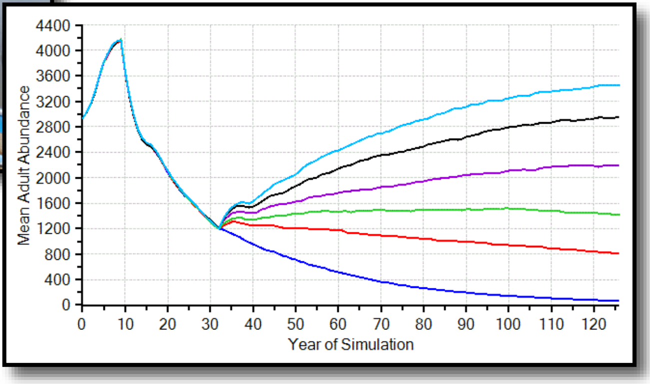
Population Viability Analysis for the Colorado Pikeminnow (*Ptychocheilus lucius*)

An Assessment of Current Threats to Species Recovery and Evaluation of Management Alternatives

USFWS



Report prepared by

Philip S. Miller, Ph.D.
Senior Program Officer
IUCN SSC Conservation Planning Specialist Group

In consultation with

The Colorado Pikeminnow PVA Technical Team

Population Viability Analysis for the Colorado Pikeminnow (*Ptychocheilus lucius*)

An Assessment of Current Threats to Species Recovery and Evaluation of Management Alternatives

Report prepared by

Philip S. Miller, Ph.D.
Senior Program Officer
IUCN SSC Conservation Planning Specialist Group

In consultation with

The Colorado Pikeminnow PVA Technical Team

Prepared for

U.S. Fish and Wildlife Service
Upper Colorado Endangered Fish Recovery Program
Post Office Box 25486, DFC
Denver CO 80225

Final Report
28 June 2018

Population Viability Analysis for the Colorado Pikeminnow (*Ptychocheilus lucius*)

An Assessment of Current Threats to Species Recovery and Evaluation of Management Alternatives

TABLE OF CONTENTS

Population Viability Analysis for the Colorado Pikeminnow (*Ptychocheilus lucius*):

An Assessment of Current Threats to Species Recovery and Evaluation of Management Alternatives

Philip S. Miller, Ph.D.
Senior Program Officer
IUCN SSC Conservation Planning Specialist Group

In consultation with

The Colorado Pikeminnow PVA Technical Team

Executive Summary

This document describes a demographic analysis and quantitative risk assessment for the Colorado pikeminnow (*Ptychocheilus lucius*) across its current range. The purpose of the analysis is to evaluate the cumulative impact of current threats to the species, to project the likely fate of river subbasin populations if current conditions are to persist, and to examine the potential for specific management alternatives – targeting different aspects of the species' life history – to contribute to long-term recovery of those populations and, by extension, the species as a whole. Population viability analysis (PVA) can be a very useful tool for investigating current and future demographic dynamics of Colorado pikeminnow populations across their range. The need for and consequences of alternative management strategies can be modeled to suggest which practices may be the most effective in managing Colorado pikeminnow populations. *Vortex*, a simulation software package written for PVA (Lacy et al. 2017), was used here as a vehicle to study the interaction of a number of Colorado pikeminnow life history and population parameters, and to test the effects of selected management scenarios.

The Colorado pikeminnow is distributed within the Colorado River Basin, specifically within three subbasins: the Green River subbasin, the Upper Colorado River subbasin, and the San Juan River subbasin (Figure 1). The PVA features separate analyses for each subbasin, using demographic, ecological and hydrological data specific to that subbasin to the greatest extent possible. Following a detailed review of these subbasin demographic models, the subbasin-specific datasets will then be combined into selected analyses that feature a metapopulation structure, where specific subbasins are demographically connected through age/sex-specific dispersal processes. Using this approach, threats to each subbasin and their management can be assessed independently, and can also be brought together in a metapopulation context to evaluate overall species dynamics and future viability across the range.

An important foundation for construction of predictive models is the retrospective analysis of demographic information that serves as the basis for parameter estimation in the model itself. This analysis quickly revealed interesting insights into past changes in population abundance in both the Green and Upper Colorado River subbasins. More specifically, these insights yielded alternative hypotheses about the dynamics of interannual changes in adult pikeminnow abundance. In what has become the "dual-phase dynamic" hypothesis, substantial rates of observed population growth in the 1990s gave way to apparent sharp and sustained declines in both subbasin populations in the early years of the decade 2000 – 2010. Future projections of subbasin abundance are then directly tied to the rate of population change inferred from the more recent period of population decline. While a detailed explanation of the precise mechanisms that may have generated this inferred inflection point is not yet in place, some evidence does exist that may link these changes in abundance trends to deterministic changes in ecological conditions – annual spring/summer spawning flows, nonnative fish densities, and the like.

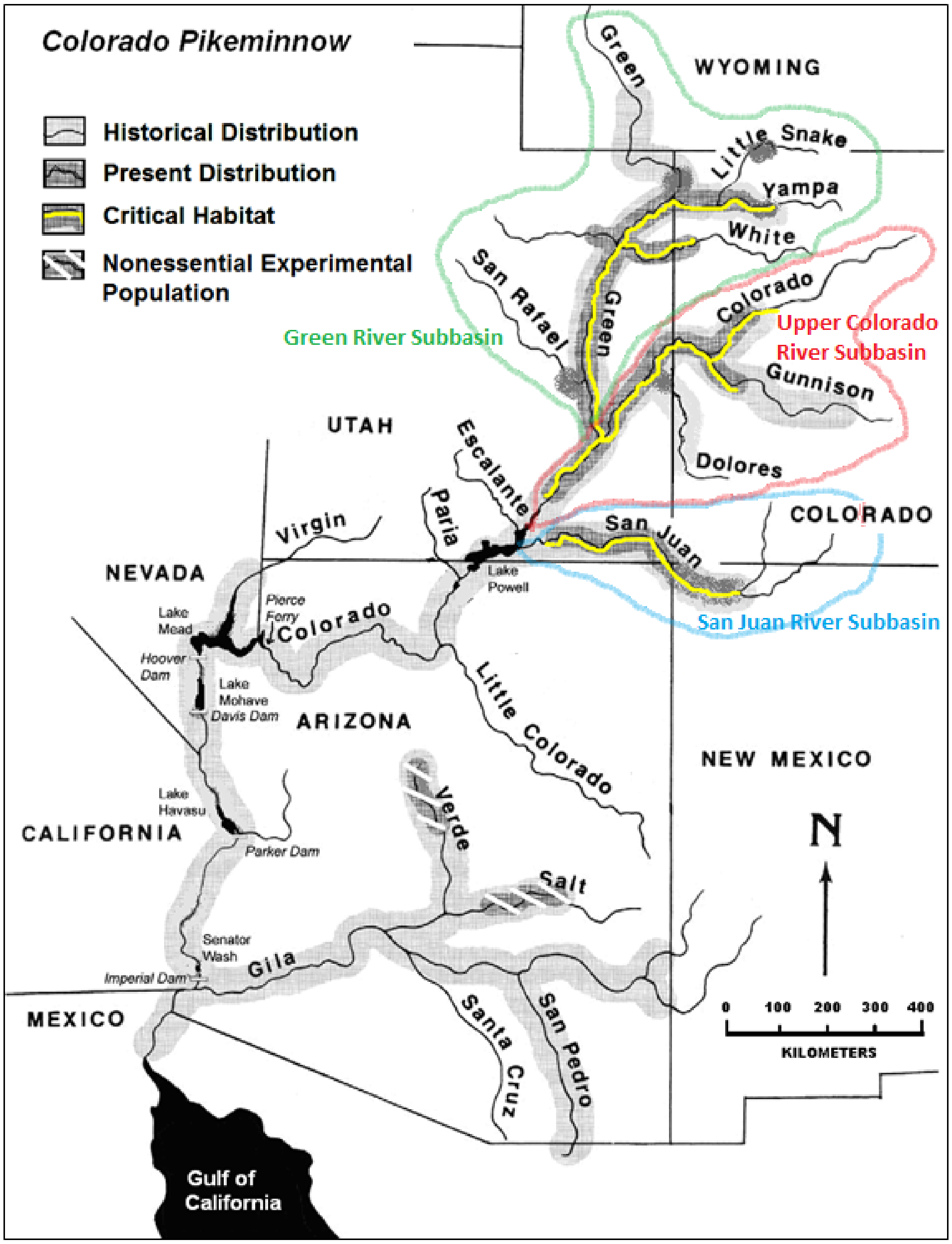


Figure 1. Distribution of the Colorado Pikeminnow in the Colorado River Basin (from USFWS 2014).

Alternatively, the "single-phase dynamic" hypothesis states that the observed changes in adult abundance over the full period of observation are nothing more than shorter-term random fluctuations that are part of the longer-term stochastic population dynamic. Therefore, projections of future population abundance are based on a single estimate of past population growth that utilizes the entire dataset from 1991 to 2015.

It may not yet be possible to distinguish between these alternative hypotheses of past population dynamics of Colorado pikeminnow in the Green and Upper Colorado River subbasins. It is important to recognize, however, that both hypotheses feature a declining population abundance in both river subbasins over at least the past 15-20 years, with the dual-phase hypothesis featuring a more rapid rate of decline. If this viability analysis is to generate recommendations for the types and, more importantly, the intensity of population management to implement to achieve positive population growth, it is important to adopt one or the other hypothesis as a more realistic portrayal of pikeminnow population dynamics. From a statistical analysis point of view, this choice may be possible only after the accumulation of more data on annual adult population abundance over the next decade. Because of the ambiguity in distinguishing among these two hypotheses of past population dynamics, our PVA includes both the dual-phase and single-phase dynamics as plausible starting points for considering future projections of pikeminnow population responses to management in the context of recovery.

The Upper Colorado River subbasin apparently includes an additional layer of demographic complexity in the form of “spawning spikes” as demonstrated by the extreme estimate of offspring production measured in 2015. Although an attenuated form of this event has been included in the prospective models for this subbasin, it is unclear how frequently this extreme event will occur in the future and what kind of impact the event will have on the population as a whole. It will be very valuable to conduct a detailed analysis of the number of fish from this 2015 spike that are recruited into the population as adults at the appropriate future point in time, e.g., 6-9 years after the spike (2021-2024). It may perhaps be possible to refine PVA model structure and input parameter specification with this important knowledge in hand following the “spawning spike” monitoring effort.

To define offspring production for each subbasin in the PVA model, data on Age-0 abundance from ISMP counts were assembled for those years in which adult abundance data were also available. Assuming an equal sex ratio among adults, the number of Age-0 fish per successfully breeding female counted during ISMP sampling was calculated. These data were then plotted against mean August-September flow data to obtain estimates of mean offspring production when flows were within or outside of recommended levels designated for each subbasin. These analytically-derived relationships between annual summer flows and estimated production rates are a key feature of these simulation models. Available data on survival of adult fish were used in conjunction with the production data and other information to construct realistic age-specific survival schedules for each subbasin, assuming equal survival probabilities for males and females.

Using the full extent of demographic, ecological and hydrologic data available, the PVA Technical Team was able to construct accurate depictions of past population performance under both dynamics hypotheses, suggesting that our models can be highly informative in predicting future population-level responses to changes in the underlying demographic characteristics of subbasin-specific pikeminnow populations. Additionally, the information obtained from the demographic sensitivity analysis reported in the earlier PVA for this species (Miller 2014) highlights the importance of both adult female fecundity (a combination of larval production (maternity) and Age-0 survival) and adult mortality as determinants of long-term population growth in this species. This result emerges from our understanding of the pikeminnow’s life history which is characterized by both high levels of offspring production (and associated low offspring survival) and a long lifespan. This insight is even more valuable when combined with knowledge of the many factors that impact offspring production and survival – frequency of optimal river flows in spring and summer to facilitate successful spawning events, predation by native and nonnative fish, availability of backwater nursery habitats, etc. From these analyses, it becomes clear that the predictive power of this and future PVA efforts can be strengthened by improved estimates of early life-stage demographics, namely, offspring production rates and the survival of Age-0 fish through the first 1-3 years of life.

If current management conditions are allowed to persist into the future, our models suggest that the Green and Upper Colorado River subbasin populations will continue to decline at an annual rate of 6 – 7% if we assume a dual-phase demographic dynamic, and a rate of 1 – 2% per year under the assumption of a single-phase dynamic. These results indicate the importance of implementing targeted management strategies that mitigate the forces acting to reduce offspring production and survival rates across all age classes.

The current PVA tests a suite of alternative management options that are believed likely to improve long-term viability of Colorado pikeminnow populations in the three subbasins defining their current distribution. Specifically, these options include managing summer flows to boost larval survival; managing nonnative fish populations to increase early lifestage survival; managing adult mortality; and managing a broad range of age-class mortalities through managing the Green River Canal diversion. These management options were tested individually or in various combinations across both the Green River and Upper Colorado River subbasins, assuming either a dual-phase or a single-phase demographic dynamic. In addition, selected modified subsets of these management options were applied to the San Juan River subbasin, in the presence of continued stocking of Age-0 fish (as is currently practiced) or in the absence of this stocking regime.

We assume that implementing the types of management activities listed above will elicit a positive demographic response in a given pikeminnow population. However, it is critically important to appreciate, in the context of this PVA, that we cannot yet predict the extent of activity that is required to achieve a desired demographic response. For example, we may want to increase early lifestage annual survival from *x* to *y* through nonnative fish removal, based on a general understanding of the impact of this form of predation on young pikeminnow survival and recruitment. However, we do not have field data on the functional numerical relationship between the number of nonnatives in a subbasin and the number of young pikeminnow they consume per unit time. Consequently, the PVA cannot provide insights that lead to specific recommendations for the number of nonnatives to remove in order to achieve the desired improvement in survival. This argument applies to the full suite of other management activities considered in this analysis. Readers of this report must keep this reality in mind when observing and interpreting model results. Instead of making specific predictions of required management efforts, the PVA should be seen as exploring various hypotheses about management efficacy. On a related note, it is important to recognize a feature common to all PVA models: the predictive models cannot by themselves generate the desired functional relationships, but instead use those relationships – derived through external analysis of appropriate field data – to evaluate potential impacts of management activities on population demographic performance.

Managing summer flows can be an effective method for generating positive population growth in the Green subbasin and, to a lesser extent, the Upper Colorado River subbasin. For the Green River subbasin, under a dual-phase dynamic, the annual target flows (1700 – 3400 cfs) must be met at least 60% of the time for the population to show a positive trend in abundance, which represents a substantial increase from the present 10% rate of achievement of these target flows. Under a single-phase dynamic, the target flows have been achieved approximately 33% of the time over the full period of observation used in this analysis (1991 – 2013). This prescribed increase in target flow achievement may be achievable, but its feasibility has not yet been assessed. For the Upper Colorado subbasin, management of summer flows is a less viable option as the rate of target flow (3000 – 6400 cfs) achievement is already quite high – 100% or 86% for the dual-phase or single-phase dynamic, respectively. Therefore, summer flow management does not seem to be a promising option for significantly increasing long-term adult abundance in this subbasin population.

In contrast, increasing early lifestage survival and increasing the extent of available habitat (by reducing interspecific competition) through nonnative fish management appears to dramatically impact long-term Colorado pikeminnow abundance trends in both of these subbasins. In the Green River subbasin, proportional increases in survival of Age-0 to Age-4 fish of 10 – 15%, combined with a corresponding increase in the extent of available habitat (expressed in the model as an increase in the habitat carrying capacity, *K*) of about 10 – 30%, results in substantial increases in population growth rate and long-term abundance. The extent of increase in the growth rate is a function of the increased juvenile and subadult survival, while the long-term abundance is also influenced by the increase in habitat availability over time. In the Upper Colorado River subbasin, substantial increases in the population growth rate are realized with a 5 – 10% increase in early lifestage survival, paired with a corresponding increase in the extent of available habitat of 10 – 40%. While this management option appears to show considerable promise as a tool to improve the long-term viability of Colorado pikeminnow populations across the species' range, the actual extent of nonnative fish management that is required to achieve these changes in pikeminnow survival remain unknown. Establishing some useful form of functional relationship between nonnative fish management and the resulting impact on pikeminnow populations remains a vital area of study in the larger context of science-based population management of Colorado pikeminnow.

Improving the rates of adult pikeminnow survival also contribute to improvements in long-term population growth and stability. However, the existing survival rate of adult pikeminnow (approximately 82%) is already rather high, with relatively few known factors contributing to reducing the baseline natural rate of survival. Consequently, the targeted management of adult survival does not appear to be effective as a single tool for generating significant changes to pikeminnow population growth. Instead, these methods can and should be considered as complementary tools to be used in conjunction with other options that may be expected to yield more effective results.

Increasing the survival rate of all pikeminnow age classes in the Green River subbasin population through the management of the Green River Canal diversion resulted in a dramatic increase in pikeminnow population viability – particularly under the assumption of a single-phase demographic dynamic. The extent of demographic improvement when testing this management option was unexpected, particularly when considering the absolute level of decrease in age-specific mortality: an additive reduction of 1.76% among adults, and of 3.52% among all other age classes. On the other hand, the compounded benefit of reducing mortality among all age-classes is to be expected given the long lifespan of the species and the relatively later onset of reproductive capability. The analysis of McAbee (2017b) provides some valuable quantitative evidence for the potential value of this management option, although additional analysis of the available data is warranted to give greater weight and validity to the assumptions carried throughout these calculations.

Assessment of combined management approaches as applied in the Green and Upper Colorado River subbasins suggests that rather modest application of at least a subset of the available management alternatives could result in substantial increases in adult pikeminnow abundance on a relatively short timeline (a few decades). In particular, management of the Green River Canal diversion is likely to be a vital component of any combined management option, along with a more broadly applied management activity targeting nonnative fish species.

Under the conditions explored in this analysis, successful management of Colorado pikeminnow in the San Juan subbasin, if stocking is to be removed as a viable long-term management strategy, requires extensive increases in offspring production and associated reductions in mortality across all age classes. As with the other subbasin population analyses, the actual nature and extent of management activities required to achieve these demographic gains is not yet known. It may be possible to achieve shorter-term viability in this subbasin under a combined management regime that includes some level of periodic or annual stocking that compensates for less effective management of pikeminnow demography. However, it is realistic to conclude that long-term viability of the subbasin population can only be achieved through demographic management to a degree where stocking with hatchery-raised fish is no longer necessary for continued population stability or growth.

We developed a small set of metapopulation scenarios, in which the Green and Upper Colorado River subbasins are connected through periodic and low-level movement of individuals (fish from the San Juan

River subbasin have not been observed in either subbasin since data collection began, instead becoming trapped in Lake Powell). If we assume no change in current management activity (the familiar “status quo” scenario discussed previously), the metapopulation model results demonstrate very little gain in subbasin population abundance arising from the dispersal mechanic. This result it also seen in scenarios in which combined management activities are implemented in each subbasin, although there is some degree of added benefit seen in the smaller Upper Colorado River subbasin population as it receives a net positive input of individuals from the larger Green River subbasin. Although the demographic consequences of metapopulation connectivity may be minimal, there may be important genetic exchange between these subbasins that helps to reduce the loss of genetic variation and improve the overall stability of each population.

It is important to remember that these conclusions are drawn from scenarios that represent our best understanding of the many and varied factors that contribute to Colorado pikeminnow population growth, and the inherent uncertainty in the detailed interactions between those factors. In addition to the sources of uncertainty addressed in this analysis, we recognize that future impacts of climate change may be a significant impediment to long-term recovery of fish like the Colorado pikeminnow in the southwestern United States. Although we do not have specific data on the predicted impacts of this global process on native fish viability in this region, it is reasonable to suspect that a warmer and more variable climate will put additional stress on riverine systems and the wildlife species therein. This will no doubt continue to be an important target of study among researchers in the endangered species conservation biology community. Despite these concerns, the insights gained from the analyses described here provide important guidance for the adoption of future management and research activities targeting long-term recovery of the Colorado pikeminnow throughout its range.

The current quantitative abundance criteria for recovery, as defined in updated USFWS recovery documents for the species, are based in part on population demographic assumptions that are not a feature of the current PVA model structure. It will no doubt be valuable to use the information contained within this report to critically re-examine the existing recovery criteria for the Colorado pikeminnow, and to perhaps adjust the criteria to align more closely with the underlying demographic characteristics of the species as defined through consensus by the pikeminnow PVA Technical Team along the course of developing the predictive model structure, its underlying input data and assumptions, and the full suite of alternative management scenarios.

Population Viability Analysis for the Colorado Pikeminnow (*Ptychocheilus lucius*):

An Assessment of Current Threats to Species Recovery and Evaluation of Management Alternatives

Philip S. Miller, Ph.D.
Senior Program Officer
IUCN SSC Conservation Breeding Specialist Group

In consultation with

Colorado Pikeminnow PVA Technical Team

Introduction

This document describes a demographic analysis and quantitative risk assessment for the Colorado pikeminnow (*Ptychocheilus lucius*) across its current range. The purpose of the analysis is to evaluate the impact of current threats to the species, to project the likely fate of river subbasin populations if current conditions are to persist, and to examine the potential for specific management alternatives – targeting different aspects of the species' life history – to contribute to long-term recovery of those populations and, by extension, the species as a whole.

Population viability analysis (PVA) can be a very useful tool for investigating current and future demographic dynamics of Colorado pikeminnow populations across their range. The need for and consequences of alternative management strategies can be modeled to suggest which practices may be the most effective in managing Colorado pikeminnow populations. *Vortex*, a simulation software package written for PVA (Lacy et al. 2017), was used here as a vehicle to study the interaction of a number of Colorado pikeminnow life history and population parameters, and to test the effects of selected management scenarios.

The *Vortex* package is a simulation of the effects of a number of different natural and human-mediated forces – some, by definition, acting unpredictably from year to year – on the health and integrity of wildlife populations. *Vortex* models population dynamics as discrete sequential events (e.g., births, deaths, sex ratios among offspring, catastrophes, etc.) that occur according to defined probabilities. The probabilities of events are modeled as constants or random variables that follow specified distributions. The package simulates a population by recreating the essential series of events that describe the typical life cycles of sexually reproducing organisms. See Figure 1 for a generalized diagram of a typical annual life-cycle (or timestep) as simulated in *Vortex*.

PVA methodologies such as the *Vortex* system are not intended to give absolute and accurate "answers" for what the future will bring for a given wildlife species or population. This limitation arises simply from two fundamental facts about the natural world: it is inherently unpredictable in its detailed behavior; and we will never fully understand its precise mechanics. Consequently, many researchers have cautioned against the exclusive use of absolute results from a PVA in order to promote specific management actions for threatened populations (e.g., Ludwig 1999; Beissinger and McCullough 2002; Reed et al. 2002; Ellner et al. 2002; Lotts et al. 2004). Instead, the true value of an analysis of this type lies in the assembly and critical analysis of the available information on the species and its ecology, and in the ability to compare the quantitative metrics of population performance that emerge from a suite of simulations, with each simulation representing a specific scenario and its inherent assumptions about the available data and a proposed method of population and/or landscape management. Interpretation of this type of output depends strongly upon our knowledge of Colorado pikeminnow biology, the environmental conditions affecting the species, and possible future changes in these conditions. Under thoughtful and appropriate interpretation, results from PVA efforts can be an invaluable aid when deriving meaningful and justifiable endangered species recovery criteria (Doak et al. 2015). Overall, population models used in PVA provide a framework not only for analyzing complex situations impacting endangered species persistence, but also for documenting assumptions and methods underlying the analyses, reviewing and improving population assessments, and integrating new threat information into our collective understanding of species dynamics.

