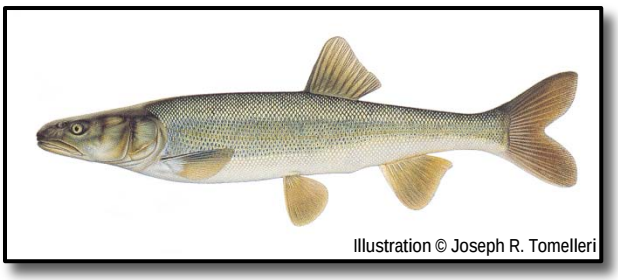
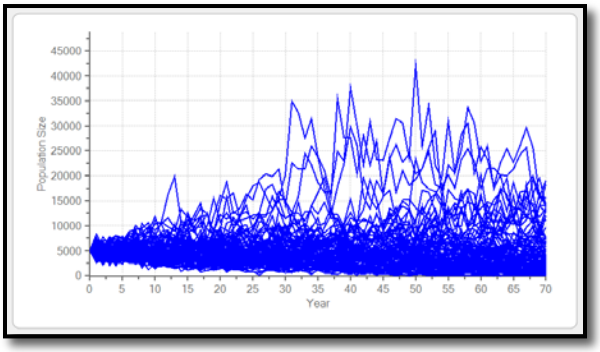
A Population Viability Analysis for the Colorado Pikeminnow (*Ptychocheilus lucius*) in the San Juan River





Report prepared by:

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In coordination with:

The Colorado Pikeminnow PVA Team

7 July 2014

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Executive Summary

This document describes the structure and implementation of a demographic model of the San Juan River population of the Colorado pikeminnow (*Ptychocheilus lucius*; hereafter referred to as pikeminnow). The model is being used in the context of a population viability analysis (PVA) for the species that is intended to inform a formal Section 7 consultation process for the Four Corners Power Plant and Navajo Mine Energy Project (FCPP&NMEP) in San Juan County, New Mexico. Objectives for this analysis were:

- To develop a realistic and credible model of current pikeminnow population dynamics in the San Juan River;
- To identify specific demographic parameters – fecundity (offspring production), age-specific mortality, etc. – that are important drivers of population growth or decline;
- To ascertain for purposes of the PVA model the potential impacts of specific anthropogenic processes – namely, deposition of mercury (Hg) in the watershed and river ecosystem and resulting bio-accumulation in individual fish – on long-term pikeminnow population persistence; and
- To identify other threatening factors and how those threats could be evaluated using this demographic model in order to inform the consultation process.

VORTEX, a simulation software package developed for population viability analysis, was used here as a vehicle to conduct the analysis. 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.

A team of eight experts in pikeminnow biology, wildlife toxicology, and ecological risk assessment was created to assemble demographic information on the species, and to develop a quantitative functional relationship between Hg accumulation in pikeminnow and resulting demographic impairment among individuals in the San Juan River pikeminnow population. This Team began its work in July 2013 and participated in five face-to-face meetings (2013: August and December; 2014: March, April, May) and a number of conference calls to summarize available information, evaluate data gaps, and discuss hypotheses and proposals around demographic model construction and function. These data were used as input parameters for specific *VORTEX* model scenarios. The PVA Team made every effort to identify key areas of uncertainty in the models, where appropriate data are scarce or absent. In such cases, the Team was forced to rely on data on pikeminnow populations from other river systems, on data from other closely-related species, and on expert judgment to derive appropriate model input parameters. In these cases, the assumptions underlying derivation of the estimates were identified and explicitly stated in order to provide the necessary context for model structure and function.

A majority of the data on pikeminnow fecundity (reproductive success) and survival come from hatchery studies, which are likely to be optimistic estimates compared to those derived from wild populations. To confirm this hypothesis, direct use of the hatchery-derived data in *VORTEX* resulted in a simulated population growth rate that grossly overestimated the actual growth dynamics of the wild San Juan River pikeminnow population. Therefore, the subsequent scenarios described in this analysis are based on revised "reference models" that were constructed to represent two alternative demographic states: (A) "Rapid Decline", representing a population with a very rapid rate of decline in abundance in the face of multiple threat factors (lack of nursery habitat, predation by / competition with non-native fish species, entrainment in diversion structures, etc.) that is likely to be descriptive of the San Juan River pikeminnow population in the 1980s and 1990s before stocking was initiated; and (B) "Lambda = 1", a population with nearly constant abundance through time, characterized by annual population growth rate $\lambda \approx 1.0$ (instantaneous stochastic growth rate $r_s \approx 0.0$) in the presence of stocking. These models were used to

explore a variety of questions of interest, including stocking rates required to achieve population stability, overall demographic sensitivity, and impairment of demographic rates due to mercury (Hg) accumulation.

Sensitivity analysis is a critical component of any credible wildlife population viability analysis. The PVA team conducted two forms of sensitivity analysis, calculating elasticity (proportional sensitivity) values for a suite of demographic parameters as well as using logistic regression methods to estimate the importance of these same parameters on estimates of extinction risk. Both of these approaches identify adult survival as a key driver of pikeminnow population growth. This result is typical of species with life histories featuring a long reproductive lifespan, even when fecundity is relatively high with associated low juvenile survival as in the case of the Colorado pikeminnow. Care must be used, however, when interpreting these results in the context of future population management as the highly sensitive parameter may not be the target of threat factors that lead to population decline and risk of local extinction. This appears to be the case for Colorado pikeminnow, where recent declines in population abundance appear to be primarily caused by very low levels of reproductive success among adult females, including survival of the earliest life stages.

The PVA team developed a detailed analysis of the rate of Hg accumulation in Colorado pikeminnow, the demographic impacts (% injury) of that accumulated burden, and the projected future increase in environmental Hg concentration in the San Juan River subbasin from local, regional and global industrial and other activities. We defined the demographic impacts of Hg accumulation in terms of fecundity among spawning females (offspring production), and age-specific survival across the full lifespan of the species. We acknowledge the potential for impairment of behavior among individual fish through Hg accumulation. However, we were unable to extrapolate quantitative measures of behavioral impairment to associated reductions in fecundity and/or survival of impaired fish. Therefore, the team agreed by consensus to exclude Hg-mediated behavioral impairment from this analysis.