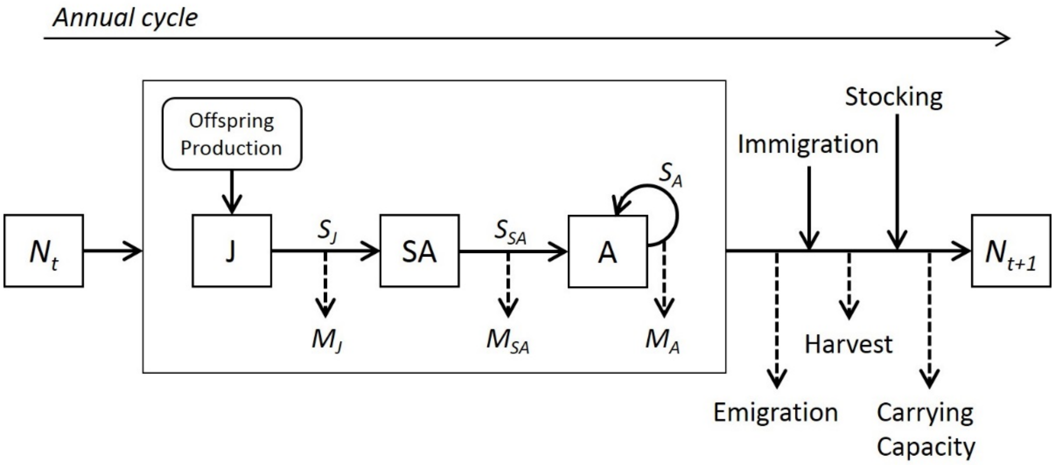


Figure 1. General schematic diagram depicting the series of events making up a typical annual cycle (timestep) in the PVA modeling software package *Vortex,* representing simulated change in population abundance from N_t to N_{t+1}. Enclosed portion of the diagram shows the production of juveniles (J) and the transition of individuals among the juvenile, subadult (SA) and adult (A) stages, determined by annual age-specific survival (S_x) rates and their complimentary mortality (M_x) rates. On the right side of the diagram, processes above the timeline act to increase population abundance, while those below the timeline decrease abundance. The aggregate effect of these various demographic processes results in a new population abundance at the end of the timestep. For more information on *Vortex*, see Lacy et al. (2017).

Guidance for PVA Model Development

PVA Meeting Structure

The analyses presented here are the product of a series of meetings from March to August 2016, and thereafter followed by a series of virtual meetings (conference calls, online collaborative sessions) through September 2017. Attendees to these physical and virtual meetings comprised the Colorado Pikeminnow PVA Technical Team:

Name	Affiliation
USFWS Program Leads	
Tom Chart / Tom Czapla, Ph.D.	Upper Colorado River Endangered Fish Recovery Program
Sharon Whitmore	San Juan River Basin Recovery Implementation Program
PVA Model Developer	
Philip S. Miller, Ph.D.	IUCN/SSC Conservation Planning Specialist Group
Species Experts	
Kevin Bestgen, Ph.D.	Larval Fish Laboratory, Colorado State University
Dale Ryden	U.S. Fish and Wildlife Service, Region 6
Scott Durst	U.S. Fish and Wildlife Service, Region 2
Nathan R. Franssen	U.S. Fish and Wildlife Service, Region 2
Advisors	
Henry Maddux	Utah Department of Natural Resources
Kevin McAbee	Upper Colorado River Endangered Fish Recovery Program
William J. Miller, Ph.D.	Miller Ecological Consultants, Inc.
Robert Muth, Ph.D.	U.S. Fish and Wildlife Service, Region 6
Richard Valdez, Ph.D.	SWCA
Seth Willey	U.S. Fish and Wildlife Service, Region 6

Spatial Organization of Species Data for Analysis

The Colorado pikeminnow is distributed within the Colorado River Basin, specifically within three subbasins: the Green River subbasin, the Upper Colorado River subbasin, and the San Juan River subbasin (Figure 2). Extensive pikeminnow research and monitoring efforts have been conducted over the past few decades on the Green and Upper Colorado subbasins, with similar efforts beginning more recently on the San Juan subbasin.

The PVA features separate analyses for each subbasin, using demographic, ecological and hydrological data specific to that subbasin to the greatest extent possible. The subbasin-specific datasets are then combined into selected analyses that feature a metapopulation structure, where specific subbasins are demographically connected through age/sex-specific dispersal processes. Using this approach, threats to each subbasin and their management can be assessed independently, and can also be brought together in a metapopulation context to evaluate overall species dynamics and future viability across the range.

Much of the information used to generate subbasin-specific demographic input datasets for this PVA was gleaned from the extensive biological data assimilation document (Valdez 2018) prepared on behalf of the Colorado Pikeminnow PVA Technical Team (see Supporting Information for the full document). In addition, this PVA stimulated extensive new analysis of existing demographic data in order to quantify specific demographic relationships that are key to evaluating impacts of threats and their subsequent management. This information is discussed in detail in the next section.

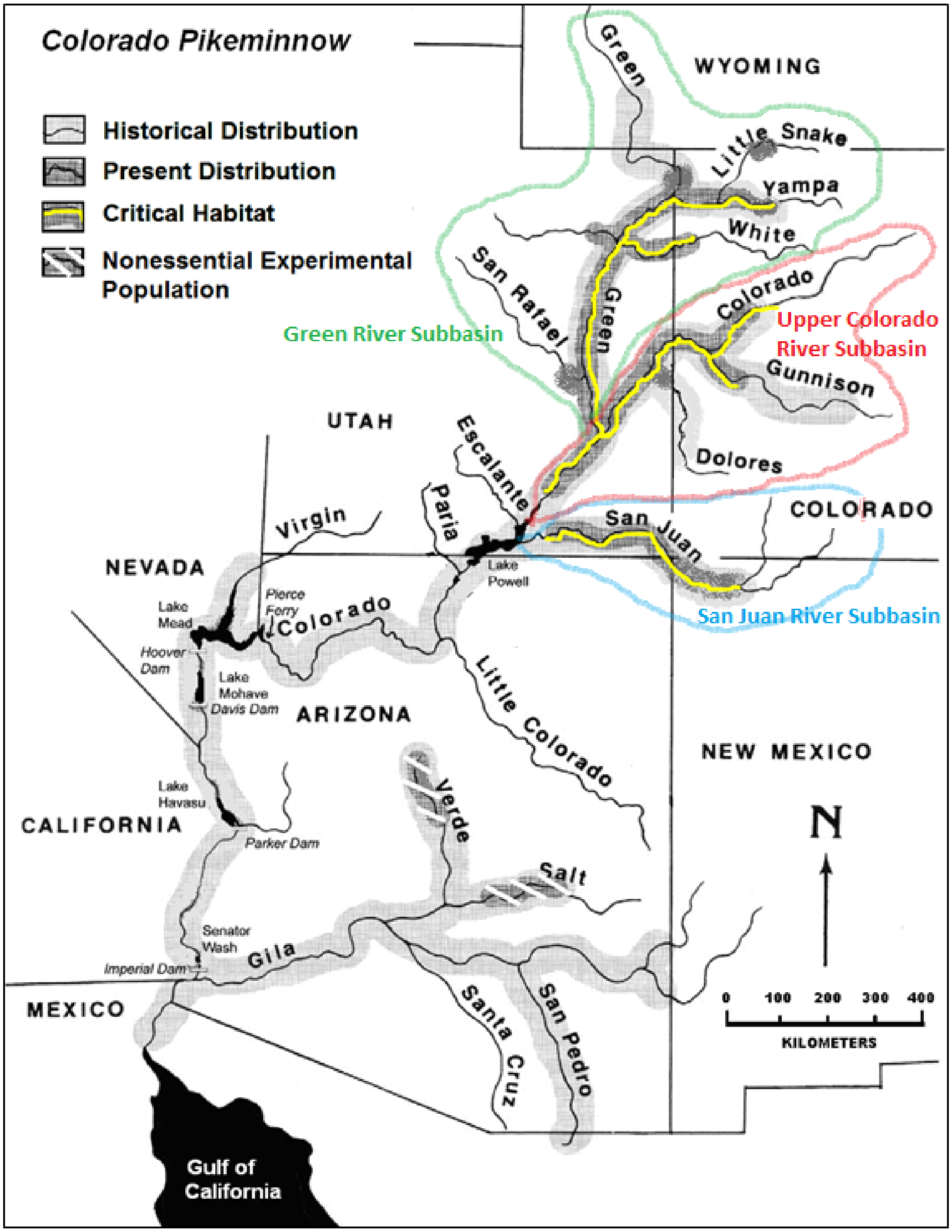


Figure 2. Distribution of the Colorado Pikeminnow in the Colorado River Basin (from USFWS 2014).

Retrospective Analysis of Population Dynamics in the Green and Upper Colorado River Subbasins

Annual adult abundance estimates are available for the Green and Upper Colorado River subbasins dating back to 1991 and 1992, respectively. These estimates are based on mark-recapture methods, with the exception of the 1991-1999 estimates for the Green River subbasin which are based on ISMP CPUE data. Inspection of these abundance data suggest two alternative interpretations to explain inter-annual changes in the number of adults:

1. Dual-phase dynamic – an early phase characterized by population growth in the 1990s followed by a transition to population decline in the early- to mid-2000s that reflects a systematic change in underlying population demographics; or
2. Single-phase dynamic – the full range of adult abundance data is described by a single demographic profile, with changes in abundance reflecting stochastic fluctuations in annual rates of reproduction and/or age-specific survival

Figures 3 and 4 show the results of non-linear regression of adult abundance data for these subbasins under the two alternative interpretations (see Supporting Information for details of the regression analysis). Break-points defining the transition between population growth and decline were determined by visual inspection of the abundance data. For the Green River subbasin (Figure 3), a dual-phase dynamic is strongly supported by the analysis, resulting in approximately 3.5% annual growth over the time period 1991 – 2000 ($P = 0.0002$), and followed by a transition to an annual rate of about 5.5% decline during the period 2000 – 2013 ($P < 0.0001$). A single-phase dynamic is also well-supported over the full range of adult abundance data, although not to the level emerging from the dual-phase analysis ($P = 0.012$).

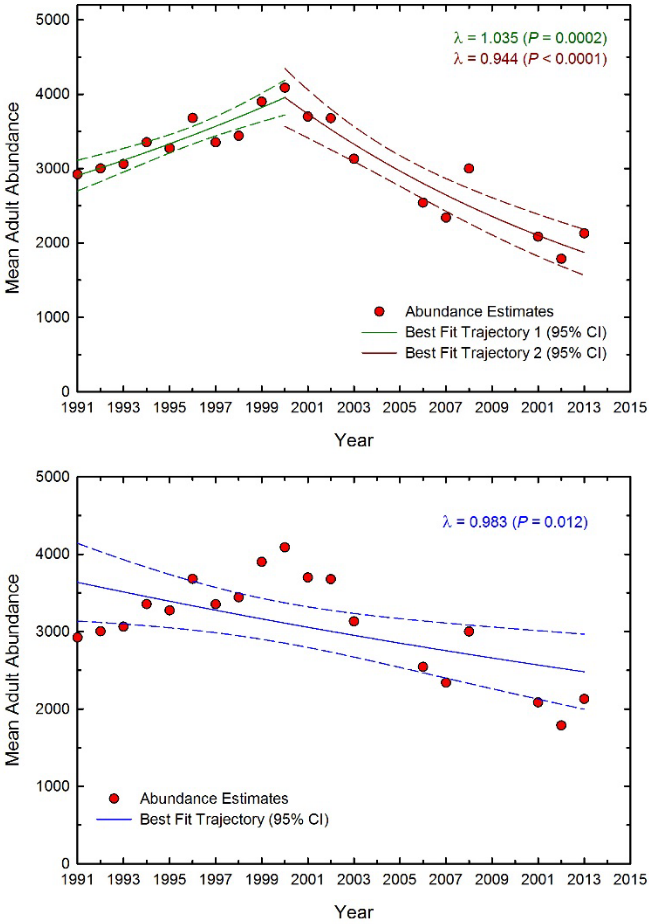


Figure 3. Historical abundance data for adult Colorado pikeminnow in the Green River Subbasin, with statistical trend analysis under the assumption of a dual-phase (top panel) or single-phase (bottom panel) demographic dynamic. Abundance estimates from Bestgen et al. (2016) and Bestgen (unpubl.).

Assuming a single-phase dynamic, the Green River subbasin adult population is assumed to be declining at an average annual rate of about 1.7%.

The Upper Colorado River subbasin abundance data show a more uncertain dynamic (Figure 4), with neither the dual-phase nor the single-phase assumptions receiving significant statistical support when using the same non-linear regression methods as those used in the analysis of the Green River subbasin data. Although there is some support for a recent period of adult population decline of more than 7% annually from 2005-2015 ($P = 0.015$), the assumption of a separate period (1992-2005) of more than 2% annual growth is not statistically robust ($P = 0.098$). Similarly, the observation of a long-term trend of nearly 1.5% annual decline in adult abundance under the assumption of a single-phase dynamic is not well supported.

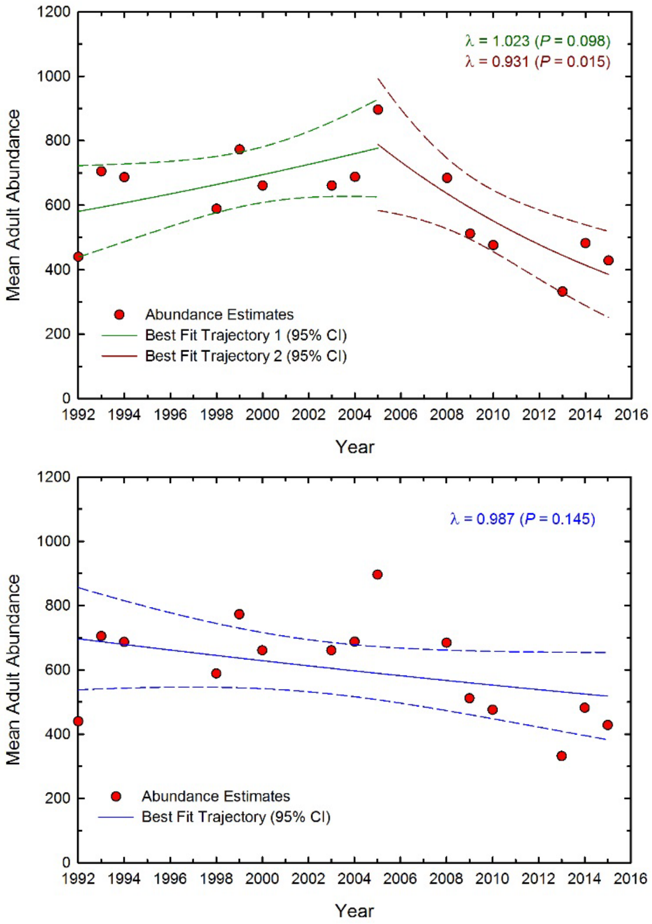


Figure 4. Historical abundance data for adult Colorado pikeminnow in the Upper Colorado River Subbasin, with statistical trend analysis under the assumption of a dual-phase (top panel) or single-phase (bottom panel) demographic dynamic. Abundance estimates from Osmundson and White (2009, 2014) and D. Ryden (pers. comm.).

All in all, the analyses summarized here cannot unambiguously reject one or the other assumption regarding the dynamics underpinning annual changes in adult abundance of Colorado pikeminnow in the Green and Upper Colorado River subbasins since the early 1990s. There is, however, some evidence linking specific environmental processes, such as spring/summer river flows or non-native predator density, to associated demographic parameters and the presumed changes in those parameter values that would characterize a dual-phase dynamic for either river subbasin. In light of this information, PVA models have been developed using each of the two alternative assumptions, with mean estimates of reproductive output and mortality rates chosen to be consistent with the assumptions underlying one or the other demographic dynamic. Differences in adult population growth rates emerging from these analyses can have important implications for future viability of subbasin populations, and the extent of demographic management required to generate a more favorable long-term projection of population performance.

Input Data for PVA Simulations

General Species Life-Cycle and Threat Specification

Before we move through the details of specifying detailed demographic rates for the Colorado pikeminnow population across the three subbasins, it is instructive to display the life-cycle of the species and the various factors that influence the rates of reproduction (fecundity) and survival of individuals as they age. This diagram is shown in Figure 5.

The conceptual model was built on an age-structured population. The production of offspring (juveniles) is described by the rate of fecundity of adults, or F_{Ad}. This variable is itself a function of the proportion of females that successfully spawn, the number of larvae that survive to be counted in the November – December ISMP sampling period – defined here as individual female maternity, or m_{Ad} – and the survival of those larvae to just before one year of age at the onset of the next spring's spawning season, or S_0. Our model tracks changes in population abundance on a timestep of one year; consequently, our survival rates (S_x) describe the mean proportion of individuals of one age class that are expected to survive from age class x to $x+1$ over the course of one year. Since the adult age class spans multiple years, we treat this group of individuals as a stage, where fish remain in that class until they die.

Figure 5 also identifies a suite of threat factors that are thought to impact these demographic rates from one year to the next. The various factors are an extension of those proposed by Bestgen et al. (2006) in their study of the factors affecting Colorado pikeminnow recruitment, and represent the collective information discussed by the PVA Technical Team during model development. It is valuable to consider these factors in order to better understand their relative importance in driving mean demographic rates, and to help identify appropriate management strategies that may reduce the detrimental influence of one or more threatening processes. The list of threats identified here is not meant to be exhaustive, but instead highlights those factors that were discussed by the Technical Team in their process of information assembly and analysis, specifically for consideration in the PVA.

A more detailed discussion of demographic rates as portrayed in Figure 5 is presented in the following subsections.

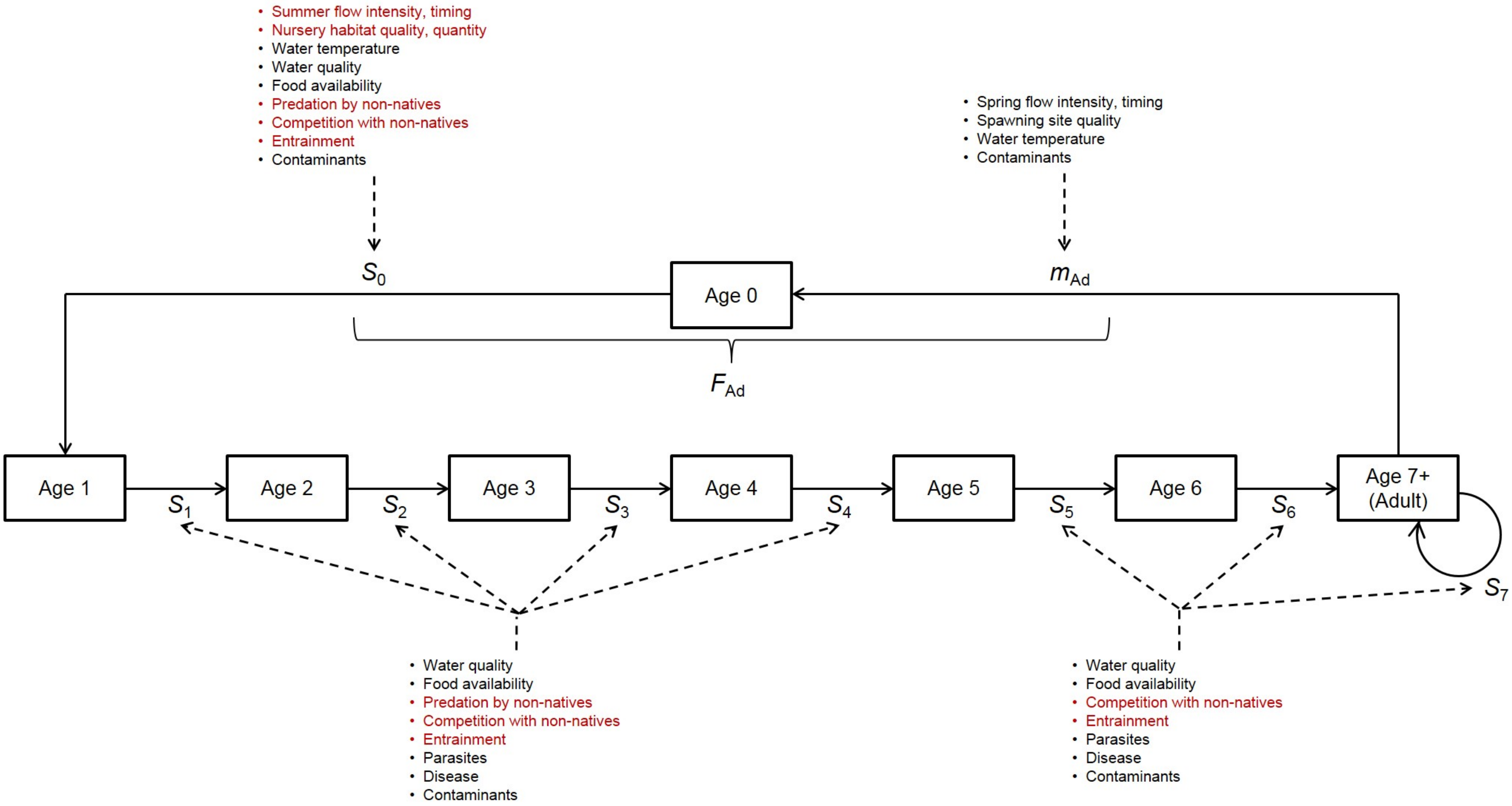


Figure 5. Graphical representation of the life cycle of the Colorado pikeminnow. The fecundity rate of adults (F_{Ad}) is deconstructed into the production of larvae that are counted by ISMP sampling methods in November - December (defined here as maternity, m_{Ad}) and the survival of those young of the year to the next spawning season the following spring (S_0). Annual survival rates of older age classes are represented as variables S_1 – S_7. Threats modifying demographic rates are listed and linked to specific variables through dashed arrows, with factors in red highlighted as subject to various management scenarios considered in this report. Figure modified from Bestgen et al. (2006).

General Characteristics of Model Structure

Simulation mode: Population-based model. The potentially large number of offspring generated in a given year greatly increases computational complexity. As a result, *Vortex* is run in a population-based mode where individuals are not tracked separately but are instead treated as members of an age/sex-specific cohort that is tracked as a numerical unit. Because of this simulation mechanism, exploration of population-level genetic structure as a function of individual heterozygosity is unavailable, as is the inclusion of inbreeding depression affecting demographic processes. The PVA Technical Team concludes that these limitations to modeling population genetic processes do not adversely impact model performance.