Under the assumptions built into our models, the analysis suggested that if we assume a constant environmental Hg burden into the future (i.e., no future increase in the rate of environmental deposition), we may expect reproductive success to be reduced by about 2% among newly-recruited adult females compared to those adults in an environment free of this type of Hg burden. As these females age, the % injury was expected to increase to an asymptotic maximum of about 5%. Under a reasonable model of future increase in environmental Hg concentration in the San Juan River, these injury estimates may increase to approximately 3.5% to 9%, respectively. Injury to adult survival increases from approximately 0.35% to 0.85% under a static Hg burden, and from approximately 0.65% to 1.5% if environmental Hg concentrations are assumed to increase over time.

Under the assumption of an increasing environmental Hg burden in the San Juan River, the estimated injuries to both reproductive success and age-specific survival led to observable decreases in simulated pikeminnow population growth. The intensity of this population-level effect is itself likely to be a function of the underlying growth rate assuming no Hg-mediated impact. For example, if a population is already compromised by other threatening factors so that growth is very limited, the addition of demographic injury through Hg accumulation may result in a transition to population decline (i.e., negative growth rate). On the other hand, if a population is growing relatively strongly, the consequence of Hg-mediated impairment may be smaller. It is important to note that, while the absolute magnitude of injury to adult survival is less than that for adult reproductive success, the population-level impact is nearly equal. This is a result of the large sensitivity (elasticity) of our model to changes in adult survival described above.

In addition to the explicit modeling work summarized here, the PVA team discussed four factors that may also contribute to long-term changes in Colorado pikeminnow population abundance in the San Juan River: availability of nursery (backwater) habitat, predation by and competition with non-native fish

species, entrainment of pikeminnow into unsuitable habitat or to regions outside of the model system, and reduced access to the full range of available habitat in the river system. We identified specific mechanisms for incorporating these factors into our *VORTEX*-based demographic model, and have briefly summarized the available data we could use to estimate relevant demographic parameters for appropriate model scenarios. With this information at our disposal, and given the informative model structure currently available, it is now possible to construct additional scenarios that explore management options that target these factors. The goal of these models would be to identify the extent of management necessary to achieve a specific desired future population state, whether defined by long-term population growth rate, mean long-term population abundance, etc.

Taken as a whole, it is the opinion of this report author that the general model described in these pages is of sufficient depth and realism to be regarded as a valuable tool for evaluating the relative response of a population of Colorado pikeminnow inhabiting the San Juan River to alternative future management scenarios. The extent of uncertainty present in these models makes it very difficult at best to generate an accurate prediction of future population abundance or extinction risk under any given threat scenario. In this sense, our imperfect understanding of pikeminnow biology and ecological processes leads to difficulties in deriving specific population performance targets, such as abundance, growth rate, extent of habitat occupied, etc., as long-term measures of recovery. Greater clarity on these issues will come with the collection of additional data on pikeminnow demography and ecology, hopefully guided by the insights gained by this first round of population viability analysis.

Introduction

This document describes the structure and implementation of a demographic simulation model of the San Juan River population of the Colorado pikeminnow (*Ptychocheilus lucius*; hereafter referred to as pikeminnow). The model is being used in the context of a population viability analysis (PVA) for the species that is intended to inform a formal Section 7 consultation process for the Four Corners Power Plant and Navajo Mine Energy Project (FCPP&NMEP) in San Juan County, New Mexico. The data and information discussed herein represents the current state of understanding of pikeminnow demography and ecology as they relate to an exploration of population dynamics under various scenarios of current and future conditions in the San Juan River Subbasin.

Population viability analysis can be a valuable tool for investigating current and future risk of endangered species decline under specific scenarios of human-mediated activities, locally and globally, which may compromise the ability of a wildlife population to successfully reproduce and/or survive (e.g., Morris and Doak 2002). In addition, PVA can be a key step in identifying potentially successful management options to reduce risk of population decline, and which may be highly effective in enhancing species recovery in its wild habitat. Specifically, the objectives for this analysis were:

- To develop a realistic and credible model of current pikeminnow population dynamics in the San Juan River;
- To identify specific demographic parameters – fecundity (offspring production), age-specific mortality, etc. – that are important drivers of population growth or decline;
- To ascertain for purposes of the PVA model the potential impacts of specific anthropogenic processes – namely, deposition of mercury (Hg) in the watershed and river ecosystem and resulting bio-accumulation in individual fish – on long-term pikeminnow population persistence; and
- To identify other threatening factors and how those threats could be evaluated using this demographic model in order to inform the consultation process.

PVA methodologies 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. Each simulation represents 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 pikeminnow and its habitat, the environmental conditions affecting the species, and possible future changes in these conditions.

VORTEX, a simulation software package developed for population viability analysis (Version 10: Lacy and Pollak 2014), was used here as a vehicle to conduct the analysis. 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. This software package has undergone rigorous testing since its introduction more than a decade ago, and is highly-regarded as a realistic and competent platform for conducting credible analyses of wildlife population demography.

The *VORTEX* system for conducting population viability analysis is a flexible and accessible tool that can be adapted to a wide variety of species types and life histories as the situation warrants. The program has been used around the world in both teaching and research applications and is a trusted method for assisting in the definition of practical wildlife management methodologies. For a more detailed explanation of *VORTEX* and its use in population viability analysis, refer to Lacy (2000) and Appendix E.

PVA Model Structure and Demographic Data Input

General Approach to Model Development and Treatment of Model Uncertainty

As discussed immediately above, a responsible practitioner of PVA tools and methodologies will present the results of their analysis in a comparative framework, instead of identifying precise future population outcomes arising from a demographic simulation model with any presumption of absolute accuracy. When adopting this approach, we develop one or more reference models that serve as a type of control for our analysis. These reference models will include what species experts believe are the critical elements of species biology and habitat ecology, but may not include some specific processes, such as anthropogenic or natural threats to the species, that researchers want to evaluate. These models are run for a specified duration into the future, and important output metrics – growth rate, final population size, etc. – are recorded. Following the establishment of our control, we then develop new models that may include the additional processes (threats) identified above. When the output of these models is compared to the results of the reference model, we can assess the relative impact that the threat may have on long-term population dynamics and stability. Again, what is important in this assessment is the relative change in the output metric of interest, and not the absolute value of that metric in any one model or scenario.

The need for this comparative approach to model creation and interpretation arises from uncertainty that clouds our vision of the future. It is important to recognize that uncertainty, defined as fundamental gaps in our knowledge about the elements of a system, is different from variability, that is, fluctuations across time and/or space in the values of one or more parameters that comprise that system. We must consider two primary types of model uncertainty: parameter uncertainty and process uncertainty. Parameter uncertainty, often called measurement error, arises when the exact values of a given parameter – for example, the age of sexual maturity, adult survival rates, or current population abundance – are not known or are poorly understood among researchers studying them in the system of interest. Process uncertainty, often referred to as structural uncertainty, arises from a lack of knowledge about the true biology or physics of the system of interest. Examples of process uncertainty can commonly be seen in a model's treatment of density dependence, or in the proposed mechanism by which a specific threat impacts population demographics.

When models of the type discussed in this report contain multiple sources of uncertainty, we should explore the impact of that uncertainty on overall model performance. Sophisticated statistical methods, often rooted in Bayesian analysis, can be used to explicitly incorporate parameter uncertainty in PVA models (e.g., Wade 2002). Interpretation of these methods can be quite cumbersome, particularly when communication to a diverse audience of stakeholders is required. Alternative methods take a simpler approach, combining systematic implementation of alternative models where appropriate with more

formal sensitivity analysis to gain a greater understanding of the impact of uncertainty in models of wildlife population demography.

As discussed in more detail below, our model of pikeminnow demographics includes many examples of both process and parameter uncertainty. Throughout the document, starting here with a detailed treatment of model structure and input, we identify areas of both process and parameter uncertainty. We also provide a detailed list of important assumptions, which specify the justifications we have used to derive process elements and parameter estimates in the absence of complete knowledge of the species' biology and ecology. Comparative assessment of alternative models and explicit sensitivity (elasticity) analysis are both used to evaluate the impact of uncertainty where feasible. While perhaps not exhaustive in scope, the treatment and discussion of uncertainty in this report should give the reader a working knowledge of the aspects of species biology that require more intensive study and characterization.

A Conceptual Model of Colorado Pikeminnow Demography

Before we move through the details of specifying detailed demographic rates for the San Juan pikeminnow population, it is instructive to display the life-cycle of the fish and the various factors that influence the rates of reproduction (fecundity) and survival of individuals as they age. This diagram is shown in Figure 1.

The conceptual model was built on an age-structured population. 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.

The production of offspring (juveniles) is described by the rate of fecundity of adults, or F_7 in Figure 1. This variable is itself a function of the proportion of females that successfully spawn, number of eggs laid by a typical successful female – the individual's maternity, or m_7 – and the survival of those eggs to immediately before one year of age, or S_0. First-year survival is itself broken down in our approach to a number of different steps for which data are available and subject to analysis and evaluation.

Figure 1 also identifies a suite of biotic and abiotic factors that are thought to influence these demographic rates from one year to the next. The various factors are quite similar to those proposed by Bestgen et al. (2006) in their study of the factors affecting Colorado pikeminnow recruitment. It is valuable to consider these factors in order to better understand their relative importance in driving mean demographic rates and, equally importantly in the context of stochastic model development, the variance in these mean rates over time. Additionally, the analysis can help to identify appropriate management strategies that may reduce the detrimental influence of one or more modifying factors.

A more detailed discussion of demographic rates as portrayed in Figure 1 is presented immediately below.

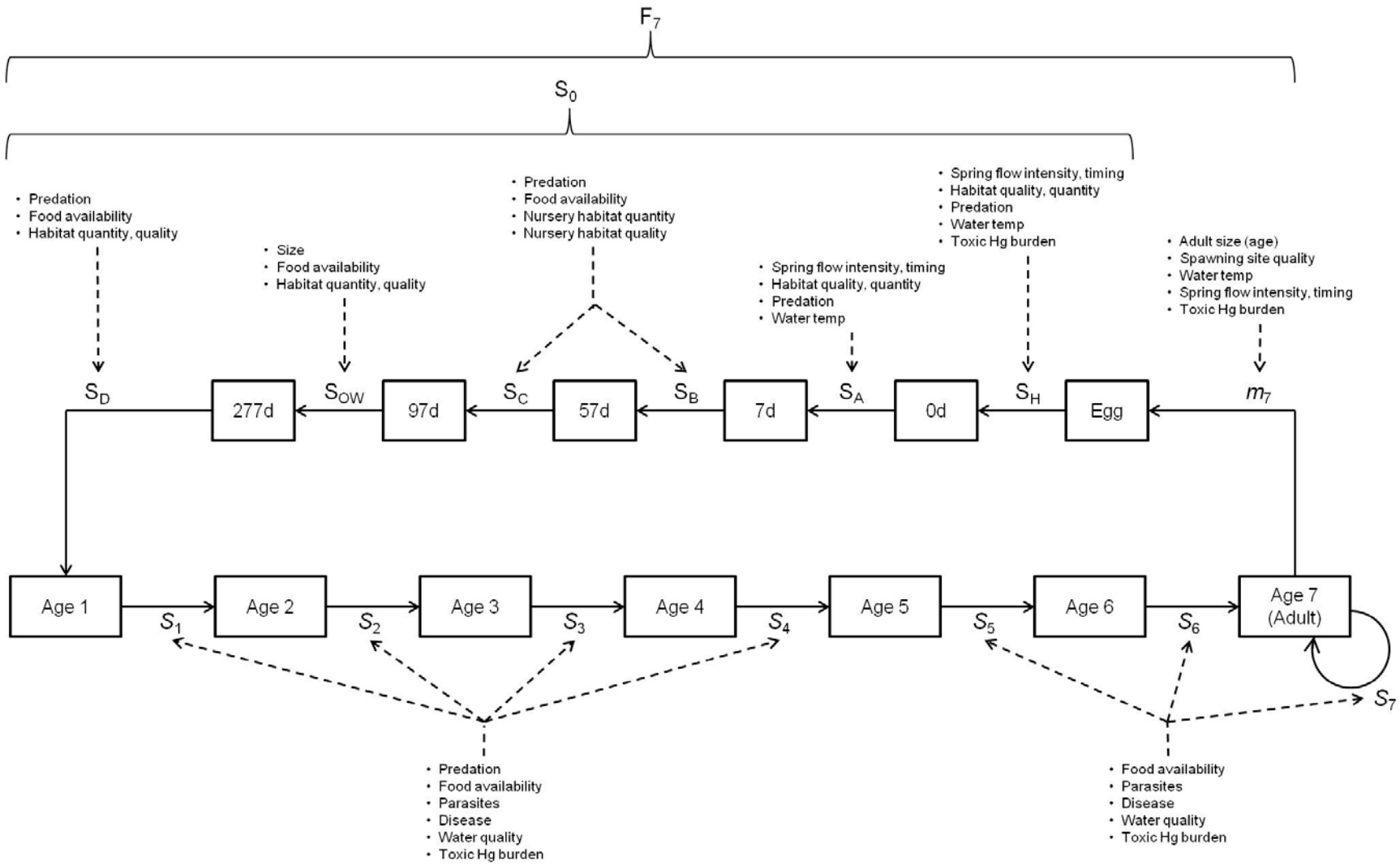

Figure 1. Graphical representation of the life cycle of the Colorado pikeminnow. Annual survival rates of age classes are represented as variables S_1 – S_7. Fecundity rate of adults (F_7) is deconstructed into egg production (or maternity, m_7) and stage-specific survival rates from hatching (S_H), through fry and early larval stages (S_A – S_C), overwintering juveniles (S_{OW}), and early juveniles surviving to their first spring after hatch (S_D). Biotic and abiotic factors modifying demographic rates are listed and linked to specific variables through dashed arrows. Figure based on Bestgen et al. (2006).