Timestep definition: Our implementation of *Vortex* for this PVA is based on a pre-breeding census, with adult abundance therefore tallied just before the onset of spawning in a given model year, i.e., June-July. As Age-0 individuals are first counted during ISMP sampling in September-October, first-year mortality is imposed from that point in the year through the next breeding cycle in spring of the following calendar year.

Number and duration of iterations: 1000 replicates for each unique input dataset (scenario), projected forward for 100 years from today.

Primary output metric: Adult population abundance. This corresponds to the main focus of population-level monitoring efforts, and is a highly informative measure of long-term impacts of demographic threats across multiple age-classes.

Common Model Input Parameters

Reproductive parameters

Breeding system: polygynous (broods from multiple females can be inseminated by a single male, as males are returned to the pool of available males after breeding with a given female)

Age of first breeding: Colorado pikeminnow begin reproducing at approximately 450 mm total body length, which is assumed to correspond to 7 years of age on average. This is assumed to be true for both females and males.

Maximum age of reproduction (lifespan): 40 years

Number of broods per year: 1

Sex ratio of offspring at birth: 0.5

Density-dependence in offspring production: None. Reproduction is assumed to be regulated if a population reaches the subbasin-specific ecological carrying capacity.

Distribution of adult males in the breeding pool: 100%, reflecting the assumption that each adult male is equally capable of successfully reproducing in a given year.

Other parameters

Catastrophes: The PVA model described here does not include a specific catastrophic event, i.e., one with a low frequency of occurrence but with the potential for a major population-level impact. Species experts involved in the development of the demographic model did not identify a specific type of event that would qualify, relying instead on other processes to generate inter-annual variation among demographic rates. Severe events such as localized chemical spills, etc. could impact portions of a subbasin population, but lack of information on both frequency and severity of candidate events made it impractical to include them in the model.

Green River Subbasin

Reproductive parameters

As described in detail by Bestgen and Hill (2016), offspring production in Colorado pikeminnow (defined by number of Age-0 fish counted during October-November ISMP sampling of backwater habitats, about four months after the June-July spawning event) appears to be linked to August-September flows that determine the extent of backwater nursery habitat necessary for survival, growth and development of larvae. Specifically, Bestgen and Hill (2016) identify the relationship as dome-shaped through polynomial regression, indicating that intermediate flows lead to larger numbers of Age-0 fish while both lower and higher mean flows result in fewer Age-0 fish. While the cited analysis was conducted on the Green River, we assume that the same general type of relationship exists in the Upper Colorado River subbasin as well. The PVA model was built to take advantage of this relationship, where Age-0 (juvenile) production is defined on a per-female basis.

To define offspring production for the PVA model, data on Age-0 abundance from ISMP counts were assembled for those years in which adult abundance data were also available. Assuming an equal sex ratio among adults, the number of Age-0 fish per successfully breeding female was calculated, assuming that approximately 80% of adult pikeminnow are able to successfully spawn and produce viable larvae that survive to the dates of ISMP sampling. These data were then plotted against mean August-September flow to obtain estimates of mean offspring production when flows were within or outside of recommended levels (Figure 6).

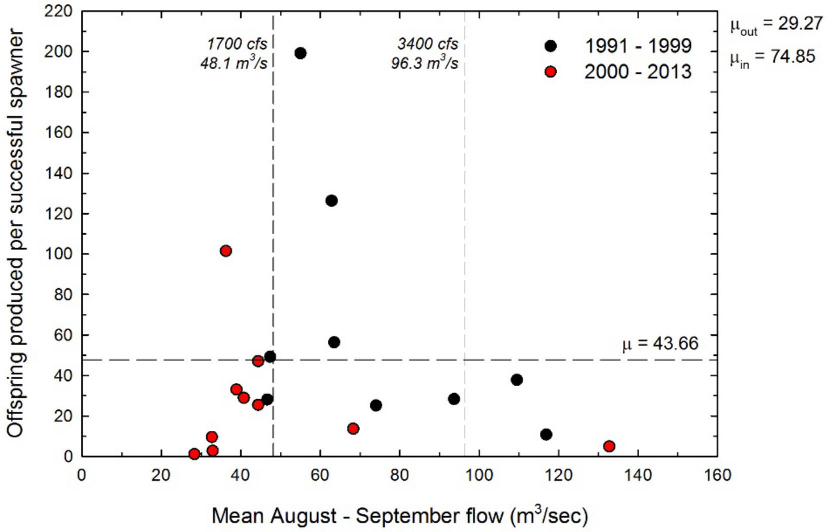


Figure 6. Mean number of Age-0 fish produced per successfully breeding adult female (as counted during ISMP sampling) as a function of mean August-September flow in the Green River subbasin, 1991-2013. Horizontal dashed line shows the mean production across all years, while μ_{in} and μ_{out} refer to mean production in those years when flow is within or outside the recommended flow targets, respectively. Vertical dashed lines delineate the recommended flow targets, based on a mean of the targets for the Middle and Lower Green River specified in Bestgen and Hill (2016).

Note that in the most recent time period (2000-2013) singled out in Figure 6, the mean August-September flow was within the recommended range only once out of the ten years for which production data can be calculated. Therefore, under an assumed dual-phase dynamic that is carried forward prospectively, we assume that the higher production value of 74.85±20 Age-0 individuals per successful female occurs during only 10% of the simulated years, with the remaining 90% of the years resulting in the lower rate of 29.27±10 Age-0 fish per female.

This functional approach is used both in retrospective analyses of model performance and in prospective models assuming no future changes in environmental conditions or management activities. Specifically, we assume for the retrospective analysis that mean production declines significantly from 124.9 to 28.4 after model year 3, which is reflected in a change in adult population growth rate in model year 10 as those individuals produced seven years earlier survive and grow to recruitment as adults at age 7. When the demographic conditions underlying the retrospective analysis are carried forward prospectively (i.e., beginning in year 2014), and under the assumption of no change in current conditions, we specify the production function as:

$$F_t = \begin{cases} \mu_{in} \text{ for } P_{\text{Target},t} < x \\ \mu_{out} \text{ for } P_{\text{Target},t} > x \end{cases}$$

$$F_t = \begin{cases} 74.85 \text{ for } P_{\text{Target},t} < 0.1 \\ 29.27 \text{ for } P_{\text{Target},t} > 0.1 \end{cases}$$

In this formulation, $P_{\text{Target},t}$ = is the probability that the summer flow in year *t* will be within the recommended range.

If the single-phase demographic dynamic is adopted, the entire 19-year dataset is used to estimate the probability of falling within the recommended flow range. Using these data, the higher production rate is expected to occur in 6 out of 19 years ($P_{\text{Target},t} = 0.316$), with the lower production occurring in 13 of 19 years ($1 - P_{\text{Target},t} = 0.684$) (Figure 5). This information would be used in the same manner as the dual-phase data for both retrospective analysis and prospective projections assuming no change in conditions.

Mortality rates

Age-specific rates of mortality for Colorado pikeminnow populations are largely unknown. Bestgen et al. (2005, 2010) provide an estimate of annual adult mortality of 0.18 for the Green River subbasin during 1991-1999. The mortality rate (and perhaps the rate of offspring production) likely changed during more recent times, as indicated by a declining adult population after the year 2000, but the specific factors influencing adult mortality are complex and not fully understood.

Based on the estimates of annual adult abundance and mean offspring production discussed above, a detailed age-specific mortality schedule was back-calculated by model iteration for each alternative demographic dynamic to produce the desired retrospective adult abundance population trajectory. These schedules are summarized in Table 1.

Note that the rates used in the single-phase dynamic model are slightly higher for the younger age classes and slightly lower for the intermediate age classes. The larger mean reproductive output for adult females under the assumption of a single-phase dynamic certainly helps to explain the higher mortality rates for the older age classes; the changes to rates for the intermediate age classes are more difficult to explain mechanistically but are important for the overall fit of the retrospective model to the available data. There are many potential factors governing the collective demographics of the dual-phase and single-phase dynamic models of past changes in Colorado pikeminnow population abundance. Definitive specification of these factors at present is not possible.

Table 1. Mean age-specific mortality rates (SD) for Colorado pikeminnow used in the PVA for the Green River subbasin, assuming either a dual-phase or single-phase demographic dynamic.

Age Class	Dual-Phase Dynamic	Single-Phase Dynamic
0-1	70 (10)	72 (10)
1-2	60 (5)	63 (5)
2-3	52 (5)	56 (5)
3-4	46 (5)	45 (5)
4-5	42 (5)	37 (5)
5-6	36 (4)	31 (4)
6-7	25 (3)	25 (3)
7+	18 (2)	18 (2)

Initial population size

All simulation models were initialized with the total number of individuals that would be expected to comprise the Green River subbasin population at the end of 1991, based on the predicted number of adults conforming to either the assumed dual-phase or single-phase dynamic. The total population is apportioned in the model according to a stable age distribution. The total number of adults in the dual-phase dynamic is 2922 (1461 females), which is the number estimated from an analysis by K. Bestgen (unpubl.) using ISMP CPUE data.

Under the single-phase dynamic assumption, the total number of adults present at the end of 1991 was assumed to be 3636 (1818 females) which is the value obtained from the regression shown in Figure 2. The disparity between this initial adult abundance estimate and that obtained from ISMP CPUE data is recognized, but the assumptions underlying the single-phase dynamic require readjustment of this parameter to generate consistent retrospective and prospective analyses of pikeminnow population dynamics.

Carrying capacity

In the typical *Vortex* modeling framework, a population is allowed to increase in abundance under favorable demographic conditions (and without explicit specification of density dependence) until the carrying capacity *K* is reached. When this occurs, individuals are randomly removed according to the age and sex structure of the population in order to bring the population back down to the value of *K*. In this manner, we therefore simulate a ceiling-type density dependence. Evidence for other types of more complex modes of density dependence, such as Beverton-Holt or a Ricker type of dependence, is currently not available.

The number of adults at maximum density in the Green River subbasin was estimated in 2000 to be 4,206 (Bestgen et al. 2005), or about 7.4 adults/mi (4,206/569 mi). There is no definitive evidence suggesting that this represents the true maximum density that the subbasin can support. In light of this uncertainty, we set the long-term carrying capacity to be 4,300 adults.

Upper Colorado River Subbasin

Reproductive parameters

The specification of mean annual production (Age-0 production per successfully breeding adult female) follows the same logic as that specified for the Green River subbasin data. Figure 7 shows the production data as a function of summer flow for census years in the interval 1992-2015. The observed relationship may not be as robust as that seen in the Green River subbasin analysis, but shows the same qualitative characteristic "dome-shaped" form. Note the presence of what is considered here to be an "outlier" year for offspring production: 2015, where the mean estimated production is about 14 times larger than any other year within the interval. This data point is not included in the retrospective analysis as we assume it did not occur during or immediately before the time interval of interest. Therefore, the 14 years for which we can calculate mean annual production yields an overall mean of 78.81 Age-0 fish per successful adult female. Moreover, we see that only two of the 14 years fell outside the recommended flow range of 3000 – 6400 cfs, although these two years are also associated with quite low production estimates.

If we adopt a dual-phase dynamic, we assume that mean annual production declines significantly from 103.8 to 64.9 after model year 7, which is then reflected in the onset of a decline in adult abundance beginning in model year 14. [In addition, we assume an increase in mortality among early age classes in order to fit the model to observed abundances; see the "Mortality rates" section below.] When the demographic conditions underlying the retrospective analysis are carried forward prospectively (i.e., beginning in year 2014), and under the assumption of no change in current conditions, we specify the production function as:

$$F_t = \begin{cases} 15.72 \text{ for } P_{\text{Target},t} < 0.0 \\ 89.32 \text{ for } P_{\text{Target},t} > 0.0 \end{cases}$$

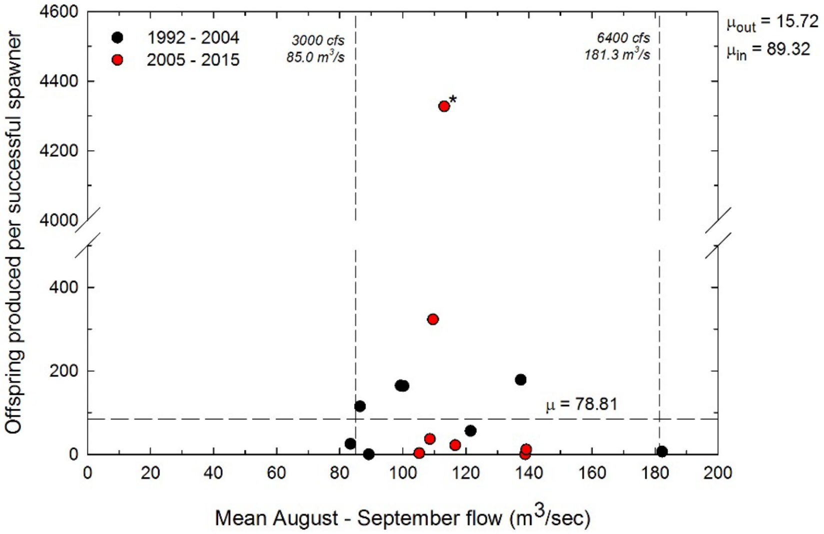


Figure 7. Mean number of Age-0 fish produced per successfully breeding adult female (as counted during ISMP sampling) as a function of mean August-September flow in the Upper Colorado River subbasin, 1992-2015. Horizontal dashed line shows the mean production across all years, while μ_{in} and μ_{out} refer to mean production in those years when flow is within or outside the recommended flow targets, respectively. Vertical dashed lines delineate the recommended flow targets identified by the PVA Technical Team, based on McAda (2003).

In other words, we expect the summer flows to be within the recommended range 100% of the time, as they were observed to be during the time period 2005-2015. This may be an optimistic assumption, but we are being true to the reproductive data currently available for the purposes of our modeling exercise.

If the single-phase demographic dynamic is adopted, the entire dataset is used to estimate the probability of falling within the recommended flow range. Using these data, the higher production rate is expected to occur in 12 out of 14 years ($P_{\text{Target},t} = 0.857$), with the lower production occurring in 2 of 14 years ($1 - P_{\text{Target},t} = 0.143$). This information would be used in the same manner as the dual-phase data for both retrospective analysis and prospective projections assuming no change in conditions.

The very large offspring production event observed in 2015 was used to parameterize a "spawning spike" in prospective analyses of pikeminnow demographic dynamics in the Upper Colorado River subbasin. This was simulated in the PVA as a probabilistic modifier to the standard specification of the number of offspring produced in a year. In the language of the *Vortex* software, the event is simulated as a "beneficial catastrophe" – similar to the specification of a traditional catastrophe that infrequently reduces survival and/or reproduction beyond the level described by typical levels of environmental variation. The modifier is described both in terms of the frequency of the spike and its demographic impact in the year that it occurs. Data on Age-0 production since 1979 provided by K. Bestgen indicates that the extremely high level of production seen in 2015 was a strong anomaly throughout the duration of observation. Therefore, we could set the frequency of this event at once in 36 years, or 0.028. However, in order to maintain a consistent framework for data analysis in this PVA, the full dataset was parsed to include the interval 1992-2015 for which adult female abundance estimates are available. This allows us to define the 2015 event in terms of offspring production instead of a more ambiguous definition of Age-0 production. Using this logic, the "spawning spike" frequency was set of (1/23) = 0.043. This frequency could be higher than what is ultimately observed in the future; on the other hand, since this event has only been observed once in the very recent past, its true frequency over the coming decades is unknown (see Supporting Information for more details).

As shown in Figure 6, the production estimate for the 2015 spike event is approximately 4200 Age-0 fish per successfully reproducing female. If we assume no additional mortality of those juvenile fish through the action of density dependent processes from the time they are counted in October-September to the beginning of the next breeding cycle (model year) the following spring, we can quantify the magnitude of the event simply by adding approximately 4000 Age-0 fish to the population in a spike year. As an alternative to this approach, we may assume some level of density-dependent mortality to act on this very large cohort of juvenile fish through increased predation, competition for food resources, etc. To evaluate this hypothesis, additional scenarios were constructed where the production was set at 2000 ("Mid Spike"), 1000 ("Low Spike"), or 500 ("Very Low Spike") in the year when the event occurred. A standard deviation of 100 was added to these specifications to allow for some level of stochasticity around the magnitude of the event.

Mortality rates

Age-specific mortality rates for the Upper Colorado River subbasin followed those estimates for the Green River subbasin, but were increased slightly in order to result in a more realistic retrospective abundance trajectory. This increase is necessary in light of the higher rates of offspring production observed in the Upper Colorado subbasin. Moreover, under the dual-phase assumption the mortality rates of the early age-classes were adjusted through model iteration to increase at model year 8 (calendar year 2000) in order to generate the desired inflection in abundance observed in the historical census data.

Table 2. Mean age-specific mortality rates (SD) for Colorado pikeminnow used in the PVA for the Upper Colorado River subbasin, assuming either a dual-phase or single-phase demographic dynamic. Numbers separated by "/" among young age-classes in the dual-phase dynamic assumption refer to mean rates for years 1-7 and years 8+ of the simulation.

Age Class	Dual-Phase Dynamic	Single-Phase Dynamic
0-1	69 / 78 (10)	75 (10)
1-2	63 / 70 (5)	69 (5)
2-3	57 / 63 (5)	60 (5)
3-4	51 (5)	51 (5)
4-5	46 (5)	40 (5)
5-6	36 (4)	31 (4)
6-7	25 (3)	25 (3)
7+	18 (2)	18 (2)

Initial population size

All simulation models were initialized with the total number of individuals that would be expected to comprise the Upper Colorado River subbasin population at the end of 1992, based on the predicted number of adults conforming to either the assumed dual-phase or single-phase dynamic. The total population is apportioned in the model according to a stable age distribution. The total number of adults in the dual-phase dynamic is 580 (290 females), which is the abundance estimated from regression analysis of abundance data over the time period 1992-2005 (Figure 4).

Under the single-phase dynamic assumption, the total number of adults present at the end of 1992 was assumed to be 698 (349 females) which is the value obtained from regression analysis of abundance data over the time period 1992-2015 (Figure 4). As with the analysis of the Green River subbasin abundance data, the intent to generate long-term population dynamics consistent with historic abundance trends over time prompted the use of initial abundances derived from regression analyses instead of the exact abundance observed at the beginning of the time periods of interest.

Carrying capacity

The number of adults in the Upper Colorado River subbasin at maximum density was estimated to be approximately 1116 adults in 2014, or about 6.2 adults/mile (summarized in Valdez 2018). There is, however, considerable uncertainty around this parameter. As a conservative estimate of carrying capacity in this system, we set K for the Upper Colorado River subbasin at 1000 adults.

San Juan River Subbasin

The structure of the demographic model for the San Juan River subbasin follows broadly the analysis of Miller (2014) on the impacts of a suite of threats to Colorado pikeminnow in this river system. There are a number of specific changes to reproduction and mortality parameters, however, in keeping with overall model structure consistency with the other river subbasins comprising the current PVA.

Recent study of Colorado pikeminnow in the San Juan River subbasin (e.g., Farrington et al. 2012) provides strong evidence over the past 10-15 years that, while some larval fish produced in the wild are being collected, the reproductive output of pikeminnow in the river is very low, in some years even below the levels of detection of larval fish surveys dedicated to documenting this process. Factors that may help explain this observation include high levels of predation by non-native fish species, reduced availability of low-velocity nursery habitat, and high rates of larval drift down the high-gradient reaches of the lower San Juan into Lake Powell. Furthermore, as documented in Durst (2013) and Valdez (2018), the number of adult pikeminnow appears to have remained rather small – on the order of 50 – 100 individuals – and rather constant over the period 1990 – 2010. We may therefore surmise that recent and current growth of the San Juan River pikeminnow population through natural reproduction is very limited, with any observed increase in abundance most likely due to survival of younger fish that are part of the ongoing stocking program started in 1996 and formalized in 2002. This information formed the basis of our demographic characterization of the Colorado pikeminnow population currently occupying the San Juan River subbasin. It is also important to note that abundance data are insufficient to distinguish between dual-phase or single-phase demographic dynamics like those defined for the Green and Upper Colorado River subbasins. Therefore, we adopt a comparatively simple single-phase dynamic for the San Juan River subbasin population.

Reproductive parameters

In keeping with the recent observations of almost negligible reproductive success among wild Colorado pikeminnow in the San Juan subbasin, we assign a mean annual level of offspring production for successfully breeding adult females of just 5.0 (SD 2.0) Age-0 fish. Furthermore, we assume that only 70% of adult females are successful spawners in a given year. While specific field data are not available to support this lower spawning rate, this assumption is intended to represent higher levels of spawning failure, simulating the observed very low levels of offspring production that characterize recent population demographics in this subbasin. Data are not available for us to link Age-0 production to flow in a manner similar to that undertaken for the Green and Upper Colorado River subbasin populations.

Mortality rates

Age-specific mortality rates for the San Juan River subbasin have been studied for a rather short period of time. Estimation of these rates is complicated by the fact that stocked fish make up the overwhelming majority of the population. Overall, morality rates were chosen to calibrate model performance against the expectation of a long-term adult population growth rate of λ ≈ 1.0 (Table 3).

Table 3. Mean age-specific mortality rates (SD) for Colorado pikeminnow used in the PVA for the San Juan subbasin, assuming a single-phase demographic dynamic.

Age Class	Mortality Rate
0-1	90 (5)
1-2	80 (5)
2-3	70 (5)
3-4	60 (5)
4-5	50 (5)
5-6	40 (4)
6-7	30 (3)
7+	18 (2)

Since the completion of this analysis, new data on larval production and survival have been collected in the San Juan (S. Durst, pers. comm.). New observations of greater levels of reproductive success, perhaps in association with high spring releases of water from Navajo Dam, suggests some level of enhanced demographic performance in this population above what is currently simulated in this PVA.

Initial population size

Only 17 wild adults were captured in the entire San Juan River between 1991 and 1995, and biologists suspected that there were fewer than 40 adults in the entire San Juan River as of October 1995 (Holden 1999). The numbers of wild fish from 1996 to 2001 was down to probably fewer than 20 (Ryden 2003a, 2004; SJRIP 2006). In 2009, Ryden (2010) estimated 26 adult Colorado pikeminnow (> 450 mm TL) from electrofishing data using a 5% capture probability. More recent analyses from S. Durst (USFWS) presented to the PVA Team provides some evidence of up to about 100 adults currently present in the San Juan River. In order to provide a consistent basis for comparison of demographic performance across model scenarios, we chose a somewhat arbitrary value of 88 adults (44 males, 44 females) as the initial adult stage abundance.

Carrying capacity

Miller and Lamarra (2006) developed a population dynamics model for the San Juan River subbasin through the use of bioenergetics which included an estimate of the carrying capacity of Colorado pikeminnow. They developed an original estimate of 800 adults that could inhabit the river across the six geomorphic reaches modeled from Piute Farms to about the confluence of the Animas River. This estimate was based on a hypothesis that management actions would result in an increase in prey abundance river-wide to a level similar to the San Juan near the Animas River confluence. The actions of flow management, non-native removal and augmentation has in fact not resulted in the expected increased prey abundance in the lower San Juan River. Based on this information, a revised estimate for carrying capacity was recalculated in 2013 using the estimated densities of prey for each of six river reaches at that time. Based on these data, it was surmised that carrying capacity of adult Colorado pikeminnow would decrease similar to prey availability among reaches. Hence, the revised carrying capacity for the river was 400 adults, or about 2.26 fish/mi (1.4 fish/km) for the 180 mi (290 km) included in their model (Miller 2013).