Input Parameters for Stochastic Population Dynamics Simulations

The biological information used to derive demographic input parameters for this PVA comes from a variety of peer-reviewed journal articles and a variety of other published and unpublished sources. These sources, and the analysis of the relevant data therein, have been the subject of considerable discussion among members of the PVA Team constructed for the purposes of this analysis. Members of the PVA Team include:

Dave Campbell, US Fish and Wildlife Service
Scott Durst, US Fish and Wildlife Service
Joel Lusk, US Fish and Wildlife Service
Phil Miller, Conservation Breeding Specialist Group
William Miller, Miller Ecological Consultants, Inc.
Mark Shibata, Environmental Resources Management, Inc.
Rich Valdez, SWCA, Inc.
Sharon Whitmore, US Fish and Wildlife Service

Others involved in the PVA process described here include:

Project proponents / participants:

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Patty Corbetta, BHP Billiton Mine Management Co.*
Richard Grimes, Arizona Public Service
Brent Musselwhite, BHP Billiton Mine Management Co.*
Maria O'Brien, Modrall Sperling
*Successor in interest to BHP Navajo Coal Company (BNCC)

Observers:

Alex Birchfield, Office of Surface Mining Reclamation and Enforcement
Steve Huntley, Cardno ENTRIX
Larry Wise, Cardno ENTRIX

This Team began its work in July 2013 and participated in five face-to-face meetings (2013: August and December; 2014: March, April, May) and a number of conference calls to summarize available information, evaluate data gaps, and discuss hypotheses and proposals around demographic model construction and function. As a result, while discussion by the PVA Team revealed uncertainties about selected elements of the data that will only be resolved with additional investigation, and while significant gaps in our definitive knowledge of the species' biology remain, the information discussed below represents an effective consensus regarding our collective understanding to date of Colorado pikeminnow demography and population ecology. Much of this information has been summarized by selected team members (Durst 2013; Valdez 2014) and these documents are used here as primary references (see Appendices).

It is important to note that, because of the very sparse dataset on population demography of the San Juan River pikeminnow population, we are forced to derive parameter estimates for this population through a combination of approaches. Where available and appropriate, existing data on pikeminnow populations occupying the Green, Yampa and Upper Colorado River subbasins were used to derive estimates for the San Juan subbasin population. In cases where data of any sort were absent for a given demographic parameter, the PVA Team used collective expert judgment to derive an appropriate estimate.

Finally, it is worth noting here that this analysis features the use of *VORTEX* in a population-based mode, instead of the usual individual-based approach typically adopted by most users of the software. This

feature is new to the latest version of the *VORTEX* package. When run in a population-based mode, *VORTEX* no longer keeps track of every individual and their specific characteristics (e.g., age, sex, parentage, inbreeding coefficient, etc.). Instead, the software aggregates all individuals within a given age-sex class into a single quantity and then applies the appropriate mean demographic rates to that aggregated number of individuals. This facilitates the analysis of much larger populations of individuals and the model runs much faster compared to the individual-based mode. On the other hand, all genetic options and modeling (e.g., of inbreeding depression) are disabled when *VORTEX* is run in population-based mode, as is individual variation (demographic stochasticity). As this analysis is not considering specific issues around genetic factors influencing long-term viability of Colorado pikeminnow in the San Juan River, it is the judgment of this author, in consultation with the Team, that a population-based modeling approach is appropriate for this PVA.

Iterations and years of projection

Stochastic projections of population abundance through time were simulated 1000 times, with each projection extending to 70 years. This choice of duration was dictated largely by the availability of predictive data for future mercury deposition rates in the San Juan River system (see below for more detailed information on this process). Secondarily, given the relatively long generation time for this species, it is important to extend these projections far enough into the future to be able to see demographic dynamics across multiple generations. By default, *VORTEX* conducts a pre-breeding census, meaning that population abundance is calculated immediately before the year's breeding season. In the case of pikeminnow, this means that the census would be taken approximately 1 July, before the beginning of the spawning season. Demographic information may be obtained at annual intervals throughout the duration of the simulation. All simulations are conducted using *VORTEX* version 10.0.6 (May 2014).

Geographic population structure in the San Juan River subbasin

For the purposes of this PVA, we focused our attention on that portion of the San Juan River from Piute Farms (RM 0) to near the confluence of the Animas River (RM 180) (Figure 2). Therefore, we did not include any portion of Lake Powell in this analysis; we assume that the waterfall at the northern entrance to the lake effectively blocks upstream movement of pikeminnow back into the San Juan River. Therefore, we assumed that fish moving downstream into the lake were removed from the system and therefore not included in calculations of simulated population abundance. While other demographic models of fish species in the San Juan River (e.g., Miller and Lamarra 2006) subdivide this same stretch of habitat into multiple reaches with designated dispersal rates among them, we did not include this level of geographic structure in our *VORTEX* model. Consequently, we treated the full 180 miles of the river as a congruous habitat housing a single demographically intact population of pikeminnow, without metapopulation dynamics.

We also assumed for this analysis that the pikeminnow population currently inhabiting the San Juan River subbasin is demographically isolated from both the Green and Upper Colorado River subbasin populations (more information on this assumption can be found in Appendix B). Therefore, the San Juan River pikeminnow population does not receive immigrants from the other river systems.