Simulating stocking of hatchery-raised fish in the San Juan River

Experimental stocking of Colorado pikeminnow into the San Juan River began in 1996. The San Juan River Basin Recovery Implementation Program has been stocking juvenile (Age-0) Colorado pikeminnow under a formal augmentation plan since 2002 (Ryden 2003; Furr 2012). Over the recent past, the stocking program involves introducing about 400,000 Age-0 fish to the river each year, approximately in November.

Because our implementation of the *Vortex* model structure includes the annual census of the population just before the next spawning season, we must therefore account for mortality of the stocked fish from the time they are added to the river in November of year x to the subsequent census event before spawning in year x+1. Moreover, since our implementation of stocking occurs late in the sequence of events within a given model timestep, stocked fish are actually considered to be one year of age at the time of stocking. This is accounted for by proper specification of “effective” stocking rates and post-stocking mortality rates to end with the desired number of individuals present in the population at the time of the next census and subsequent spawning event (onset of the next model year).

Taking the above information into account, approximately 3000±2000 fish that survive from the date of stocking to the onset of the next breeding cycle are added to the population each year through this “effective” stocking process. This is consistent with estimates of immediate post-stocking survival provided to the PVA Team by S. Durst (USFWS).

PVA Model Results

Retrospective Model Performance

The Green River subbasin retrospective models show good concordance with the historical abundance estimates over the period 1991-2013, assuming either a dual-phase or single-phase dynamic (Figure 8). During the growth period of the dual-phase dynamic, the simulated population grew at an annual rate of just under 4% (λ = 1.039), which was then followed by a period of decline of approximately 6% per year (λ = 0.941). Under the assumption of a single-phase dynamic, the simulated population declined at a rate of just under 2% per year (λ = 0.983), essentially identical to that predicted from regression analysis of the adult abundance data over the full period of interest.

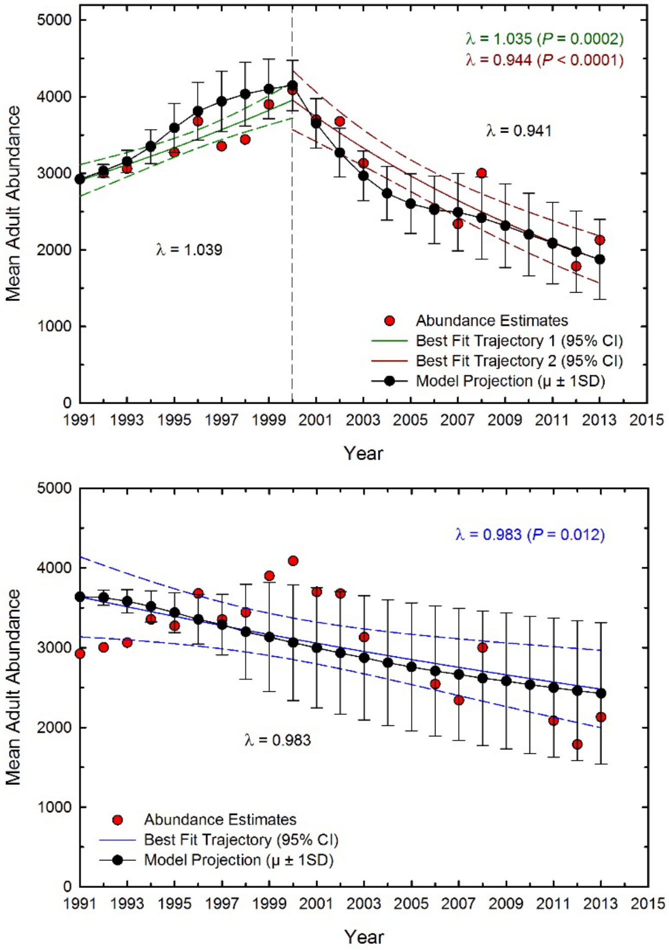


Figure 8. Retrospective trajectories of simulated Colorado pikeminnow adult abundance in the Green River subbasin, alternatively assuming a dual-phase (top panel) or single-phase (bottom panel) demographic dynamic. Growth rate (λ) estimates in the upper-right corner of each panel are derived from non-linear regression analysis of actual abundance estimates, while the estimates in the middle of each panel are derived from model simulation runs.

Similarly, the retrospective model projections for the Upper Colorado River subbasin population perform well compared to the observed historical abundance trend under either assumption of demographic dynamic (Figure 9). Under a dual-phase dynamic, the simulated population trajectory during the observed growth period from 1992-2005 produces a mean annual growth rate of just over 2% per year (λ = 1.022), followed by a transition to a rate of decline after 2005 approaching 7% annually (λ = 0.933).

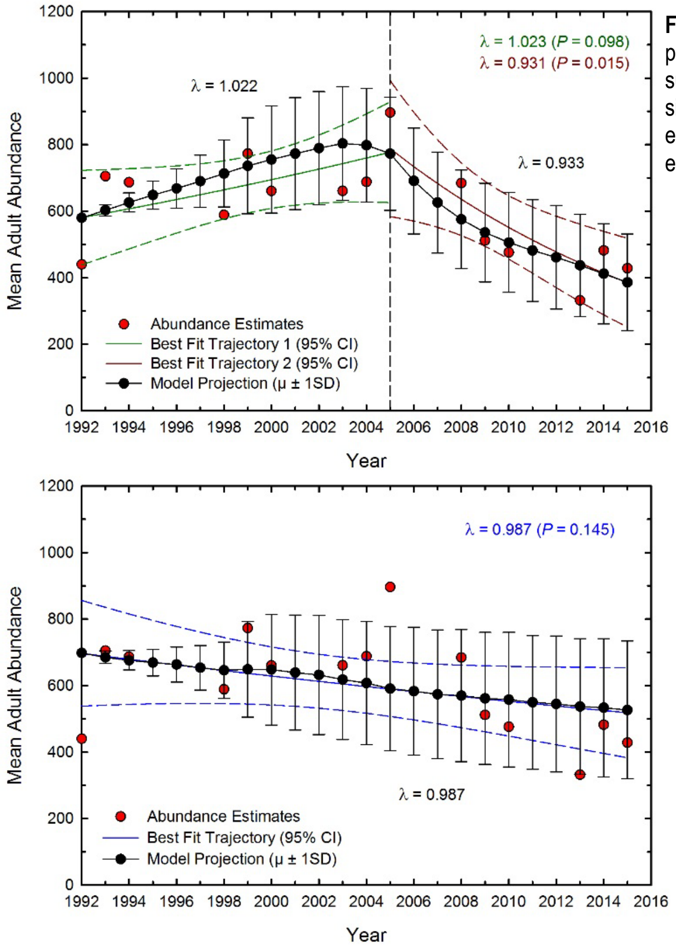


Figure 9. Retrospective trajectories of simulated Colorado pikeminnow adult abundance in the Upper Colorado River subbasin, alternatively assuming a dual-phase (top panel) or single-phase (bottom panel) demographic dynamic. Abundance estimates and results from regression analyses on those estimates included for comparison.

A similar type of detailed retrospective analysis was not conducted for the San Juan River subbasin as we do not have sufficient data on historical adult population abundance to draw comparisons with simulated population trajectories.

In both the Green River and Upper Colorado River subbasins, and under both assumptions of underlying demographic dynamic that may drive observed changes in adult population abundance, our simulation models of past population abundance are strongly concordant with dynamic changes in observed abundance estimates. Therefore, we may confidently use these models to prospectively evaluate the future adult abundance in these river systems under a variety of management scenarios designed to increase population growth rate and to minimize the risk of extinction of a particular subbasin population or even the extinction of the species across the current range.

Prospective Risk Analysis: Status Quo

We may assume that the conditions defining the recent abundance trajectories for each of the subbasin populations – both environmental drivers impacting population demography and the management activities currently in place – will remain unchanged in the future. This scenario can set a "baseline" of sorts to which other scenarios describing alternative management conditions can be compared.

The conditions defining the "status quo" scenario for the Green River subbasin include a continuation of summer flows that typically (probability 0.9, years 2000 – 2013) fall outside of the recommended range currently identified (see Figure 6). If these conditions are assumed to persist, the Green River subbasin population will continue to decline in adult abundance under either the dual-phase or single-phase demographic dynamic assumption (Figure 10). At the end of the simulation (model year 125), the mean adult abundance under the dual-phase dynamic is 58 individuals, while the projection under single-phase assumption produces a final abundance of 425 individuals. The probability of extinction under the dual-phase assumption is 0.006, indicating that a very small number of long-lived adults continue to persist at low density for many years.

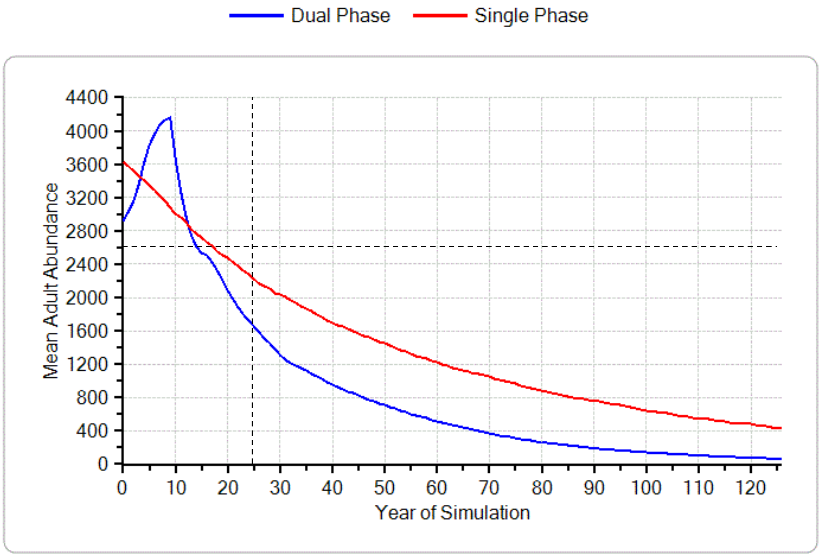


Figure 10. Simulated adult population abundance for Colorado pikeminnow in the Green River subbasin, under alternative assumptions of model demographic dynamic and assuming a "status quo" condition of no change in current management conditions in an unchanging environment. Vertical dashed line identifies the current calendar year, with retrospective trajectories included for reference. Horizontal dashed line identifies the current recovery criterion for adult abundance in the subbasin.

The "status quo" conditions for the Upper Colorado are largely governed by the flow conditions shown in Figure 7 and the mortality rates summarized in Table 2. However, future predictions of adult pikeminnow abundance in this system will be influenced by our assumption regarding the impact of the "spawning spike" of 2015 as discussed in the section on model input. Figure 11 shows the results of scenarios featuring alternative assumptions regarding the intensity of the spike, under both dual-phase and single-phase demographic dynamic assumptions.

The projections in Figure 11 clearly indicate that this observed occasional spike in Age-0 production can have a significant impact on future population performance. Under the assumption of a dual-phase dynamic, the adult population abundance appears to stabilize at approximately 300 individuals, with the lower-intensity spike scenarios showing negative rates of population growth but with increases in abundance compared to the scenario where the spike is absent. Extinction risks range from 0.364 in the "None" spike scenario to 0.022 in the "Full" spike scenario. Under the single-phase dynamic, all but the "Very Low" and "None" spike scenarios show negative growth of the adult population, with the other three scenarios appearing to stabilize in abundance at approximately 500 individuals. Only the "None" scenario presents any risk of subbasin population extinction (probability = 0.004).

The apparent stabilization in abundance shown in both sets of scenarios presented in Figure 11 results from an interaction between the very large increase in adult abundance predicted by the spike and the restriction in adult abundance imposed by the ecological carrying capacity. Under the "Full" spike to "Low" spike scenarios, the predicted number of adults produced by the spike event far exceeds the subbasin carrying capacity, which results in the final abundance for that year in which the cohort is recruited into the adult stage to be limited to *K* = 1000 adults. In any one iteration of a scenario, the trajectory will be characterized by likely population decline (defined by the "None" scenario) punctuated by very large increases in adult abundance to 1000 individuals in just one year as the fish produced during the previous spike grow and mature into adults. Over the 100 years of any one iteration of the scenario, and across 1000 iterations, the spike occurs in nearly every iteration-year, thereby leading to the apparent population stabilization. This effect is even more pronounced in the single-phase demographic dynamic scenarios, where the underlying higher growth rate leads to a larger number of years in which the impact of the event is truncated by carrying capacity.

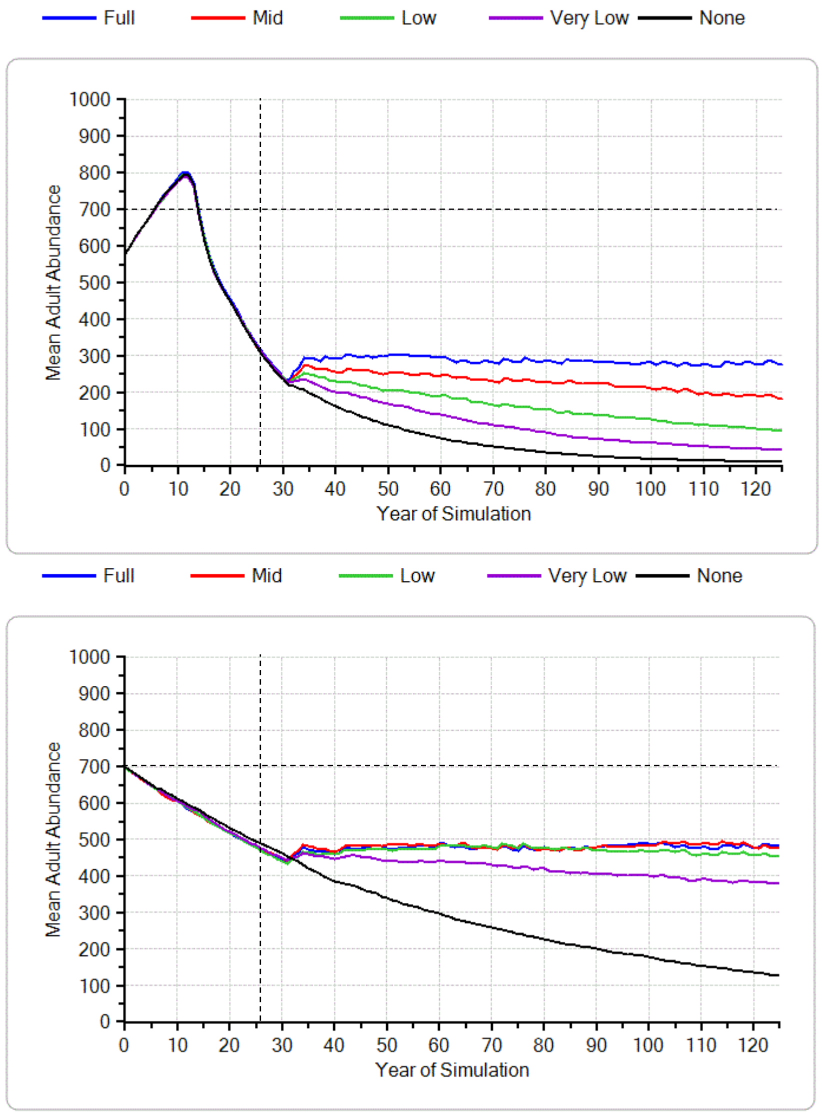


Figure 11. Simulated adult population abundance for Colorado pikeminnow in the Upper Colorado River subbasin, under alternative assumptions of model demographic dynamic and assuming different intensities of a future "spawning spike" based on the 2015 event. Vertical dashed line identifies the current calendar year, with retrospective trajectories included for reference. Horizontal dashed line identifies the current recovery criterion for adult abundance in the subbasin.

As stated previously, the true long-term impact of the 2015 spike in Age-0 production on adult abundance is unknown. Nevertheless, there is a general agreement among PVA Team members that spawning spikes such as this have in the past resulted in some later increase in the number of adults; therefore, an event of this nature should be included in prospective models of Upper Colorado River subbasin population viability. All subsequent models of this river system will therefore include the "Mid" form of the 2015

Age-0 production event. This is considered to be a reasonable intermediate characterization of the event, but is subject to re-evaluation in future revisions of this analysis.

Prospective Risk Analysis: A Preamble to Evaluating Alternative Management Activities

The following subsections present results of model scenarios that feature alterations to specific demographic input parameters, which are assumed to reflect the implementation of certain management activities within targeted subbasins. These activities are designed to alleviate given threats to Colorado pikeminnow populations within individual subbasins. Additional details on these scenarios can be found in the Supporting Information document accompanying this report (McAbee 2017a,b,c; Valdez et al. 2017; Durst 2017).

We assume that implementing the types of management activities presented below will elicit a positive demographic response in a given pikeminnow population. Furthermore, we assume that the management activity will target the threat this is most likely responsible for reducing reproductive and/or survival rates, habitat availability, etc. For example, we may hypothesize that high levels of predation by non-native fish species is primarily responsible for depressing normal rates of survival among younger pikeminnow age classes. While this may be a logical hypothesis, there may very well be other contributing factors that a given management activity may not address. The types of management activities described below are not meant to be unwaveringly prescriptive, but can instead be considered as representative activities that are based on the best available understanding of the means by which management can address the many threats facing the Colorado pikeminnow across its current range. More specific recommendations on management activities can emerge in the future, but only after a better understanding of threats to the species emerges through more research and analysis.

It is critically important to appreciate, in the context of this PVA, that we cannot yet predict the extent of activity that is required to achieve a desired demographic response. For example, we may want to increase early lifestage annual survival from x to y through nonnative fish removal, based on a general understanding of the impact of this form of predation on young pikeminnow survival and recruitment. However, we do not have field data on the functional numerical relationship between the number of nonnatives in a subbasin and the number of young pikeminnow they consume per unit time. Consequently, the PVA cannot provide insights that lead to specific recommendations for the number of nonnatives to remove in order to achieve the desired improvement in survival. The same argument can be made for the other management activities explored in this analysis. Readers of this report must keep this reality in mind when observing and interpreting model results.

On a related note, it is important to recognize a common misperception of PVA as a predictive tool: that the analysis itself generates the quantitative form of the functional relationship between a given threatening process and the demographic response within the population. Carrying on with the nonnative fish predation threat from above, there is a common expectation that the PVA model will generate the relationship between the number of nonnative fish inhabiting a given subbasin and the estimate of reduced survival among young pikeminnow. In fact, the mechanics of PVA model projection does not yield that relationship, but can only demonstrate the impacts of that reduced survival estimate – derived through external analysis of appropriate field data – on long-term population performance, i.e., growth or decline. This is accomplished by writing explicit mathematical expressions within the PVA model structure to define the appropriate demographic rate as functions of specific external variables. In an "ideal world", with the desired functional relationship in hand, and their explicit inclusion in the model input structure, one could then predict the intensity of management that would likely be required to alleviate the threatening process of interest.

Prospective Risk Analysis: Managing Summer Flows on the Green River

The status quo projections for the Green River subbasin above assume that only 10% of the yearly summer flows will fall within the recommended range, as was the case between 2000 and 2013 (Figure 6). Age-0 production may be enhanced by increasing the frequency with which these flow targets are achieved.

If all other model conditions remain unchanged – focusing only on increasing the rate of achieving recommended flow targets – our dual-phase dynamic models suggest that attaining those flow recommendations at least 50% of the time can generate stable to positive growth trajectories (Figure 12). Under a single-phase dynamic, the minimum frequency of achieving the targets increases slightly to approximately 60%. The higher frequency of successful flow years that is required in the single-phase dynamic is due to the slightly higher mortality rates among younger age-classes that characterizes assumed dynamic.

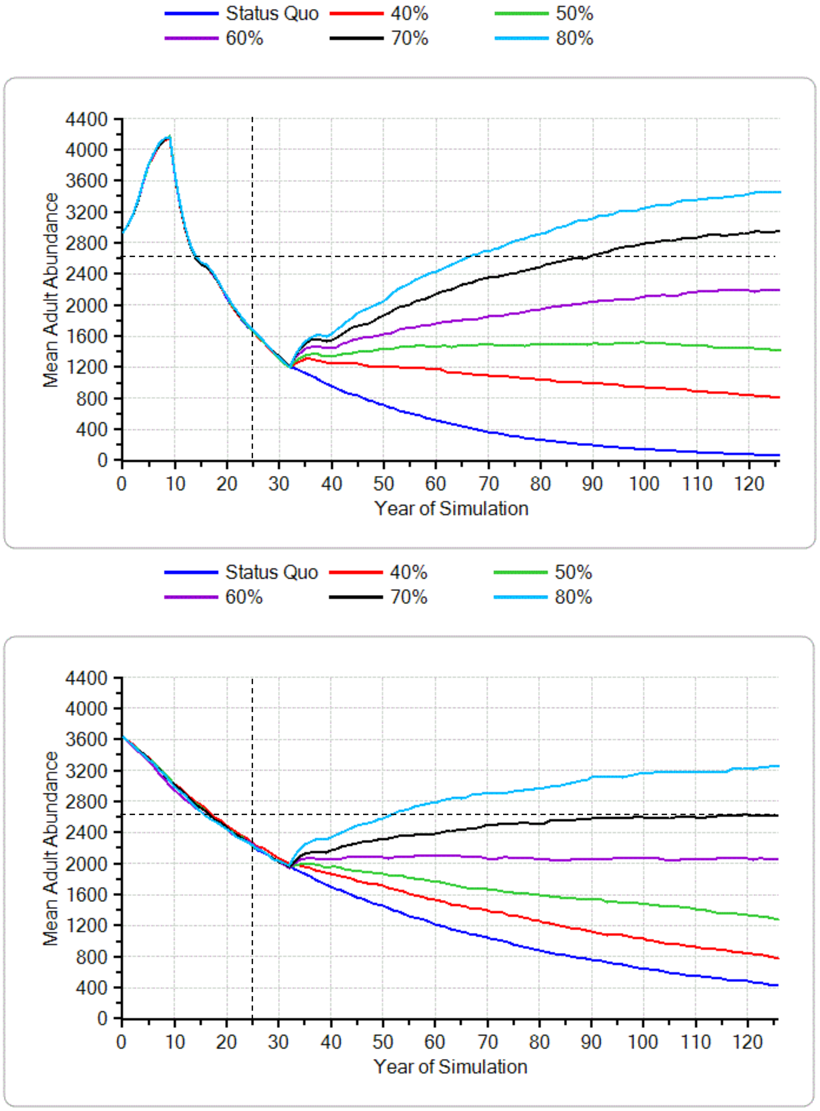


Figure 12. Simulated adult population abundance for Colorado pikeminnow in the Green River subbasin under alternative summer flow management regimes along the Green River and assuming either a dual-phase (top panel) or single-phase (bottom panel) demographic dynamic. Vertical dashed line identifies the current calendar year, with retrospective trajectories included for reference. Horizontal dashed line identifies the current recovery criterion for adult abundance in the subbasin.