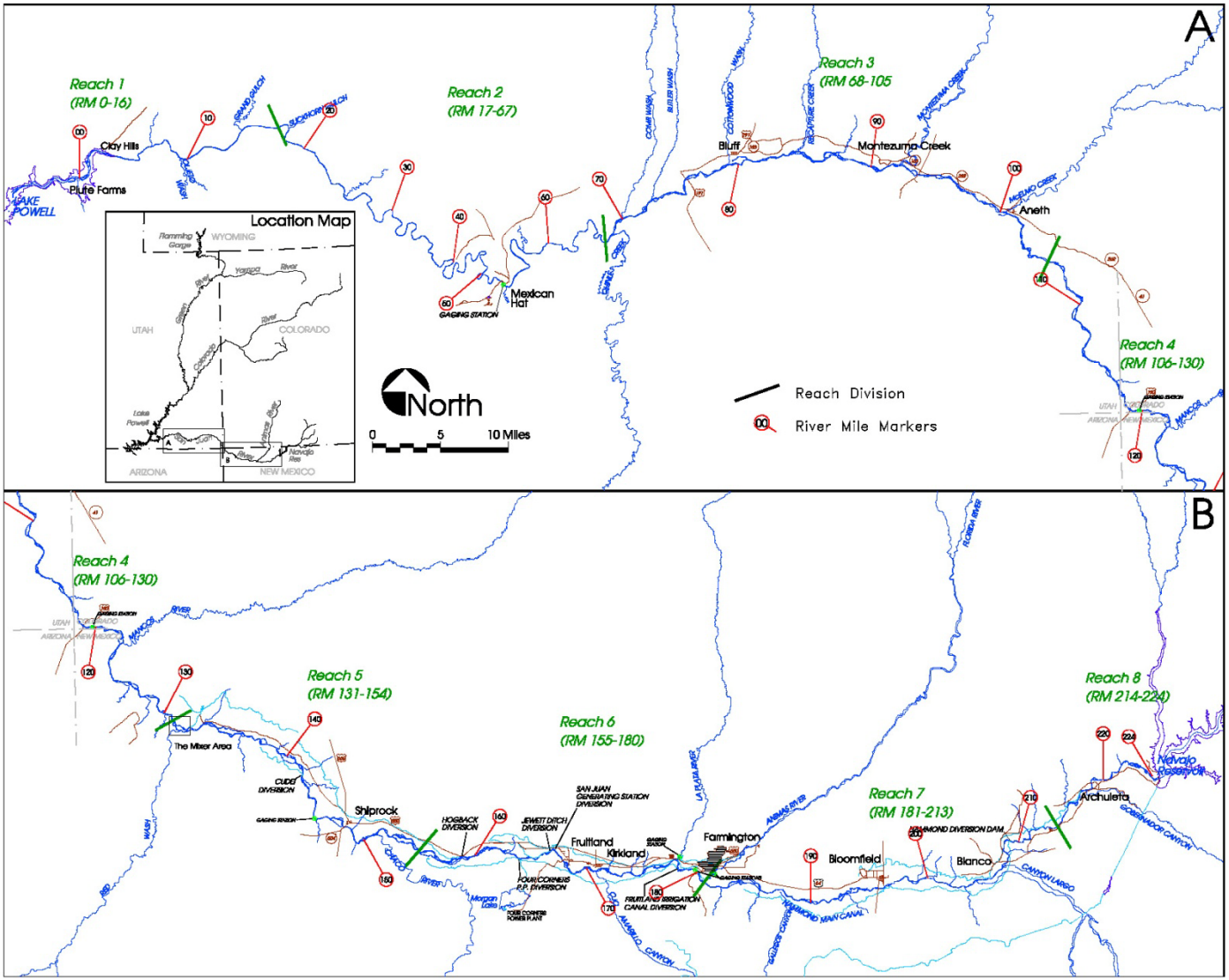

Figure 2. Map of the San Juan River that is included in this PVA. The Colorado pikeminnow population in this analysis is located between River Mile 0 at Piute Farms and River Mile 180 near the confluence of the Animas River. Map courtesy of USFWS.

Target demographic states for reference pikeminnow simulation model

Many of the model scenarios described in this analysis are based on "reference models" that were constructed to represent two alternative demographic states: (A) "Rapid Decline", a population with a very rapid rate of population decline in the face of multiple threat factors (lack of nursery habitat, predation by / competition with non-native fish species, entrainment in diversion structures, etc.) that is likely to be descriptive of the San Juan River pikeminnow population in the 1980s and 1990s before stocking was initiated; and (B) "Lambda = 1", a population with nearly constant abundance through time, characterized by annual population growth rate $\lambda \approx 1.0$ (instantaneous stochastic growth rate $r_s \approx 0.0$). These models were used to explore a variety of questions of interest, including stocking rates required to achieve population stability, overall demographic sensitivity, and impairment of demographic rates due to mercury (Hg) accumulation.

Adult breeding age

We assumed for this analysis that female Colorado pikeminnow begin spawning at approximately 450 mm in total body length (TL), which in our age-structured model translates to seven years of age, based largely on the work of Hawkins (1992) and summarized more broadly by Valdez (2014) in Appendix B. This translation to age carries with it some variability and uncertainty based on variation in individual growth rates, but for the purposes of our analysis we set this parameter at seven years of age across all scenarios, thereby allowing more meaningful comparison of model output among different scenarios. We also set the maximum adult age at 40 years, although based on the mortality rates chosen for this analysis (see below) the probability of a newly-recruited adult living to that maximum age is quite small (approximately 0.4%).

Fecundity

In general terms, fecundity in *VORTEX* is defined as the average number of offspring that are generated per reproductively successful adult female and that survive to the next census period, i.e., to one year of age. For mathematical convenience in our model, we defined "offspring" as larvae that survive to approximately 97 days of age. Fecundity is described in *VORTEX* by three separate parameters: the proportion of adult females that successfully spawn in a given year, the average number of offspring produced per spawning event, and the survival of those offspring to one year of age. Of course, any number of specific combinations of parameter values can be identified that yield a given value for overall fecundity. Practitioners of PVA often resort to "reverse engineering" parameter values in order to achieve a desired level of fecundity that is consistent with an observed or suspected population growth rate.

We do not have specific data on the proportion of adult females that successfully spawn in an "average" year on the San Juan River. Although many data sources suggest that a large proportion of the adult cohort may spawn, there is also evidence to suggest that Colorado pikeminnow and other similar species in the southwest United States may be "skip spawners" (e.g., Yackulic et al. 2014; R. Valdez and W. Miller, pers. comm.). In this case, we assumed that only about 50% of adult female pikeminnow successfully spawn in a given year, with young surviving to the next simulated population census.