Prospective Risk Analysis: Managing Summer Flows on the Upper Colorado River

Summer flows may be managed on the Upper Colorado River in the same manner as they are on the Green River. Under the assumption of a dual-phase demographic dynamic, 100% of the recent flows (i.e., since 2005) have been within the recommended targets (see Figure 7). Therefore, we may want to explore the impact of occasionally failing to achieve the proper flow. Approximately 85% of the summer flows fall within the recommended target under the single-phase demographic dynamic assumption, so it is instructive to explore the impact of improving flow management to achieve the targets with greater frequency.

Relatively modest changes in predicted adult abundance are seen under both demographic dynamic assumptions when flows are managed across the range of achievement frequencies considered (Figure 13). Reducing the efficacy of flow target management below 100% assuming a dual-phase dynamic and a "Mid Spike" Age-0 productive event reduced the final adult abundance to approximately 100 individuals. This is compared to the "status quo" scenario when flow targets are achieved 100% of the time, when the final adult abundance as approximately 200 individuals.

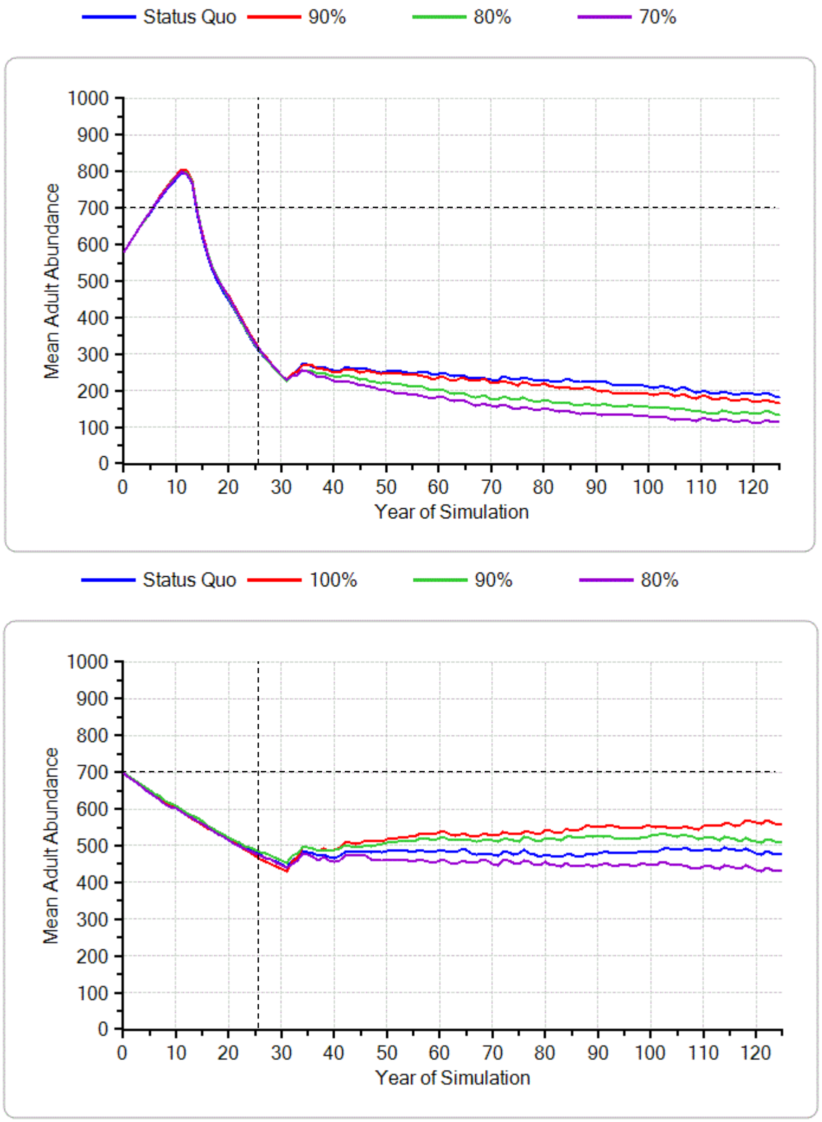


Figure 13. Simulated adult population abundance for Colorado pikeminnow in the Upper Colorado River subbasin under alternative summer flow management regimes along the Upper Colorado River, assuming a "Mid Spike" Age-0 production event and either a dual-phase (top panel) or single-phase (bottom panel) demographic dynamic. Vertical dashed line identifies the current calendar year, with retrospective trajectories included for reference. Horizontal dashed line identifies the current recovery criterion for adult abundance in the subbasin.

Increasing the rate of achieving the recommended flow targets for the Upper Colorado River from the "status quo" rate (85%) to 100% led to a slight increase in the mean adult population abundance. However, given that the base achievement rate is already rather high, the small increases in flow management that are possible do not facilitate a substantial change in adult abundance over the long term.

Prospective Risk Analysis: Managing Impacts of Non-Native Predators in the Green River Subbasin

Managing non-native predators in the Green River subbasin via removal is considered to be beneficial for two aspects of Colorado pikeminnow population dynamics: increasing the survival of young pikeminnow, and improving both the quality and quantity of available habitat (and therefore increasing carrying capacity) through decreased competition.

Specifically, non-native predator management was simulated in this PVA through the following two proposed mechanisms, with the precise nature of the functional relationship as yet unspecified:

1. An increase in the mean annual survival rate of Colorado pikeminnow from age-class 0 (young of the year) to age-class 4, employing incremental proportional increases of 5% to 20% across each of the stated age classes in increments of 5%; and
2. An increase in the habitat carrying capacity, from the "status quo" value of 4300 adults to 4600 at the lowest level of non-native predator management (corresponding to 5% increase in survival described above) to 5500 at the highest level of non-native predator management (corresponding to 20% increase in survival). Carrying capacity increases in increments of 300 in conjunction with the incremental increase in survival through management.

Substantial increases in long-term adult population abundance are observed in our simulations of this management option – even with potentially relatively modest levels of successful management (Figure 14). Under the assumption of a dual-phase demographic dynamic, as much as 10% annual proportional increase in annual survival through non-native predator removal appears to generate a positive growth rate for the adult Colorado pikeminnow population. Increasing the intensity of non-native predator removal to a level that is commensurate with a 15% annual proportional increase in younger pikeminnow results in a large increase in population growth rate, with the adult population increasing from approximately 1500 fish seven years after the initiation of management to more than 4500 fish at the end of the simulation. If we assume a single-phase demographic dynamic, the response to non-native predator removal is even more robust – owing to the lower baseline mortality rates that define this assumed dynamic. A positive growth rate for the simulated adult pikeminnow population is possible with as little as a 6-7% increase in annual survival of younger pikeminnow, while a 10% increase in that survival yields a final adult population abundance of nearly 4000 by the end of the simulation. It is important to note that the transition to positive long-term population growth in these scenarios can only be achieved through improving survival of the younger age-classes; in other words, such population growth cannot be achieved through increasing only habitat carrying capacity. Of course, increasing *K* will facilitate growth of the population to long-term abundances that would be unachievable without expanding the availability of pikeminnow habitat.

As stated throughout this report, the exact relationship that defines the extent of non-native predator removal required to achieve a given increase in young (i.e., 0-4 years old) pikeminnow survival rate is currently unknown. However, it may be possible through targeted study design and implementation to assess the impacts of a specific management action on survival of these younger fish, which can then guide predator removal activities to achieve the desired demographic outcome.

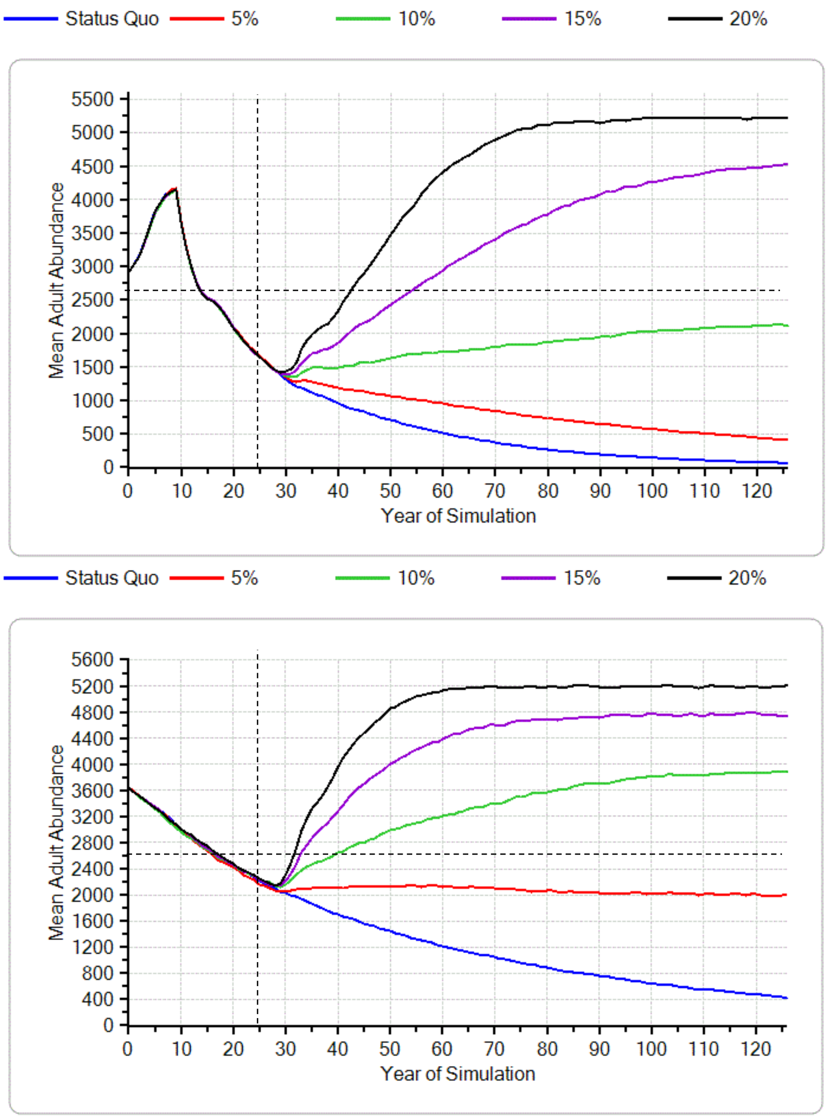


Figure 14. Simulated adult population abundance for Colorado pikeminnow in the Green River subbasin under alternative non-native predator management regimes and assuming either a dual-phase (top panel) or single-phase (bottom panel) demographic dynamic. Vertical dashed line identifies the current calendar year, with retrospective trajectories included for reference. Horizontal dashed line identifies the current recovery criterion for adult abundance in the subbasin.

Prospective Risk Analysis: Managing Impacts of Non-Native Predators in the Upper Colorado River Subbasin

The analysis also considers a similar type of non-native predator removal program for the Upper Colorado River subbasin, subject to the following proposed conditions:

1. An increase in the mean annual survival rate of Colorado pikeminnow from age-class 0 (young of the year) to age-class 4, employing incremental proportional increases of 5% to 20% across each of the stated age classes in increments of 5%; and
2. A simultaneous increase in the habitat carrying capacity, from the “status quo” value of 1000 adults to 1100 at the lowest level of non-native predator management (corresponding to the 5% increase in survival described above) to 1400 at the highest level of non-native predator management (corresponding to 20% increase in survival). Carrying capacity increases in increments of 100 in conjunction with the incremental increase in survival through management.

As with the Green River subbasin models, our analyses suggest that the Upper Colorado River subbasin population may show significant response to non-native predator management (Figure 15). A proportional increase of just 5 – 10% in the survival of the younger age-classes of Colorado pikeminnow yields positive population growth rates assuming either the dual-phase or single-phase demographic dynamic. The response of the population to a given level of non-native predator management is more robust under the single-phase dynamic assumption, once again resulting from the lower overall mortality rates that define this hypothesized dynamic. As before, the influence of the "spawning spike" is evident in the approach to a long-term equilibrium in population abundance that is a balance between the occasional nature of the event and its significant benefit to the population which is ultimately attenuated by the habitat carrying capacity.

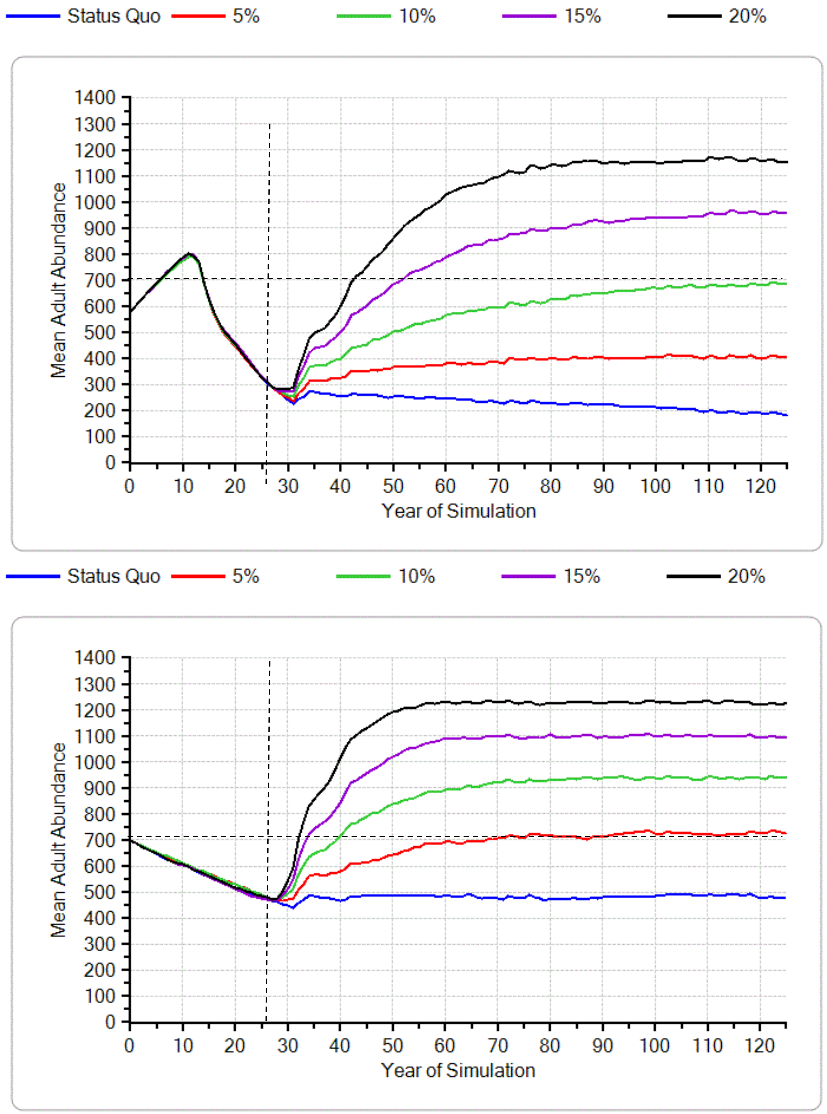


Figure 15. Simulated adult population abundance for Colorado pikeminnow in the Upper Colorado River subbasin under alternative non-native predator management regimes along the Upper Colorado River, assuming a "Mid Spike" Age-0 production event and either a dual-phase (top panel) or single-phase (bottom panel) demographic dynamic. Vertical dashed line identifies the current calendar year, with retrospective trajectories included for reference. Horizontal dashed line identifies the current recovery criterion for adult abundance in the subbasin.

Prospective Risk Analysis: Managing Adult Mortality in the Green River Subbasin

While there may be fewer proposed direct threats to mortality of adult Colorado pikeminnow in comparison to younger age classes, it is nevertheless instructive to evaluate the extent of adult mortality management that would lead to pikeminnow adult abundance increases relative to our "status quo" baseline scenario. This was implemented for both the Green and Upper Colorado River subbasin population models, with the annual adult mortality rate modified from the "status quo" value of 18% down to a minimum value of 10% in increments of 2%. The results of these scenarios are shown for the Green River subbasin population in Figure 16.

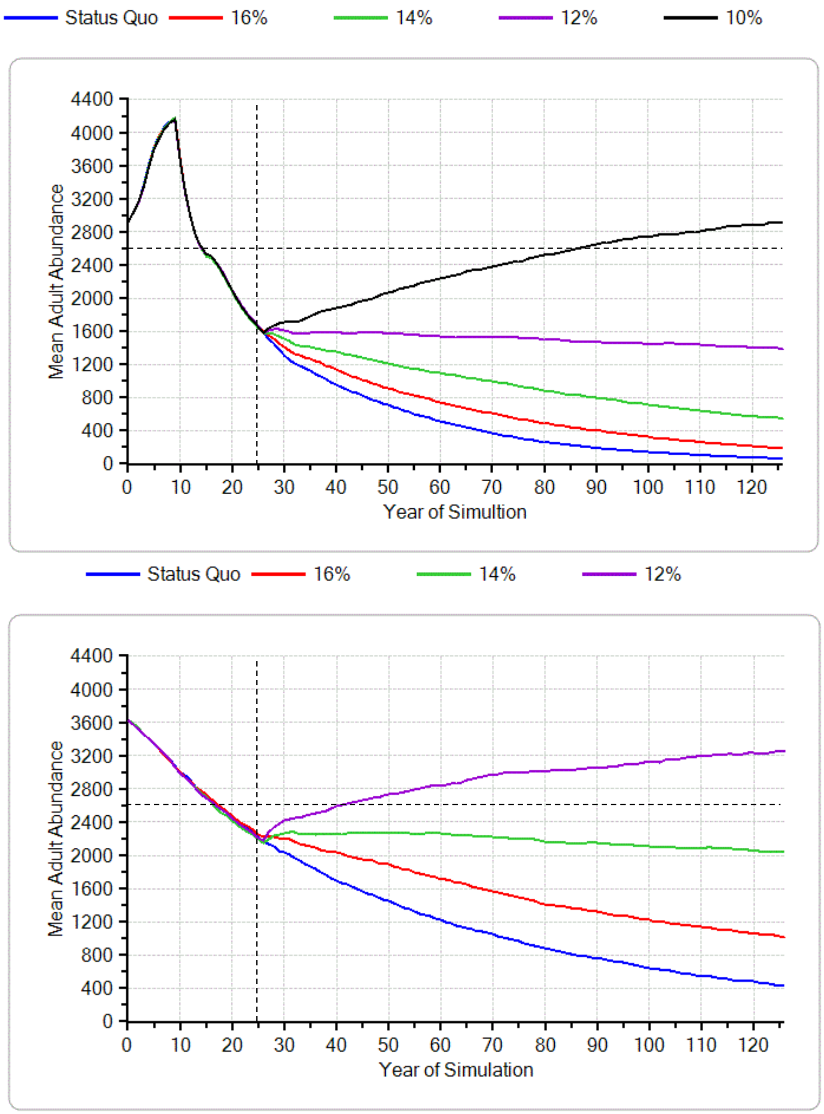


Figure 16. Simulated adult population abundance for Colorado pikeminnow in the Green River subbasin under alternative adult mortality management regimes and assuming either a dual-phase (top panel) or single-phase (bottom panel) demographic dynamic. Vertical dashed line identifies the current calendar year, with retrospective trajectories included for reference. Horizontal dashed line identifies the current recovery criterion for adult abundance in the subbasin.

The simulations summarized in Figure 16 suggest that Colorado pikeminnow populations are also quite responsive to changes in adult mortality. Under the dual-phase demographic dynamic assumption, a reduction in mortality from the "status quo" value of 0.82 to 0.88 results in a simulated population that is very close to displaying long-term growth in the absence of other demographic revisions. For reference, the aforementioned reduction in mortality corresponds to roughly a 7% proportional increase in mean annual adult survival. This is similar to the magnitude of proportional change in young pikeminnow survival required to achieve a positive growth rate through non-native predator removal (Figure 14), although it is important to remember that the increase in survival effected through non-native predator removal is applied to the five youngest age classes of pikeminnow in our model.

A comparatively smaller reduction in annual adult mortality is required to achieve growth in adult pikeminnow abundance under the assumption of a single-phase demographic dynamic. Based on the results shown in Figure 15, positive growth would be expected with annual adult mortality just under 14% instead of the 12% necessary for growth in the dual-phase dynamic. Again, this is not surprising given that the single-phase dynamic assumes a lower rate of annual mortality among younger fish, thereby increasing the rate of recruitment relative to that expected under the dual-phase demographic dynamic.

Prospective Risk Analysis: Managing Adult Mortality in the Upper Colorado River Subbasin

Management of adult mortality in the Upper Colorado River subbasin also leads to a significant long-term response in adult population abundance (Figure 17). In fact, because of the marked response of this population to the included "spawning spike", the threshold levels of adult mortality required for long-term population growth are slightly lower than those required for the Green River subbasin population. Under the assumption of a dual-phase demographic dynamic, the Upper Colorado subbasin adult population shows positive growth when the mean adult mortality rate is lowered to 14% from the baseline value of 18%, while population growth is achieved under the assumption of a single-phase dynamic when adult mortality is reduced to just 16%.

To reiterate, these adult mortality management scenarios do not correspond to specific and recognizable river system management activities, although there are such activities that may include some level of adult mortality mitigation (see below). Rather, the scenarios are instructive to determine the extent of mortality mitigation necessary to observe long-term population growth, which could then stimulate discussion about the degree to which that level of mitigation is reasonable or even achievable given what is known about threats to survival of adult Colorado pikeminnow.

Prospective Risk Analysis: Managing Pikeminnow Mortality through Entrainment in the Green River Canal Diversion

McAbee (2017b) discusses in detail a proposed management action designed to screen the Green River Canal diversion just upstream of Tusher Wash, north of Green River, Utah. The existing canal results in additional mortality of all age-classes of pikeminnow through entrainment. As Age-0 individuals sampled in the autumn ISMP sampling protocol are approximately 50 mm total length, this youngest age class is included in this analysis as McAbee considers fish of this size to be susceptible to entrainment. It is believed that screening this diversion would reduce or potentially eliminate all entrainment-based pikeminnow mortality resulting from this structure.

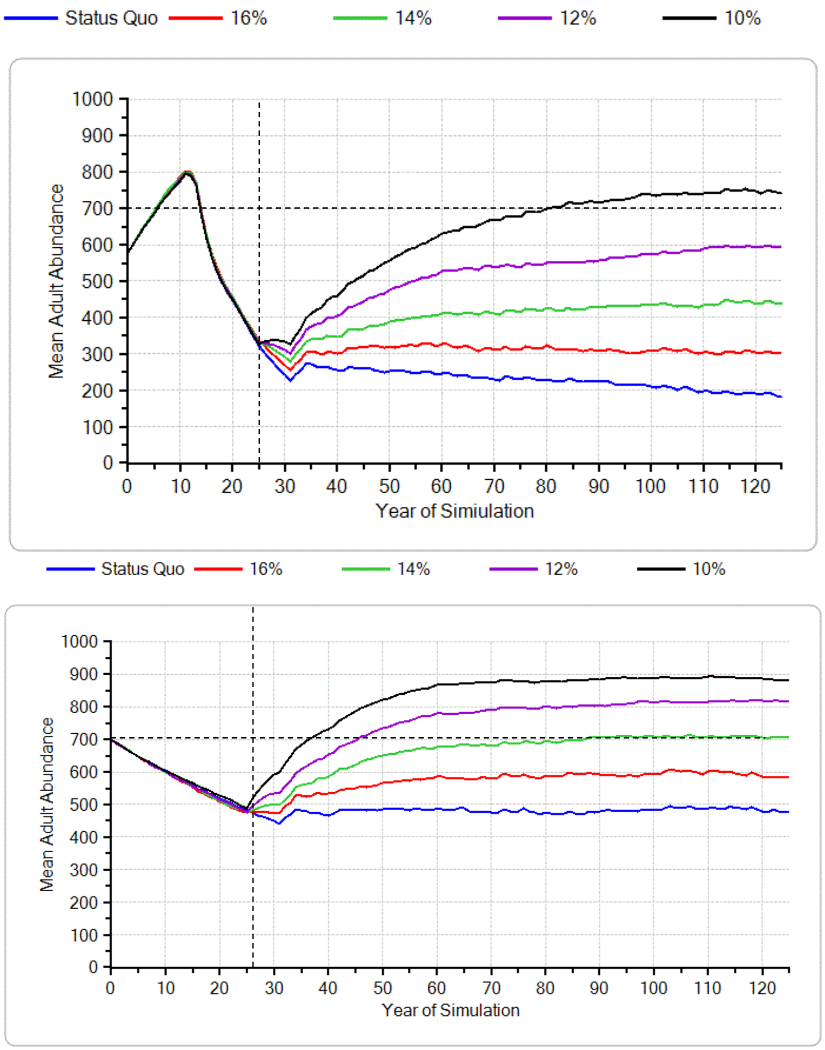


Figure 17. Simulated adult population abundance for Colorado pikeminnow in the Upper Colorado River subbasin under alternative adult mortality management regimes along the Upper Colorado River, assuming a “Mid Spike” Age-0 production event and either a dual-phase (top panel) or single-phase (bottom panel) demographic dynamic. Vertical dashed line identifies the current calendar year, with retrospective trajectories included for reference. Horizontal dashed line identifies the current recovery criterion for adult abundance in the subbasin.

Simulating the management of this diversion is implemented in this PVA through the following proposed mechanisms (again, with the nature of the functional relationship as yet undefined):

1. Reduce annual adult mortality by 1.76%. McAbee (2017b) derived this value using monitoring data from tagged fish detected (entrained) in the canal, estimating the total number of adult pikeminnow entrained annually in this diversion, and then transforming this to a proportion of the total adult population. It is important to note that this is an additive mortality impact and not proportional as was assumed for the non-native predator removal analysis.
2. Reduce annual mortality of all other age classes by 3.52%. McAbee (2017b) assumes that younger/smaller fish may become entrained in higher proportion to their adult counterparts. An initial estimate of this increased susceptibility is to double the rate of entrainment-based mortality. Therefore, screening this structure would result in a reduction in mortality of double the adult rate (the “High Impact” scenario). The magnitude of this differential impact on younger fish is uncertain. In order to test the sensitivity of our model to this parameter, an additional scenario was created in which the impact on mortality of younger fish was assumed to be of equal

magnitude to the impact on adult fish – i.e., an additive 1.76% reduction in mortality (the "Low Impact scenario).

The results of these management analyses are shown in Figure 18. The successful screening of the Green River Canal diversion, as simulated in this PVA, can have a significant impact on the long-term abundance of adult Colorado pikeminnow. Under the assumption of a dual-phase demographic dynamic, the "Low Impact" management scenario leads to a continued decline in adult abundance, though the rate of decline is substantially less than the "status quo" scenario. In contrast, the "High Impact" scenario results in strong population growth, reaching nearly 3200 adult fish by the end of the simulation. Under the assumption of a single-phase demographic dynamic, both the "Low Impact" and "High Impact" scenarios result in sustained population growth throughout the timeframe of the simulation, with the latter scenario approaching the assumed habitat carrying capacity of 4300 adults.

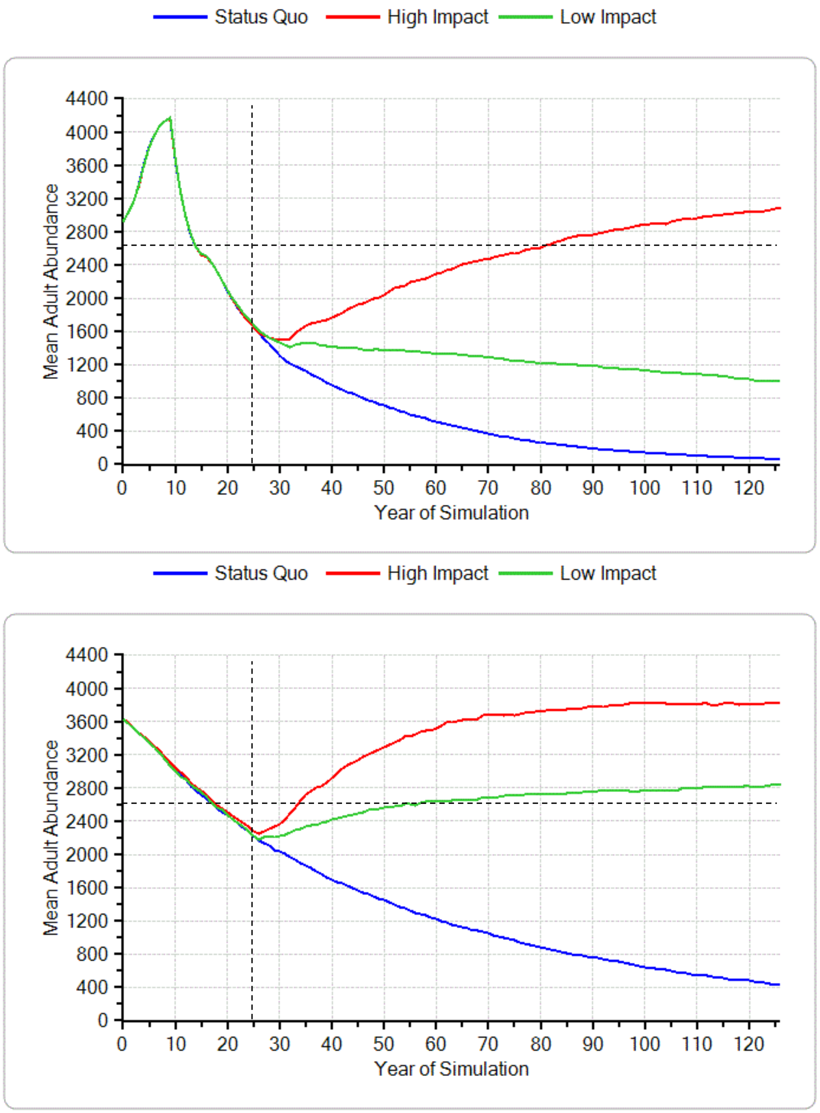


Figure 18. Simulated adult population abundance for Colorado pikeminnow in the Green River subbasin under alternative Green River Canal diversion management regimes and assuming either a dual-phase (top panel) or single-phase (bottom panel) demographic dynamic. Vertical dashed line identifies the current calendar year, with retrospective trajectories included for reference. Horizontal dashed line identifies the current recovery criterion for adult abundance in the subbasin.

Prospective Risk Analysis: Combined Management of Multiple Threats in the Green River Subbasin

The specific pikeminnow conservation activities that could be implemented in the Green River subbasin – summer flow management, non-native predator removal, and Green River Canal entrainment screening – have all been evaluated as singular activities. In reality, it is likely that one or more of these management activities will be conducted simultaneously, with the hypothesis that relatively smaller investments in any one activity, when implemented in conjunction with one or more additional management scheme, may yield significant benefits to the pikeminnow population. In this spirit, the current PVA conducts an exploration of a selected set of combined management schemes for the Green and Upper Colorado River subbasin populations of Colorado pikeminnow.

The Green River subbasin scenarios evaluate the combined impact of roughly intermediate levels of the three broad management options listed above. Specifically, the combined management scenarios feature the following management components:

1. Summer flow management – recommended flow targets are achieved in 50% of years;
2. Non-native predator removal – management sufficient to realize a 5% proportional increase in annual survival in pikeminnow age-classes 0 through 4; and
3. Green River Canal diversion screening – Both the “Low Impact” and “High Impact” scenarios are evaluated.

Each of these options is implemented in pairs (e.g., [flow management + predator removal]), or as a full-scale management activity involving all three components.

Figure 19 summarizes the results of the various activities that make up the combined management scenarios. All combined management scenarios generate significant growth in the adult pikeminnow population, although some combinations perform more vigorously than others. Under the assumption of a dual-phase demographic dynamic, the combined action of a low level of non-native predator removal, resulting in a 5% proportional increase in young pikeminnow survival, and the “Low Impact” mode of Green River Canal diversion screening resulted in the most modest increase in adult pikeminnow abundance, with the final abundance reaching 3200 individuals. Combining the same level of non-native predator removal with a 50% summer flow target activity performed slightly better, with the final adult population increasing to 3600 individuals, while the 50% flow target activity combined with a “Low Impact” Canal diversion scenario culminated in 3800 adults at the end of the simulation. As expected, combination scenarios including the “High Impact” Canal diversion scenarios consistently led to vigorous population growth. Combining this with the 50% summer flow target activity yields high adult abundances early in the prospective trajectory, but ultimately the “High Impact” Canal diversion scenario combined with the low level of non-native predator removal performs better through the inclusion of an expanded habitat carrying capacity gained through predator management. Finally, and certainly not surprisingly, the full combination scenarios perform the best, with final adult population abundances reaching 4300 to 4400 indiviuals as a function of the strength of the Canal diversion screening impact.

The results of the combined management analysis under the assumption of a single-phase demographic dynamic are quite similar to those of under the dual-phase assumption. However, the scenarios involving management pairs that include the low level of non-native predator removal perform markedly better under the single-phase dynamic. This is most likely due to the lower levels of young pikeminnow mortality that are already in play at the beginning of the simulated trajectory, thereby amplifying the impact of additional reductions to mortality among those important age-classes.

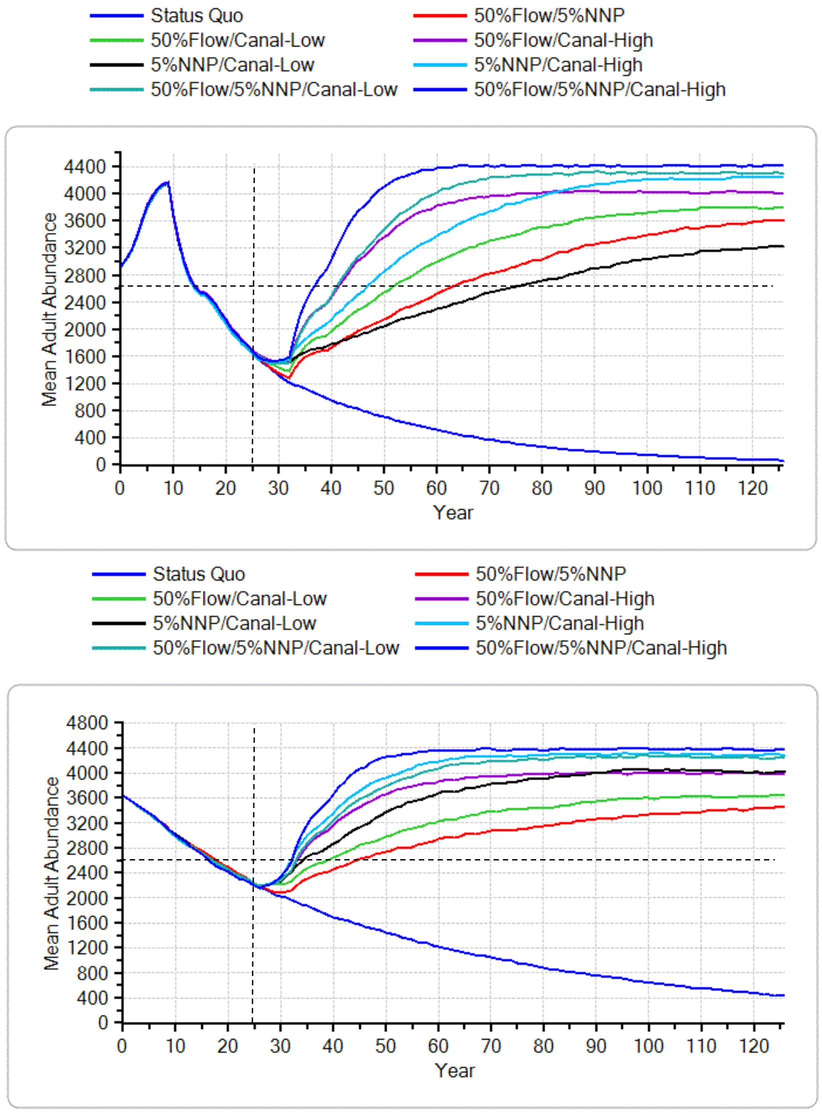


Figure 19. Simulated adult population abundance for Colorado pikeminnow in the Green River subbasin under a suite of combined management scenarios and assuming either a dual-phase (top panel) or single-phase (bottom panel) demographic dynamic. Vertical dashed line identifies the current calendar year, with retrospective trajectories included for reference. Horizontal dashed line identifies the current recovery criterion for adult abundance in the subbasin.

Prospective Risk Analysis: Combined Management of Multiple Threats in the Upper Colorado River Subbasin

The Upper Colorado River subbasin scenarios evaluate the combined impact of roughly intermediate levels of two broad management options. The dual-phase demographic dynamic scenarios assume that flow targets will consistently be met each year, in accord with observations across the recent past (2005-2015). In the single-phase demographic dynamic, summer flow management becomes an option for overall species management. All combined management scenarios include the “Mid-Spike” Age-0 reproductive event and feature the following management components:

1. Summer flow management (single-phase only) – recommended flow targets are achieved in 100% of years;
2. Non-native predator removal – management sufficient to realize a 5% or 10% proportional increase in annual survival in pikeminnow age-classes 0 through 4; and

3. Expansion of pikeminnow range through implementation of fish passage – This management activity has not yet been assessed as its primary demographic impact would be on increasing habitat carrying capacity. As described in detail in Valdez et al. (2017), the fish passage structures recently installed in the Upper Colorado River at the Grand Valley Water User's Dam (RM 194) now open up as many as 38 miles of suitable habitat to the thermally-derived upstream boundary at Rulison (RM 232). Depending on the choice of estimate for pikeminnow density that could persist in this area (11.6 adults/mile vs. 7.5 adults/mile), this new habitat could possibly support between 285 and 441 additional adults. Using a similar argument, the selective fish passage installed on the Gunnison River's Redlands Water and Power Company diversion at RM 3.0 opens up as many as 37 miles of new habitat. This could potentially support up to 278 additional adults based on the upper density estimate of 7.5 adults/mile obtained from the Upper Colorado River analysis just described. Taken together, this information leads to two alternative fish passage scenarios for analysis: a "Low" scenario with new habitat to support up to (285+287) 572 adults, and a "High" scenario with new habitat to support up to (441+287) 728 adults. These scenarios assume that the new habitat will be available immediately, although it is more likely to be gained gradually over a period of years. This simplification is not expected to alter the outcome of the analyses.

Under the dual-phase dynamic assumption, each of these options is implemented in pairs defined by strength of non-native predator removal and the extent of new habitat (increased carrying capacity) through the implementation of fish passages along the Upper Colorado and Gunnison Rivers. Under the assumption of a single-phase demographic dynamic, the three options are implemented in pairs or as the full combination of all three management components.

Under the assumption of a dual-phase demographic dynamic (Figure 20), the addition of the fish passage management component adds substantially to the growth rate and final population abundance when compared to implementing a non-native removal program in the absence of adding fish passage (see Figure 14 for comparison). Without fish passage, the final adult abundance is about 400 or 680 individuals under a 5% or 10% proportional increase in young pikeminnow survival, respectively, while the addition of fish passage increases this abundance to approximately 600 (5% survival increase) or 1000-1100 (10% survival increase) adults. The increased benefit of adding both extended areas of habitat is relatively small as the underlying demographic rates for the fish passage scenarios are the same.

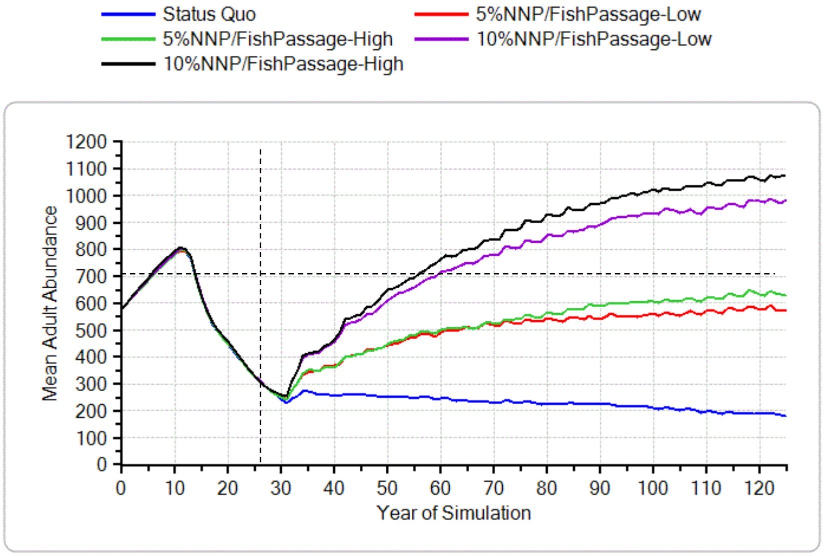


Figure 20. Simulated adult population abundance for Colorado pikeminnow in the Upper Colorado River subbasin under a suite of combined management scenarios, assuming a "Mid Spike" Age-0 production event and a dual-phase demographic dynamic. Vertical dashed line identifies the current calendar year, with retrospective trajectories included for reference. Horizontal dashed line identifies the current recovery criterion for adult abundance in the subbasin.

The suite of alternative combination management scenarios is expanded under the assumption of a single-phase demographic dynamic (Figure 21). Modest levels of non-native predator removal, combined with the added habitat made available through installation of fish passages along the Upper Colorado and Gunnison Rivers, can yield strong population growth rates and final adult population abundances near the maximum habitat carrying capacity of about 1700 individuals in the “High” fish passage scenarios. The addition of more stringent summer flow management (flows within recommended range 100% of years) on top of the combined non-native predator removal and fish passage installation adds somewhat to the adult population growth potential, but does not yield the same level of benefit relative to the low to modest level of non-native predator removal featured in these scenarios.

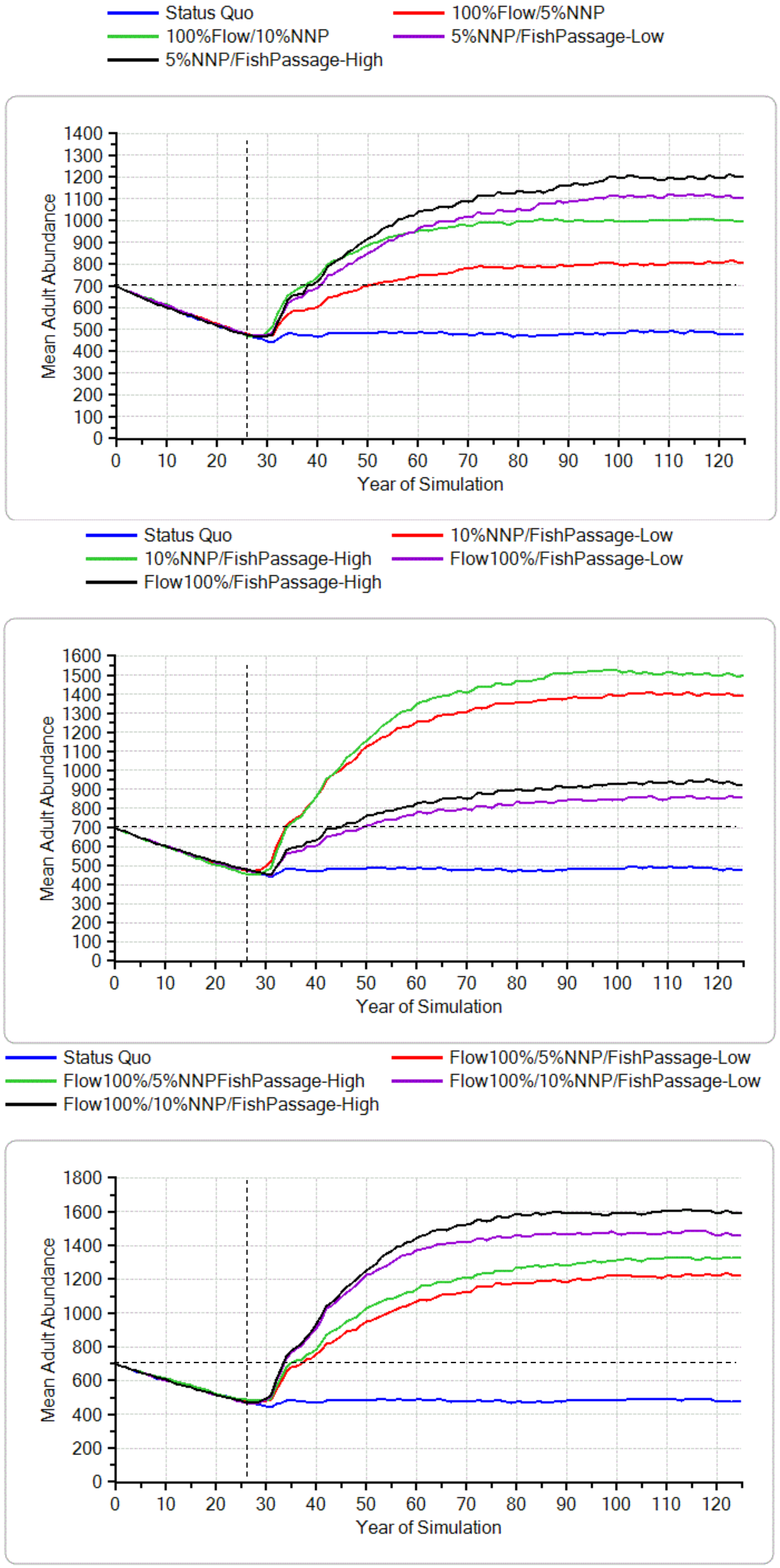


Figure 21. Simulated adult population abundance for Colorado pikeminnow in the Upper Colorado River subbasin under a suite of combined management scenarios, assuming a "Mid Spike" Age-0 production event and a single-phase demographic dynamic. Vertical dashed line identifies the current calendar year, with retrospective trajectories included for reference. Horizontal dashed line identifies the current recovery criterion for adult abundance in the subbasin.