Data on egg production (maternity) came primarily from Hamman (1986), who reported data on induced spawning of hatchery-reared Colorado pikeminnow aged 9 and 10 years. Across both age classes, average egg production was approximately 50,000 eggs/kg adult female body mass. Given that the average weight of adult fish in the study was 1.4 kg, we can estimate total egg output per adult spawning female at 70,000 eggs. More recent information (W. Wilson, Southwestern Native Aquatic Resources and Recovery Center, pers. comm. with R. Valdez: 29 January 2014) provides evidence for lower maternity rates among wild pikeminnow adults. Therefore, our best estimate for this parameter was approximately 50,000 eggs per reproductive female. We assume here that the sex ratio of eggs is 50:50.

Data on egg survival came from Hamman (1986) where eggs were held at 22ºC in Heath trays or jars, and the number of viable eggs enumerated after 48 hr of the stated 100-hr incubation period. Estimates of hatching success were then computed by expanding the 48-hr viability counts to estimated viability after 100 hr of incubation (to hatching). The 48-hour egg viability estimate reported by Hamman (1986) was 0.573, which equates to an hourly "survival" rate of $(0.573)^{1/48} = 0.9885$. Therefore, after 100 hours, the final estimate of egg survival is $(0.9885)^{100} = 0.3145$. This was taken as the hatching rate of eggs collected for the reported study.

Survival of hatched fry to 97 days: Data from Hamman (1986, 1989) was available to estimate the total survival of newly-hatched pikeminnow to 97 days as 0.176. See Appendix B for more information on the calculation of this parameter.

Overall, then, our reference estimate of offspring production (age 97 days) for Colorado pikeminnow in the San Juan River, based on available data from hatchery studies, was (50,000)(0.3145)(0.176) = 2,768 individuals. In combination with mortality rates also derived in the context of the two alternative reference models described above, we found that the "Rapid Decline" reference model state (A) can be described by a very low rate of offspring production of just 20±5 individuals per successfully spawning female. This low productivity is consistent with recent data collected by researchers during annual spawning survey efforts, where very small numbers of larvae are found each year (e.g., Farrington et al. 2012). Additionally, the "Lambda = 1" reference model state (B) can be achieved with a mean rate of offspring production of 500±100 individuals per successfully spawning female.

Survival of offspring to Age 1: Survival of offspring, defined here as 97 days old, to one year of age was estimated from both overwinter survival rates (Days 98 – 277) and spring survival rates (Days 278 – 365). Catch rates from the Green and Upper Colorado Rivers analyzed by Valdez and Cowdell (1996) indicated that an estimate for total survival during this period was 0.178; therefore, the mortality used by *VORTEX* to define 0-1 mortality (where "Age 0" is actually 97 days old, given our definition of "offspring" above) 0.822, or 82.2%. See Appendix B for more information on the derivation of this parameter. We assumed that survival of offspring to one year of age is independent of their mother's age.

It is important to recognize that many of these demographic rates – particularly among the earliest life stages – are derived from experimental observations under hatchery conditions or from catch rate indices in uncontrolled field settings. This may result in high estimates of specific maternity and/or early-life-stage survival rates relative to those that would come from direct observation in wild populations, leading to an overestimate of the growth rate of the current Colorado pikeminnow population in the San Juan River.

Mortality

VORTEX defines mortality as the annual rate of age-specific death from year x to $x + 1$; in the language of life-table analysis, this is equivalent to $q(x)$. We assumed that our model, intended to reflect the current pikeminnow population in the San Juan River, broadly includes the effects of human disturbance among age-specific mortality rates. However, as discussed in Valdez (2014, see Appendix B) and other sources, survival rates for Colorado pikeminnow in the San Juan River have been studied on a limited basis for hatchery stocked fish with small numbers of fish across specific age classes to facilitate meaningful statistical analysis. We therefore must turn to similar studies on the species inhabiting nearby subbasins, specifically the Green and Upper Colorado Rivers.

Table 1 below gives the mean annual mortality values for each of the age classes included in our model. See Appendix B for more information on deriving these parameter values.

Table 1. Mean annual mortality rates of each age class of Colorado pikeminnow derived from literature for this demographic analysis. The specified rates describe the average proportion of individuals age *x* that dies before reaching age (*x*+1). Numbers in parentheses indicate the annual environmental variability, expressed as a binomial standard deviation.

Age (*x*)	Mean mortality,% (SD)
0	82.2 (5.0)
1	45.3 (5.0)
2	27.1 (5.0)
3	15.3 (5.0)
4	27.5 (5.0)
5	23.0 (4.0)
6	18.0 (3.0)
Adult (7+)	15.0 (2.0)

Mortality rates of age classes 1 through 3 were estimated from numbers of stocked fish captured by year in the San Juan River (U.S. Fish and Wildlife Service 2014). Survival of age classes 4 through adult were estimated from survival curves of wild fish from the Upper Colorado River (Osmundson and White 2009). The average of survival for the "upper reach" and the "lower reach" were used for a specified fish length that corresponded to age (e.g., 260 mm Total Length (TL) = Age 4; 335 mm TL = Age 5, given sexual maturity is reached at 450 mm TL = Age 7).

In addition to the mortality rates given in Table 1, we derived additional sets of mortality data that were consistent with the two reference model states described above: "Rapid Decline" (A), a population with a very rapid rate of population decline in the face of multiple threats that is likely to be descriptive of the San Juan River pikeminnow population in the 1980s and 1990s before stocking was initiated; and "Lambda = 1" (B), a population with nearly constant abundance through time, characterized by annual population growth rate $\lambda \approx 1.0$ (instantaneous stochastic growth rate $r_s \approx 0.0$). These data are given in Table 2. It is also important to note that these two population states are also defined by different rates of offspring production (fecundity) per successfully spawning female, as shown in Table 2.

Table 2. Mean age-specific annual mortality rates for Colorado pikeminnow under alternative conditions of population growth. Alternative conditions also determined by rate of annual fecundity, *F*, defined as number of 97-day-old offspring produced per successfully spawning female. Data definitions per Table 1.

	Mean mortality,% (SD)	
Age (*x*)	Rapid decline (*F* = 20±5)	Lambda = 1 (*F* = 500±100)
0	50.0 (5.0)	50.0 (5.0)
1	90.0 (5.0)	89.0 (5.0)
2	80.0 (5.0)	78.0 (5.0)
3	70.0 (5.0)	67.0 (5.0)
4	50.0 (5.0)	45.0 (5.0)
5	30.0 (4.0)	30.0 (4.0)
6	18.0 (3.0)	18.0 (3.0)
Adult (7+)	15.0 (2.0)	15.0 (2.0)

Sources of variability in demographic rates

Annual environmental variation (EV) in demographic rates is simulated in the stochastic modeling environment of *VORTEX* by specifying a standard deviation (SD) that is applied each year to the base rates in order to simulate fluctuations due to extrinsic factors (both natural and anthropogenic) in the environment within and near the San Juan River. Environmental variation is assumed to follow binomial distributions for both birth and death rates (see Lacy et al. (2014), Lacy (2000) and Appendix E for more information).