Prospective Risk Analysis: Managing Threats in the San Juan River Subbasin

The scenarios described below are loosely based on a subset of proposed management alternatives described in Durst (2017). Given our best estimates of population demographic processes governing the growth of Colorado pikeminnow in the San Juan River subbasin, and if we assume that those processes remain unchanged into the future (likely a dubious assumption at best, as is the case with the other river systems discussed here), we can maintain a population of adult pikeminnow in the San Juan River subbasin at an abundance that is consistent with recent overall abundance esimates of approximately 80-100 individuals (Figure 21). However, this is dependent on the continued stocking of Age-0 to Age-1 fish in the river at annual intervals in order to overcome the various processes (predation, river hydrology, toxins, etc.) that combine to greatly restrict reproduction and recruitment in wild pikeminnow inhabiting this river system.

In order to explore the demographic conditions required for sustainable population growth of San Juan River subbasin pikeminnow, a series of scenarios was constructed that incrementally increased both Age-0 production and survival of the younger age-classes through targeted non-native predator removal in accord with that implemented in scenarios evaluating the Green and Upper Colorado River subbasins. Specifically, mean annual Age-0 production was increased from the "status quo" value of just five individuals among successfully spawning females to as high as 60 individuals, and predator removal was assumed to be conducted at a level that would result in a 25% to 50% increase in survival of individuals in age-class 0 to age-class 4. Note that this seemingly large increase in survival rate of younger fish represents a rather small change in the absolute rate, owing to the very low assumed survival of these fish in the subbasin. For example, a 25% increase is survival among Age-0 and Age-1 fish means that survival changes from 10% to 12.5% and from 20% to 25%, respectively.

The results of the varous management analyses shown in Figure 22 suggest that considerable demographic improvements are required if the Colorado pikeminnow is to survive in the San Juan River subbasin. Based on the conditions set forth in this set of analyses, a stable population can be maintained in the absence of stocking only if the apparent reproductive rate is increased by more than an order of magnitude, and the baseline mortality rates are greatly improved. Specifically, the demographic conditions that lead to long-term population stability include (1) the mean rate of successful spawning among adult females increases from the baseline rate of 70% to 80%; (2) mean Age-0 production among successfully breeding females of no less than 60 individuals per successful female; and (3) an approximate increase in mean survival rates among juvenile and subadult pikeminnow age-classes of between 150% and 11%, respectively, relative to their baseline values (Table 4). If the demographic profile of the population does not meet this standard, the long-term adult abundance trajectory will resemble those in Figure 22 where the population declines rapidly to extinction when stocking is ceased. Continued stocking in the early years of the prospective trajectory, in the presence of management aimed at improving underlying population demographics, can facilitate rapid growth of the population to a point where stocking can be removed from the managment regime when the population abundance nears its habitat carrying capacity.

An additional set of management scenarios was proposed that involved expanding the range of Colorado pikeminnow beyond their current distribution within this subbasin. Specifically, one could consider thermal modifications to upstream reaches of the San Juan River below Navajo Dam, as well as opening up areas of the Animas River upstream to Durango, CO by managing passage barriers and entrainment risks. Proper management in these areas could potentially increase the subbasin habitat carrying capacity by a substantial amount, although the true extent of this increase remains unknown. However, simply increasing the amount of available habitat by itself, without some associated improvement in the underlying demographic characteristic of this population, will not lead to a change in the overall growth dynamic of this subbasin population. It has been suggested that increased availability of upstream habitat in this subbasin could result in better overall larval survival, since the larvae produced upstream may be able to find suitable low-velocity nursery habitat before drifting downstream into high-gradient, higher-velocity habitats that terminate at the waterfall into Lake Powell. In this case, the increased habitat carrying capacity would have the potential to improve overall demographic performance due to the associated impact on larval survival. Unfortunately, we have no appropriate information at present on the extent to which larval survival would be improved by expanding pikeminnow range into these upstream habitats. Because of these data limitations, and due to a host of other factors impeding progress on implementing this type of broad management action, the option of range expansion in the San Juan subbasin was not explicitly evaluated in this PVA. Further exploration of this management option can and should be considered as the species management program evolves.

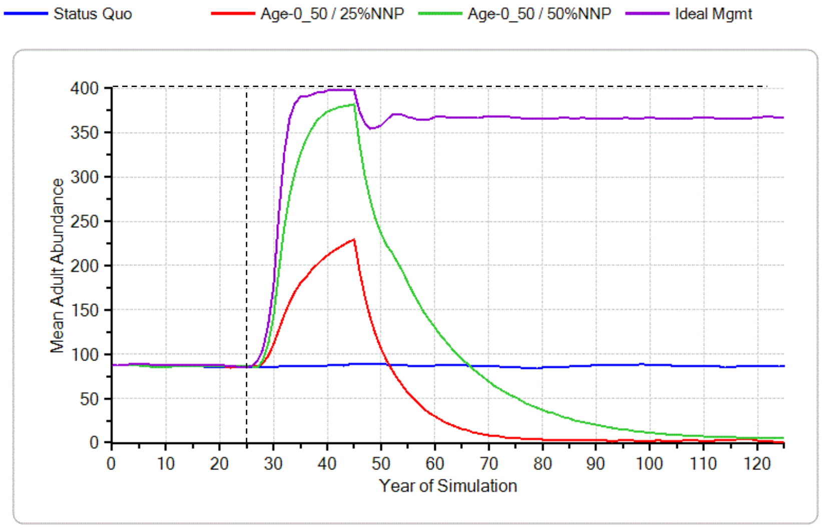


Figure 22. Simulated adult population abundance for Colorado pikeminnow in the San Juan River subbasin under a suite of combined management scenarios. Stocking of Age-0 fish at the levels discussed in the text is halted at model year 40 in all simulations. Vertical dashed line identifies the current calendar year, with retrospective trajectories included for reference. Horizontal dashed line identifies the current approximate recovery criterion for adult abundance in the subbasin.

Table 4. Age-specific mortality rates for Colorado pikeminnow used in the PVA for alternative scenarios exploring population dynamics in the San Juan subbasin. Stocking of juvenile is continuous in the "Status Quo" scenario and terminated at year 40 in the "Ideal Mgmt" scenario.

Age Class	"Status Quo" scenario	"Ideal Mgmt" scenario
0-1	90	75
1-2	80	65
2-3	70	55
3-4	60	40
4-5	50	30
5-6	40	25
6-7	30	22
7+	18	18

Prospective Risk Analysis: Managing Threats in the Colorado Pikeminnow Metapopulation

With the component subbasin populations fully analyzed, we can explore the dynamics of the complete metapopulation as a platform to determine realistic management scenarios across the range of the species. The metapopulation analysis requires the specification of a few additional model parameters, which are discussed below.

Characteristics of dispersing individuals

We assume that both male and female pikeminnow could move among selected river subbasins. Furthermore, we assume that while younger fish in both the Green and Upper Colorado River subbasins may move more easily downstream and end up in the northern reaches of Lake Powell, only larger fish (> ≈250 mm TL) are capable of moving upstream among these two subbasins. For our model structure, we therefore specify that fish greater than four years of age are capable of dispersing among these two subbasins.

Dispersal rates among subbasins

The recent study of Osmundson and White (2017) provides important information for estimating the annual rate of movement of the appropriate age cohort of fish between the Green and Upper Colorado River subbasins. Based on extensive analysis of tagged fish captures during the period 1991 – 2013, they estimated an annual rate of movement of 6.5 Age-5+ fish per year from the Green to the Upper Colorado subbasin. Our demographic analyses of adult mean abundance in the Green River subbasin during that same period was used to estimate the mean total abundance of the Age-5+ cohort over the period 1991 – 2013 as approximately 5500 individuals. Therefore, we estimate the annual rate of interbasin movement, expressed in terms of the percentage of the total mean cohort abundance, as (6.5)/(5500) = 0.00119 or 0.12% per year. This parameter value is used to predict the annual number of Age-5+ fish moving from the Green to Upper Colorado River subbasin, as a function of the fluctuating annual abundance of that Green River subbasin cohort. We assume that this rate of movement is symmetrical, i.e., the rate of movement from the Upper Colorado to the Green River subbasin is also 0.12% per year. While the proportional movement rate may be equivalent, the absolute numbers of fish moving between the two subbasins will be different owing to the different total abundances of the Age-5+ cohort occupying each subbasin.

Because of the location of the San Juan River subbasin population, with Lake Powell forming the intervening habitat south of the Green and Upper Colorado River subbasins, we assume that the San Juan River subbasin is effectively demographically isolated from these two portions of the species' range. This is supported by Osmundson and White (2017) who note that no movement of fish between the San Juan River subbasin and either the Green or Upper Colorado River subbasins has ever been recorded.

When the Green and Upper Colorado River subbasins are connected in a metapopulation configuration, under the conditions summarized above and when assuming no change in current management activity (the familiar "status quo" scenario discussed previously), the model results demonstrate very little gain in subbasin population abundance (Figure 23) arising from the dispersal mechanic. Not surprisingly, the Upper Colorado subbasin shows a slightly greater benefit from this metapopulation structure as it receives a larger number of fish than it loses to the Green River subbasin, owing to the Green subbasin's larger overall abundance. This benefit is seen in the early stages of the trajectory, while the Green River subbasin population is still relatively large; when that source population declines to low levels, the net immigration of fish into the Upper Colorado subbasin becomes negligible. Overall, the inclusion of a metapopulation dynamic into our PVA model structure does not appear to result in a significant change in subbasin population dynamics.

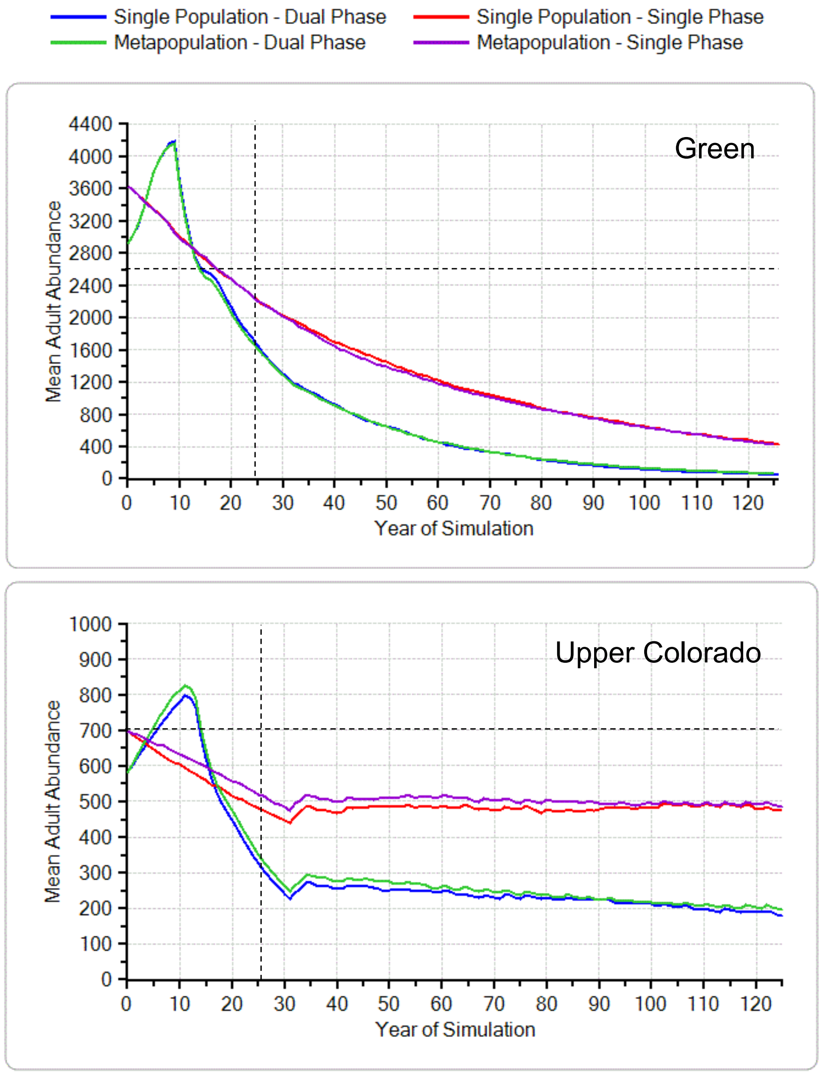


Figure 23. Simulated adult population abundance for Colorado pikeminnow in the Green River (top panel) and Upper Colorado (bottom panel) subbasins, assuming demographic connectivity through a metapopulation structure and a "status quo" condition of no change in current management conditions in an unchanging environment. Single (isolated) subbasin-specific population trajectories from Figures 10 (Green) and 11 (Upper Colorado) included for reference. Upper Colorado models include a "Mid-Spike" reproductive event. Vertical dashed line identifies the current calendar year, with retrospective trajectories included for reference. Horizontal dashed line identifies the current approximate recovery criterion for adult abundance in each subbasin.

In addition to the "status quo" scenarios that were evaluated in a metapopulation configuration, representative subbasin management models were developed that are drawn from the subbasin-specific combined management scenarios presented earlier in this report. Specifically, our management scenarios are structured in the following manner:

- <u>Green River subbasin</u>: achieve summer flow targets 50% of the time (50%Flow); increase age-specific annual survival by 5% and increase habitat carrying capacity through non-native predator control (5$%NNP); further increase age-specific survival by implementing the "Low" version of the Green River Canal diversion management activity (Canal-Low);
- <u>Upper Colorado subbasin</u>: achieve summer flow targets 100% of the time (100%Flow); increase age-specific annual survival by 10% and increase habitat carrying capacity through non-native predator control (10%NNP); further increase habitat carrying capacity through implementing the "High" version of the fish passage management activity (FishPassage-High).

As before, each of these combination management strategies was implemented across subbasins while assuming either a Dual-phase or a Single-phase demographic dynamic.

Once again, the inclusion of a metapopulation configuration leads to, at best, only marginal gains in subbasin population abundance relative to the earlier models featuring no such configuration, and this gain is seen only in the Upper Colorado subbasin under the assumption of a dual-phase dynamic (Figure 24). This can be explained by the fact that, under the Upper Colorado combined management scenario chosen for this analysis, the expected growth rate for this subbasin is relatively lower than that emerging from the same subbasin in a single-phase dynamic. The added input through immigration from the connected Green River subbasin therefore provides a greater boost to population growth. In comparison, the relatively more robust underlying growth rate for the Upper Colorado subbasin, assuming a single-phase dynamic, acts to dampen out this added immigration benefit.

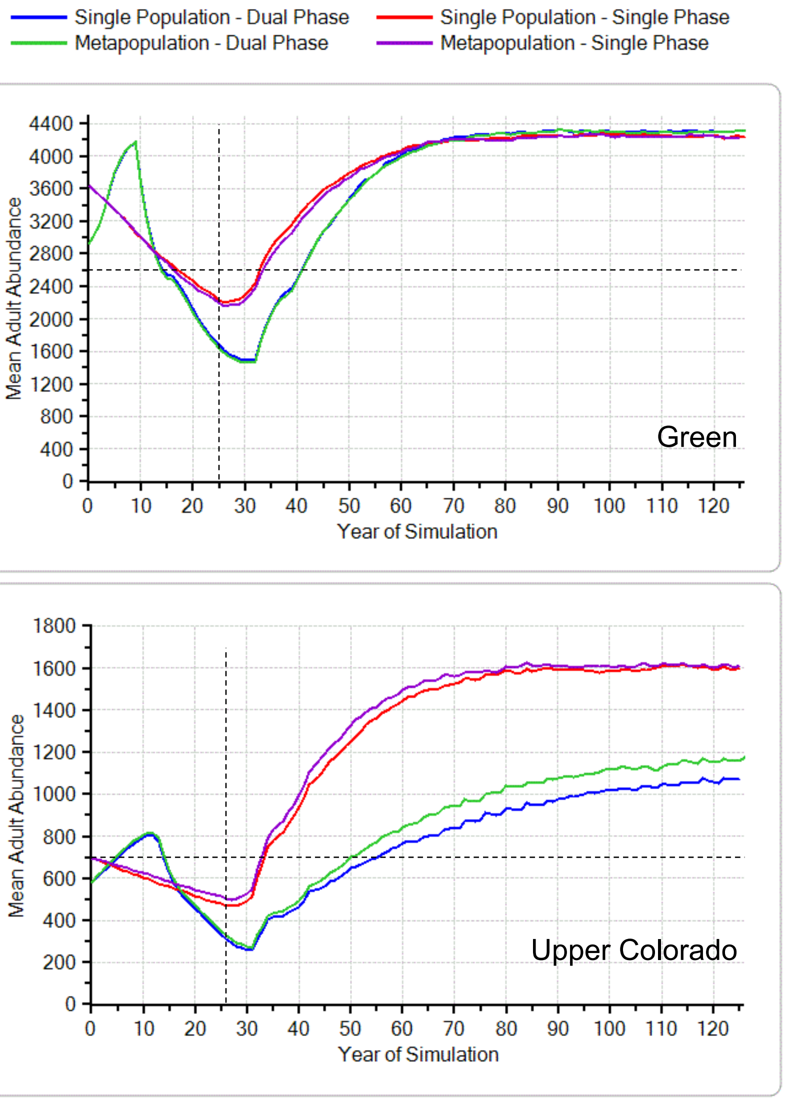


Figure 24. Simulated adult population abundance for Colorado pikeminnow in the Green River (top panel) and Upper Colorado (bottom panel) subbasins, assuming demographic connectivity through a metapopulation structure and subbasin-specific combined management strategies as described in the text. Single (isolated) subbasin-specific population trajectories from Figures 19 (Green) and 20-21 (Upper Colorado) included for reference. Upper Colorado models include a “Mid-Spike” reproductive event. Vertical dashed line identifies the current calendar year, with retrospective trajectories included for reference. Horizontal dashed line identifies the current approximate recovery criterion for adult abundance in each subbasin.

Discussion

This report provides a detailed description of a complex, age-specific stochastic model of Colorado pikeminnow demography, designed to explore future options for management of the species distributed across the three river subbasins defining its current range. During the process of model development, the team of species experts and simulation model practitioners made full use whenever possible of the extensive historical datasets on pikeminnow abundance, fecundity, and survival, as well as the various natural and human-mediated ecological factors that influence these rates through time – both in the past as well as in the present. As such, this population viability analysis (PVA) likely represents the most extensive exploration to date of the expected responses to the many and varied management actions that may be implemented in the future in order to improve the pikeminnow's long-term viability.

Despite the rigor brought to this analysis by the Colorado pikeminnow PVA Technical Team, and while recognizing the extensive efforts by the many field biologists that have assembled demographic and ecological data on these populations over the past three decades, there is unanimous recognition of the considerable uncertainty that still clouds our full understanding of the impacts of threats to population demographics, and the extent to which various management activities may serve to mitigate those threats. Therefore, it is important to recognize that the analyses presented here are not to meant to be accurate predictions of future pikeminnow abundances in any given river system at a specific future time. Instead, they are best interpreted as relative predictors of expected population performance when alternative management actions are implemented as a means of mitigating threats to subbasin population persistence.

An important foundation for prospective model construction is the retrospective analysis of demographic information that serves as the basis for parameter estimation in the model itself. This analysis quickly revealed interesting insights into past changes in population abundance in both the Green and Upper Colorado River subbasins. More specifically, these insights yielded alternative hypotheses about the dynamics of interannual changes in adult pikeminnow abundance. In what has become the "Dual-Phase Dynamic" hypothesis, substantial rates of observed population growth in the 1990s gave way to apparent sharp and sustained declines in both subbasin populations in the early years of the decade 2000 – 2010. Future projections of subbasin abundance are then directly tied to the rate of population change inferred from the more recent period of population decline. While a detailed explanation of the precise mechanisms that may have generated this inferred inflection point is not yet in place, some evidence does exist that may link these changes in abundance trends to deterministic changes in ecological conditions – annual spring/summer spawning flows, nonnative fish densities, and the like.

Alternatively, the "Single-Phase Dynamic" hypothesis states that the observed changes in adult abundance over the full period of observation are nothing more than shorter-term random fluctuations that are part of the longer-term stochastic population dynamic. Therefore, projections of future population abundance are based on a single estimate of past population growth that utilizes the entire dataset from 1991 to 2015.

It may not yet be possible to distinguish between these alternative hypotheses of past population dynamics of Colorado pikeminnow in the Green and Upper Colorado River subbasins. It is important to recognize, however, that both hypotheses feature a declining population abundance in both river subbasins over at least the past 15-20 years, with the dual-phase hypothesis featuring a more rapid rate of decline. If this viability analysis is to generate recommendations for the types and, more importantly, the intensity of population management to implement to achieve positive population growth, it is important to adopt one or the other hypothesis as a more realistic portrayal of pikeminnow population dynamics. From a statistical analysis point of view, this choice may be possible only after the accumulation of more data on annual adult population abundance over the next decade. Additionally, a deeper exploration of the potential linkages between historic changes in adult abundance and the factors responsible for those changes – nonnative fish densities, hydrologic profiles, etc. – may yield the necessary insights to clarify our understanding of this population dynamic.

Because of the ambiguity in distinguishing among these two hypotheses of past population dynamics, our PVA includes both the dual-phase and single-phase dynamics as plausible starting points for considering future projections of pikeminnow population responses to management in the context of recovery. Both of these baseline model structures are characterized by significant levels of uncertainty in estimates of fecundity, age-specific survival rates, inter-subbasin movement rates, subbasin carrying capacity, etc. This parametric uncertainty makes it a rather speculative process at best to generate accurate predictions of future population abundance in the presence of any one set of proposed management conditions. Nevertheless, our success in creating accurate depictions of past population performance under both dynamics hypotheses (see Figures 7 and 8) suggests that our models can be highly informative in predicting future population-level responses to changes in the underlying demographic characteristics of subbasin-specific pikeminnow populations. Additionally, the information obtained from the demographic sensitivity analysis reported in the earlier PVA for this species (Miller 2014) highlights the importance of both adult female fecundity (a combination of successful spawning among adult females, offspring production by those successful spawners, and Age-0 survival) and adult mortality as determinants of long-term population growth in this species. This result emerges from our understanding of the pikeminnow's life history which is characterized by both high levels of fecundity (and associated low offspring survival) and a long lifespan. This insight is even more valuable when combined with knowledge of the many factors that impact offspring production survival – frequency of optimal river flows in spring and summer to facilitate successful spawning events, predation by native and nonnative fish, availability of backwater nursery habitats, etc. From these analyses, it becomes clear that the predictive power of this and future PVA efforts can be strengthened by improved estimates of early life-stage demographics, namely, offspring production rates and the survival of Age-0 fish through the first 1-3 years of life.