Unfortunately, the methods to arrive at mean estimates of Colorado pikeminnow fecundity and survival described in the preceding sections are effectively only "snapshots" of data within a short time period – often over a single year (spawning season). Moreover, the data we are using come from different river systems that may not experience the same environmental conditions within a given time period. Instead of trying to accurately assign a particular level of environmental variability to fecundity and survival rates in the absence of appropriate data, we assigned what we considered to be a reasonable level of variance to the mean fecundity and age-specific survival rates.

Furthermore, we assumed in all our models that EV for fecundity and survival will be correlated within a year; in this way, the model draws only a single random normal deviate for a population and applies that same deviate to each demographic rate.

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 68 adults (34 males, 34 females) as the initial adult stage abundance. Given some differences in mortality values across various scenarios (see below), this number of adults would translate into different values of overall initial population abundance of all age classes. Importantly, though, the number of adults would remain constant for consistency and clarity when interpreting model output. This relatively small number of adults was used to reflect the number of fish that could have recently inhabited the San Juan River.

Carrying capacity

The long-term equilibrium abundance of a given population in a specific habitat is simulated through quantifying a given habitat's population carrying capacity (K). The habitat carrying capacity defines an upper limit for the population size, above which additional mortality is imposed randomly across all age classes in order to return the population at the end of a specific timestep to the value set for K.

Miller and Lamarra (2006) developed a population model for the San Juan River 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. A new estimate for carrying capacity was recalculated in 2013 using the estimated densities of prey for each of six river reaches. 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 406 adults, or about 2.26 fish/mi (1.4 fish/km) for the 180 mi (290 km) included in their model (Table 3; Miller 2013).

Table 3. Estimated carrying capacity of adult Colorado pikeminnow in six geomorphic reaches of the San Juan River (after Miller 2013). River miles are measured from Piute Farms (RM 0.0) upstream to about the confluence of the Animas River (RM 180.0).

Reach	Length (miles)	Adults/mile	Total Adults
1	0-16 (16)	1.0	16
2	17-67 (51)	1.0	51
3	68-105 (38)	1.0	38
4	106-130 (25)	3.0	75
5	131-154 (24)	4.0	96
6	155-180 (26)	5.0	130
Totals:	**180**	**2.26**	**406**

Density-dependent regulation of demographic rates

The regulation of one or more demographic rates as a function of population density is a nearly universal phenomenon among wildlife populations. Birth and/or survival rates can be reduced when density increases to a point where competition for space or resources becomes critical; at the other extreme, very low population densities can lead to a reduction in breeding rates simply because individuals of the opposite sex have difficulties in finding each other to mate (known as the Allee effect). Therefore, a proper PVA must include at least some form of density-dependent regulation of vital rates (see Morris and Doak (2002) and references therein for more information on this topic).

At the present time, it is impossible for us to analyze spawner-recruit relationships in the San Juan River population in order to derive a reliable density-dependent stock recruitment relationship. In fact, little reliable data on density-dependent stock recruitment exist for pikeminnow populations in either the Green or Upper Colorado River subbasins. Valdez (2013) conducted an exploratory analysis of population estimation data from the Green and Upper Colorado River subbasins to derive preliminary estimates of parameters defining a Beverton-Holt style of density dependence. These analyses yield estimates of the parameter R_{Max} – defined as the maximal annual growth rate expected in the absence of density dependence and a critical parameter in the Beverton-Holt density dependence model – that far exceed what would be expected for a long-lived species such as the Colorado pikeminnow. It is likely that the small datasets available and the large degree of uncertainty around population estimates derived from those datasets make it extremely difficult to compute complex models of density dependence with a reasonable degree of accuracy. Further exploration of density dependence in our pikeminnow populations of interest is provided in Valdez (2014, Appendix B).

In light of this high level of uncertainty, we must therefore rely on other models to develop a mechanism for density dependence. As a first step in our modeling process, we assumed that Allee effects are not present, and we also assumed that processes operating at high densities are best explained by a ceiling model of density dependence. Under the ceiling type of density dependence, the population grows exponentially until it reaches the ceiling, also known as the carrying capacity, and then remains at that level if the population growth rate is sufficiently strong. For large population sizes, the population size at

t+1 is a constant function of the population size at t. A population that reaches the ceiling remains at that level until a population decline (e.g., a random fluctuation or an emigration) takes it below the ceiling. Adopting a ceiling model of density dependence is preferred to a more sensitive model, such as the Beverton-Holt or Ricker functions, particularly in the absence of reliable data that may justify the choice of such an option.

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). At present, the stocking program involves introducing about 400,000 Age 0 fish to the river each year, approximately in November. Because our model conducts its 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 on 1 July of year x+1. In other words, we must determine an "effective stocking rate" that properly accounts for this mortality. See the Results section below for a more detailed discussion on how stocking was implemented within selected scenarios.

Stocking – known in the language of *VORTEX* as "supplementation" – occurs late in the sequence of events within a given timestep, specifically after all individuals in the population go through reproduction and mortality and age one timestep or year. Therefore, the youngest age class available for stocking in the model is Age 1. This is not a problem, however, as fish within this stocked cohort will actually mature to one year of age before the model ages them to the next timestep, thereby maintaining their proper age through their lifespan in the simulation.

A Method for Incorporating Hg-Mediated Demographic Impairment into PVA Model Scenarios

The continued addition of mercury (Hg) into rivers and nearby basins through coal-based energy production activities, mining, and natural processes, both locally and worldwide, has been an issue of growing concern to many natural resource management organizations (e.g., Royal Swedish Academy of Sciences 2007). An important goal of this PVA project was to develop a method for simulating the effects of demographic impairment – specifically, reduced reproductive success and/or survival – on long-term viability of the Colorado pikeminnow in the San Juan River. This section summarizes and expands upon a more extensive analysis of Hg accumulation in pikeminnow and associated demographic injury (Shibata 2014) found in Appendix C.

Throughout this analysis, we compared models of Hg-mediated demographic impairment to a "reference model" that features no explicit impairment. We chose parameters for this model to be consistent with reference model (B) "Lambda = 1" described earlier in this report: A population with nearly constant abundance through time, characterized by annual population growth rate $\lambda \approx 1.0$ (instantaneous stochastic growth rate $r_s \approx 0.0$).