Perhaps more importantly, the value of this PVA can be enhanced through a more detailed understanding of the functional relationships between pikeminnow demographics and the factors that influence their rates. When considering the subbasin populations in their entirety, how might we explain the observed population declines in both subbasins, applying either the dual-phase or single-phase dynamics hypotheses? At a more detailed level of analysis, it appears that there is increased offspring production among adult pikeminnow in the Upper Colorado River subbasin compared to their counterparts in the Green River subbasin (compare Figures 6 and 7). What are the factors that lead to the apparently higher levels of production in the Upper Colorado River subbasin? Strengthening these research and monitoring efforts will not only improve the credibility of the retrospective analyses used to build the PVA models described here, but they will also strengthen the reliability of prospective analyses of alternative management strategies that may be more or less effective in improving long-term population outcomes for the species across its range.

The Upper Colorado River subbasin apparently demonstrates an additional layer of demographic complexity in the form of "spawning spikes" as demonstrated by the extreme estimate of production measured in 2015. This event may be diagnostic of the "periodic strategist" life-history strategy that is used to describe slow-growing, long-lived species with high fecundity (Winemiller 2005). The PVA Technical Team carefully deliberated on the nature of this data point and ultimately treated this seemingly anomalous observation as a real event that may have important implications for long-term viability of the subbasin pikeminnow population. It is also possible that such an event may occur in the Green River subbasin but, in the absence of directly observing it, the Development Team chose to exclude it from that subbasin analysis – in part, as a means of comparing the presence of the event in one subbasin with its absence from another. Although an attenuated form of this event has been included in the prospective models for the Upper Colorado subbasin, it is unclear how frequently this event will occur in the future and what kind of impact it will have on the population as a whole. It will be very valuable to conduct a detailed analysis of the number of fish from this 2015 spike that recruit into the population as adults at the appropriate future point in time, e.g., 6-9 years after the spike (2021-2024). It may perhaps be possible to refine PVA model structure and input parameter specification with this important knowledge in hand following the "spawning spike" monitoring effort.

This report presents the results of PVA model runs in terms of the mean trajectory of adult abundance through time. An additional output metric that is very commonly reported is the probability of population (here, subbasin) extinction over the simulated timeframe. Because of the pikeminnow's long lifespan and relatively high adult survival, the risk of total extinction within any one subbasin was very low across the great majority of scenarios tested here. Consequently, this output metric is not tabulated in this version of the report. An alternative associated metric could be the probability of the adult population abundance falling below some agreed-upon threshold that likely represents the lowest abundance below which the prospects for natural recovery are greatly diminished. This is commonly known as the probability of quasi-extinction. There is no commonly applied value for this threshold, which must be decided upon by consensus for each group of species experts or recovery team that is using a PVA to guide species conservation planning. Specific guidance can be given on deriving a quasi-extinction threshold if desirable. Applying this concept in the current PVA would not require modifications to the underlying model structure, but instead only slight changes to the breadth of information reported as output.

The current PVA tests a suite of alternative management options that are believed likely to improve long-term viability of Colorado pikeminnow populations in the three subbasins defining their current distribution. Specifically, these options include managing summer flows to boost offspring production; managing nonnative fish populations to increase early lifestage survival; managing adult mortality; and managing a broad range of age-class mortalities through managing the Green River Canal diversion. These management options were tested individually or in various combinations across both the Green River and Upper Colorado River subbasins, assuming either a dual-phase or a single-phase demographic dynamic. In addition, selected modified subsets of these management options were applied to the San Juan River subbasin, in the presence of continued stocking of Age-0 fish (as is currently practiced) or in the absence of this stocking regime.

Once again, it is important to remember that the conclusions to be drawn from these scenarios are based on our best understanding of selected factors that contribute to Colorado pikeminnow population growth, and the inherent uncertainty in the detailed interactions between those factors. As discussed in the preamble to the prospective analyses discussed in detail in this report, we are unable to make specific recommendations about the intensity of any given management activity that is required to achieve a particular demographic outcome. In the absence of these functional relationships quantitatively linking threats and management actions to demographic performance, we must instead rely on comparative insights into the type of management activities that may target the most sensitive aspects of pikeminnow demography. In order to make more precise recommendations on required management intensity, it will be necessary to collect additional data on threatening processes and the quantitative impact they impart on specific life-history parameters of affected populations.

Additionally, the current PVA is not structured to provide insight into the feasibility and practicality of implementing the alternative management actions described in this report. Discussions on management feasibility involve many other considerations – economic, social, technological, etc. – that are outside the boundaries of this and other PVAs that are rooted in population biology and principles of ecological risk assessment. Having said that, it is clear that these discussions are critical within the broader context of endangered species management, and the PVA results presented in this report should be a valuable component of a more comprehensive analysis of recovery planning and decision-making for Colorado pikeminnow.

Managing summer flows can be an effective method for generating positive population growth in the Green River subbasin and, to a lesser degree, the Upper Colorado River subbasin. For the Green River subbasin, under a dual-phase dynamic, the annual target flows (1700 – 3400 cfs) must be met at least 60% of the time for the population to show a positive trend in abundance, which represents a substantial increase from the present 10% rate of achievement of these target flows. Under a single-phase dynamic, the target flows have been achieved approximately 33% of the time over the full period of observation used in this analysis (1991 – 2013). This prescribed increase in target flow achievement may be achievable, but its feasibility has not yet been assessed. For the Upper Colorado subbasin, management of summer flows is a less viable option as the rate of target flow (3000 – 6400 cfs) achievement is already quite high – 100% or 86% for the dual-phase or single-phase dynamic, respectively. Therefore, summer flow management does not seem to be a promising option for significantly increasing long-term adult abundance in this subbasin population.

In contrast, increasing early lifestage survival and increasing the extent of available habitat through nonnative fish management appears to dramatically impact long-term Colorado pikeminnow abundance trends in both of these subbasins. In the Green River subbasin, proportional increases in survival of Age-0 to Age-4 fish of 10 – 15%, combined with a corresponding increase in the extent of available habitat (expressed in the model as an increase in the habitat carrying capacity, *K*) of about 10 – 30%, results in substantial increases in population growth rate and long-term abundance. The extent of increase in the growth rate is a function of the increased juvenile and subadult survival, while the long-term abundance is also influenced by the increase in habitat availability over time. In the Upper Colorado River subbasin, substantial increases in the population growth rate are realized with a 5 – 10% increase in early lifestage survival, paired with a corresponding increase in the extent of available habitat of 10 – 40%. While this management option appears to show considerable promise as a tool to improve the long-term viability of Colorado pikeminnow populations across the species' range, it is important to recognize that juvenile pikeminnow abundance was declining before non-native species such as walleye entered the system (Osmundson and White 2017). Other forces must therefore be at least partly responsible for this observed decline. Moreover, the actual extent of nonnative fish management that is required to achieve these changes in pikeminnow survival remain unknown. Determining a practical functional relationship between nonnative fish management and the resulting impact on pikeminnow populations remains a vital area of study in the larger context of science-based population management of Colorado pikeminnow.

Improving the rates of adult pikeminnow survival also contribute to improvements in long-term population growth and stability. However, the existing survival rate of adult pikeminnow (approximately 82%) is already rather high, with relatively few known factors contributing to reducing the baseline natural rate of survival. Consequently, the targeted management of adult survival does not appear to be effective as a single tool for generating significant changes to pikeminnow population growth. Instead, these methods can and should be considered as complementary tools to be used in conjunction with other options that may be expected to yield more effective results.

Increasing the survival rate of all pikeminnow age classes in the Green River subbasin population through the management of the Green River Canal diversion resulted in a dramatic increase in pikeminnow population viability – particularly under the assumption of a single-phase demographic dynamic. The extent of demographic improvement when testing this management option was unexpected, particularly when considering the absolute level of decrease in age-specific mortality: an additive reduction of 1.76% among adults, and of 3.52% among all other age classes. On the other hand, the compounded benefit of reducing mortality among all age-classes is to be expected given the long lifespan of the species and the relatively later onset of reproductive capability. The analysis of McAbee (2017b) provides some valuable quantitative evidence for the potential value of this management option, although additional analysis of the available data is warranted to give greater weight and validity to the assumptions carried throughout these calculations.

Assessment of combined management approaches as applied in the Green and Upper Colorado River subbasins suggests that rather modest application of at least a subset of the available management alternatives could result in substantial increases in adult pikeminnow abundance on a relatively short timeline (a few decades). In particular, management of the Green River Canal diversion is likely to be a vital component of any combined management option, along with a more broadly applied management activity targeting nonnative fish species.

Under the conditions explored in this analysis, successful management of Colorado pikeminnow in the San Juan subbasin, if stocking is to be removed as a long-term management strategy, requires extensive increases in offspring production and associated reductions in mortality across all age classes. As with the other subbasin population analyses, the actual nature and extent of management activities required to achieve these demographic gains is not yet known. It may be possible to achieve shorter-term viability in this subbasin under a combined management regime that includes some level of periodic or annual stocking that compensates for less effective management of pikeminnow demography. However, it is realistic to conclude that long-term viability of the subbasin population can only be achieved through demographic management to a degree where stocking with hatchery-raised fish is no longer necessary for continued population stability or growth. Wild-born pikeminnow are expected to demonstrate more robust survival rates than their hatchery-raised counterparts, further supporting the argument for additional effort being place on successful *in situ* management of pikeminnow in this subbasin population.

Adding an explicit metapopulation configuration to the demographic models, in which individuals of a particular age range are allowed to probabilistically immigrate between the Green and Upper Colorado River subbasins, does not appreciably alter the demographic outcomes of the model scenarios developed for this analysis. This is not surprising given the very low rates of movement expected to occur between these subbasins in any given year, as measured by Osmundson and White (2017). Although the demographic consequences of metapopulation connectivity may be minimal, there may be important genetic exchange between these subbasins that helps to reduce the loss of genetic variation and improve the overall stability of each population. Unfortunately, our population-based modeling approach does not allow us to track subbasin-specific levels of heterozygosity across the duration of the simulation; as a result, we are unable to simulate the potential genetic benefit of this periodic, low-level demographic connectivity.

In addition to the sources of uncertainty addressed in this analysis, we recognize that future impacts of climate change may be a significant impediment to long-term recovery of fish like the Colorado pikeminnow in the southwestern United States. Although we do not have specific data on the predicted impacts of this global process on native fish viability in this region, it is reasonable to suspect that a warmer and more variable climate will put additional stress on riverine systems and the wildlife species therein. This will no doubt continue to be an important target of study among researchers in the endangered species conservation biology community. Despite these concerns, the insights gained from the analyses described here provide important guidance for the adoption of future management and research activities targeting long-term recovery of the Colorado pikeminnow throughout its range.

Finally, it may be instructive to consider these PVA results in the context of the existing abundance recovery criteria for Colorado pikeminnow as currently defined in recovery planning documents. The abundance criteria for the Green, Upper Colorado and San Juan subbasins are currently set at 2600 adults, 700 adults, and 1000 Age-5+ fish, respectively. [Note that the San Juan River Subbasin criterion was based on an estimated carrying capacity of 800 adults, which has now been revised downwards to 400 adults and is now the basis for our carrying capacity in the current PVA model.] The model results presented in this report can be assessed for their ability to generate subbasin-specific abundances that meet or exceed these targets. Perhaps more fundamentally, however, it may be useful to consider the validity of these abundances as long-term recovery targets. The updated USFWS document outlining recovery goals for the Colorado pikeminnow (USFWS 2002) uses population genetics theory and the concept of effective population size to derive a minimum viable population (MVP) abundance as the appropriate long-term recovery target for each subbasin population. Importantly, these calculations feature an assumed 3:1 ratio of adult males to adult females, based on "…a consensus decision of biologists (Lentsch et al. 1998)". This skewed sex ratio among adults is not a feature of our model, where we assume that males and females have equal survival rates throughout their adult lifespan. Therefore, it is arguably not logical to apply the results of these PVA models to a set of abundance criteria that are based on a different set of demographic assumptions.

One option for adjusting these values to create a more logical link between the genetic basis for considering an estimate of subbasin-specific MVP and the current PVA model is to relax the assumption of a 3:1 male-biased sex ratio, and instead assume equal numbers of male and female adults in an average pikeminnow population. In this case, we would retain the desired genetic effective population size of N_e = 500, now comprised of 250 males and 250 females in a population that is now skewed towards adult females. In addition, there is justification for revising the ratio of the effective population size to the total census population size in light of an improved understanding of wildlife population biology, and in particular of fish population biology. USFWS (2002) uses a value of 0.3 for this ratio, indicating that only about 30% of adult pikeminnow contribute their genes to successive generations. However, recent analysis of the available information on this parameter for fish and other taxonomic groups (e.g., Palstra and Fraser 2012) suggests that the ratio is closer to 0.2 – a value that was originally proposed by Allendorf et al. (1997) for salmonids. Therefore, we adjust the genetic effective population size by this revised proportion to estimate a genetic census population size of N_G = 500/0.2 = 2500. This value is then adjusted by the annual average adult mortality rate (0.18) to estimate the minimum viable population size (MVP) as (2500)*(1.18) = 2950 adults, which could potentially be rounded upwards in keeping with the protocol in USFWS (2002) to yield the estimate of MVP = 3000 adults for the Green River subbasin. This value could be considered as a revision of the existing estimate of 2600 adults that emerges from the above calculation when assuming a male-biased 3:1 adult sex ratio.

The calculation above demonstrates one method for how the current Colorado pikeminnow PVA Technical Team might approach the task of re-evaluating the estimation of abundance recovery criteria. If genetics are to be considered in the derivation of these criteria, general principles such as those briefly presented above (and discussed in far greater depth in USFWS (2002)) would form an appropriate basis for estimating this value. An alternative method for deriving abundance criteria would come more directly from the PVA results, relying explicitly on the probability of population quasi-extinction to derive abundance thresholds. In this case, the quasi-extinction thresholds could represent the minimum abundance that could be "rescued" through aggressive population management. Alternatively, the threshold could be interpreted as the smallest abundance that would be considered relatively immune to the deleterious genetic consequences of inbreeding and genetic drift. This threshold may very well converge on the MVP estimate discussed above, as it is also based on considerations of the genetic viability of small populations. It is also possible that the discussions required to derive a quasi-extinction threshold could include other factors that may result in a different value for this threshold. Regardless of the final outcome, the discussion of this concept and associate numerical value – involving both quantitative and normative elements – is a valuable element of any endangered species conservation planning process.

References

Allendorf, F.W., D. Bayles, D.J. Bottom, K.P. Currens, C.A. Frissell, D. Hankin, J.A. Lichatowich, W. Nehlsen, P.C. Trotter, and T.H. Williams. 1997. Prioritizing Pacific salmon stocks for conservation. *Conservation Biology* **11**:140-152.

Beissinger, S. and D. McCullough (Eds.). 2002. *Population Viability Analysis*. Chicago, IL, USA: University of Chicago Press.

Bestgen, K.R., and A.A. Hill. 2016. Reproduction, abundance, and recruitment dynamics of young Colorado pikeminnow in the Green and Yampa rivers, Utah and Colorado, 1979-2012. Final report to the Upper Colorado River Endangered Fish Recovery Program, Project FW BW-Synth, Denver, CO. Department o fGish, Wildlife and Conservation Biology, Colorado State University, Fort Collins. Larval Fish Laboratory Contribution 183.

Bestgen, K.R., J.A. Hawkins, G.C. White, K. Christopherson, M. Hudson, M. Fuller, D.C. Kitcheyan, R. Brunson, P. Badame, G.B. Haines, J. Jackson, C.D. Walford, T.A. Sorensen, and T.B. Williams. 2005. Population status of Colorado pikeminnow in the Green River Basin, Utah and Colorado. Final Report of Colorado State University Larval Fish Laboratory to Upper Colorado River Endangered Fish Recovery Program, Denver, CO.

Bestgen, K.R., J.A. Hawkins, G.C. White, C.D. Walford, P. Badame, and L. Monroe. 2010. Population status of Colorado pikeminnow in the Green River Basin, Utah and Colorado, 2006–2008. Final Report of Colorado State University Larval Fish Laboratory to Upper Colorado River Endangered Fish Recovery Program, Denver, CO.

Bestgen, K.R., C.D. Walford, G.C White, J.A. Hawkins, M.T. Jones, P.A. Webber, M. Breen, J. Skorupski, J. Howard, K Creighton, J. Logan, K. Battige, and F.B. Wright. 2016. Population status of Colorado pikeminnow in the Green River Basin, Utah and Colorado, 2000-2013. Final Report. Colorado State University, larval Fish Laboratory to Upper Colorado River Endangered Fish Recovery Program, Denver, CO. Larval Fish Laboratory Contribution 200.

Doak, D.F., G.K. Himes Boor, V.J. Bakker, W.F. Morris, A. Louthan, S.A. Morrison, A. Stanley, and L.B. Crowder. 2015. Recommendations for improving recovery criteria under the US Endangered Species Act. *Bioscience* **65**:189-199.

Durst, S.R. 2013. Population Viability Analysis Data Input Form for Colorado pikeminnow. 8 April, 2013

Durst, S.R. 2017. San Juan River Basin scenarios for Colorado Pikeminnow PVA. Report prepared for the Colorado Pikeminnow PVA Technical Team.

Ellner, S. P., J. Fieberg, D. Ludwig, and C. Wilcox. 2002. Precision of population viability analysis. *Conservation Biology* **16:**258–261.

Farrington, M.A., W. H. Brandenburg, and S.P. Platania. 2013. Colorado pikeminnow and razorback sucker larval fish survey in the San Juan River during 2012. Report to the San Juan River Basin Recovery Implementation Program. U.S. Fish and Wildlife Service, Albuquerque, NM.

Furr, D.W. 2012. Augmentation of Colorado pikeminnow (Ptychocheilus lucius) in the San Juan River: 2011. Annual Report to the San Juan River Basin Recovery Implementation Program. U.S. Fish and Wildlife Service, Albuquerque, NM.

Holden, P.B. (ed.). 1999. Flow recommendations for the San Juan River. San Juan River Basin Recovery Implementation Program. U.S. Fish and Wildlife Service, Albuquerque, NM.

Lacy, R.C. and J.P. Pollak. 2017. *Vortex: A Stochastic Simulation of the Extinction Process*. Version 10.2.8. Brookfield, IL, USA: Chicago Zoological Society.

Lacy, R.C., P.S. Miller, and K. Traylor-Holzer. 2017. Vortex 10 User's Manual. 6 September 2017 update. IUCN SSC Conservation Planning Specialist Group, and Chicago Zoological Society, Apple Valley, MN.

Lentsch, L.D., C.A. Toline, T.A. Crowl, and Y. Converse. 1998. Endangered fish interim management objectives for the Upper Colorado River Basin Recovery and Implementation Program. Final Report of Utah Division of Wildlife Resources to Upper Colorado River Endangered Fish Recovery Program, Denver, Colorado.

Lotts, K.C., T.A. Waite, and J.A. Vucetich. 2004. Reliability of absolute and relative predictions of population persistence based on time series. *Conservation Biology* **18**:1224-1232.

Ludwig, D. 1999. Is it meaningful to estimate a probability of extinction? *Ecology* **80:**298–310.

McAbee, K. 2017a. Incorporating Recovery Program conservation actions in the PVA modeling framework: Multiple test cases. Report prepared for the Colorado Pikeminnow PVA Technical Team.

McAbee, K. 2017b. Scenario 4: Increased adult survival via screening a problematic irrigation structure. Report prepared for the Colorado Pikeminnow PVA Technical Team.

McAbee, K. 2017c. Colorado River summer base flow scenario for PVA consideration. Report prepared for the Colorado Pikeminnow PVA Technical Team.

McAda, C. W. 2003. Flow recommendations to benefit the endangered fishes in the Colorado and Gunnison rivers. Recovery Program Project Number 54. Final Report.

Miller, P.S. 2014. A Population Viability Analysis for the Colorado Pikeminnow (*Ptychocheilus lucius*) in the San Juan River. Conservation Breeding Specialist Group (IUCN/SSC), Apple Valley, MN.

Miller, W.J. 2013. Revised estimate of Colorado pikeminnow population on the San Juan River. Memorandum to Dave Campbell, U.S. Fish and Wildlife Service, Albuquerque, NM, August 8, 2013.

Miller, W.J., and V. Lamarra. 2006. FY 2005 San Juan River population model refinement and model runs. Memorandum to Mark McKinstry, Bureau of Reclamation, Salt Lake City, UT, December 30, 2005.

Osmundson, D.B., and G.C. White. 2009. Population status and trends of Colorado pikeminnow of the Upper Colorado River, 1991-2005. Final Report. U.S. Fish and Wildlife Service, Grand Junction, Colorado.

Osmundson, D.B., and G.C. White. 2014. Population structure, abundance and recruitment of Colorado pikeminnow of the Upper Colorado River, 1991-2010. Final Report. U.S. Fish and Wildlife Service, Grand Junction, Colorado.

Osmundson, D.B., and G.C. White. 2017. Long-term mark-recapture monitoring of a Colorado pikeminnow (*Ptychocheilus lucius*) population: Assessing recovery progress using demographic trends. *Endangered Species Research* **34**:131-147.

Palstra, F.P., and D.J. Fraser. 2012. Effective/census population size ratio estimation: A compendium and appraisal. *Ecology and Evolution* **2(9)**:2357-2365.

Reed, J.M., L.S. Mills, J.B. Dunning Jr., E.S. Menges, K.S. McKelvey, R. Frye, S.R. Beissinger, M.-C. Anstett, and P.S. Miller. 2002. Emerging issues in population viability analysis. *Conservation Biology* **16**:7-19.

Ryden, D.W. 2003a. Long term monitoring of sub-adult and adult large bodied fishes in the San Juan River: 1999–2001 integration report. U.S. Fish and Wildlife Service, Grand Junction, CO.

Ryden, D.W. 2003b. An augmentation plan for Colorado pikeminnow in the San Juan River. U.S. Fish and Wildlife Service, Grand Junction, CO.

Ryden, D.W. 2004. Long term monitoring of sub-adult and adult large bodied fishes in the San Juan River: 2003 interim progress report. U.S. Fish and Wildlife Service, Grand Junction, CO.

Ryden, D.W. 2010. Long term monitoring of sub-adult and adult large-bodied fishes in the San Juan River: 2009. Interim Progress Report for the San Juan River Recovery Implementation Program. U.S. Fish and Wildlife Service, Albuquerque, NM.

San Juan River Basin Recovery Implementation Program (SJRIP). 2006. Final Program Document. San Juan River Basin Recovery Implementation Program, U.S. Fish and Wildlife Service, Albuquerque, NM.

U.S. Fish and Wildlife Service (USFWS). 2014. Colorado pikeminnow (*Ptychocheilus lucius*) draft recovery plan. U.S. Fish and Wildlife Service, Mountain-Prairie Region (6), Denver, CO.

Valdez, R.A. 2018. Data Assimilation for the Colorado Pikeminnow Population Viability Analysis. Report prepared for the Colorado Pikeminnow PVA Technical Team.

Valdez, R.A., T. Francis, D. Elverud, and D. Ryden. 2017. Colorado Pikeminnow PVA Scenarios for the Upper Colorado River Subbasin. Report prepared for the Colorado Pikeminnow PVA Technical Team.

Winemiller, K.O. 2005. Life history strategies, population regulation, and implications for fisheries management. *Canadian Journal of Fisheries and Aquatic Science* **62**:872-885.