The process for incorporating Hg-mediated demographic impairment involved the following steps:

1. Using the relationship derived by J. Lusk (USFWS 2012) between whole-body tissue Hg burden and total fish length, in combination with the relationship derived by Hawkins (1992) between Colorado pikeminnow length and age using data from the Upper Colorado and Green Rivers, a relationship was developed between whole-body tissue Hg burden and fish age. The graphical representation of this relationship for adults is given in Figure 3. This curve describes the rate of accumulation of Hg in the cohort of Colorado pikeminnow that mature to 7 years of age, i.e., are

recruited into the adult component of the population in that year. An explicit assumption here is that the concentration of Hg in the environment will not change over time, so that the curve in Figure 3 describes only simple bio-accumulation of Hg in a constant environment. Under this scenario, all cohorts recruiting into the adult stage will have an initial adult-stage Hg burden of approximately 0.14 ppm as inferred from the figure.

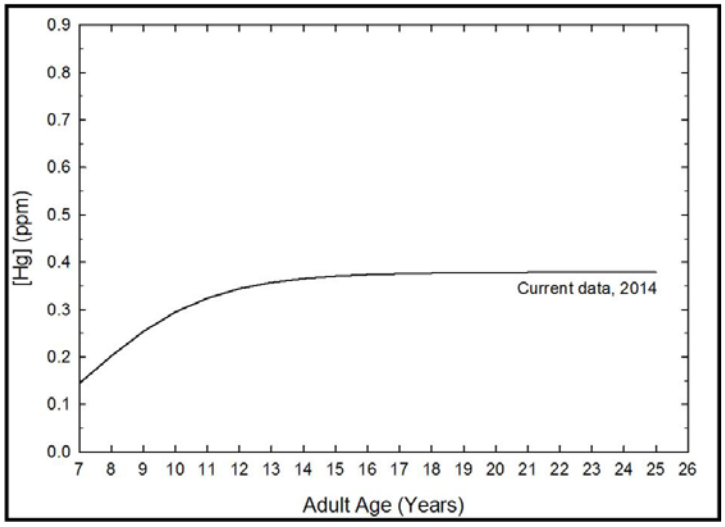

Figure 3. Whole-body mercury (Hg) burden among adult Colorado pikeminnow as a function of age. See accompanying text and Appendix C for more information on deriving the proposed relationship.

2. Recent modeling of Hg deposition and transport in the San Juan River (EPRI, Inc. 2014) indicates that, in a typical future scenario, the environmental burden of Hg in adult Colorado pikeminnow will likely increase by a factor of approximately 1.82 in the time period 2014 – 2071 (Figure 4). Using this information, we then derive a new curve that describes the rate of Hg accumulation in the cohort of Colorado pikeminnow that mature to 7 years of age in the year 2071 (Figure 5). This new curve reflects the synergistic results of both simple bio-accumulation of Hg in a given cohort and the increased environmental Hg burden 58 years into the future (assuming year 1 of the simulation is the current year 2014).

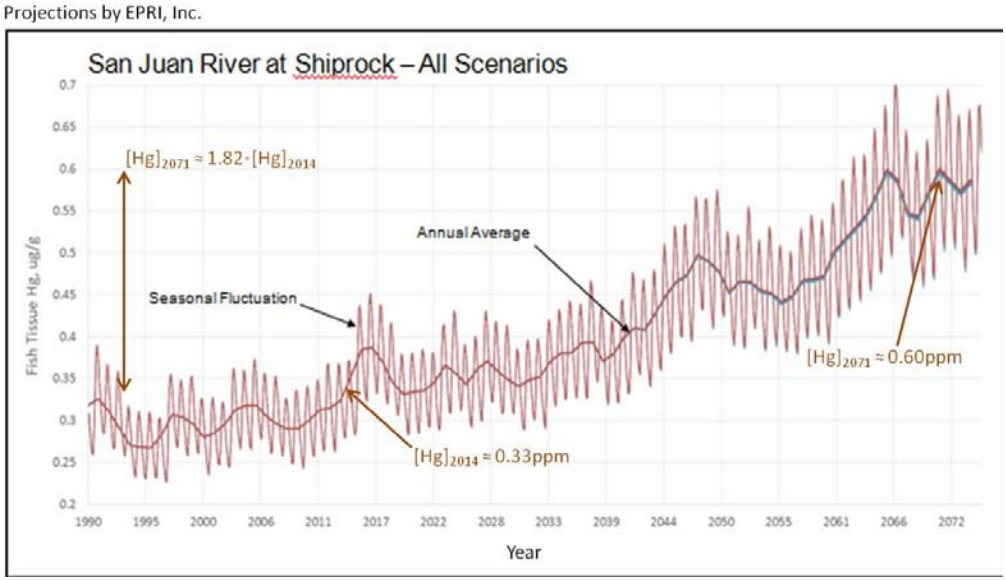

Figure 4. Projection of environmental Hg burden in adult Colorado pikeminnow in the San Juan River. See accompanying text for additional information.

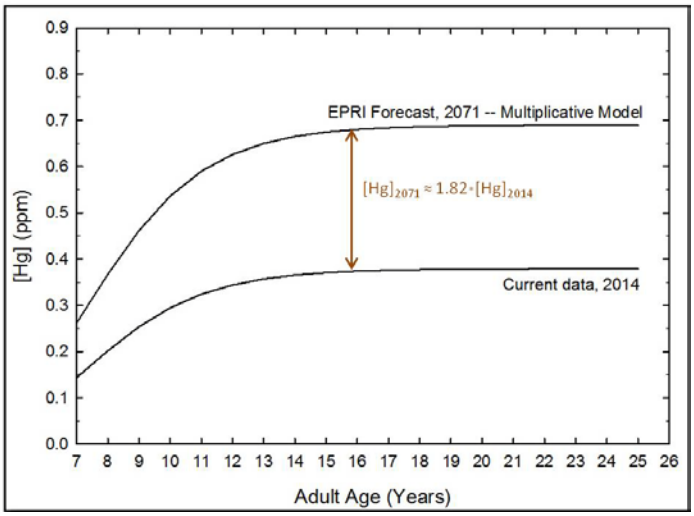

Figure 5. Whole-body mercury (Hg) burden among adult Colorado pikeminnow as a function of age, assuming either constant environmental Hg burden through time (2014 dataset) or gradual increase in environmental Hg burden into the future (2071 dataset). See accompanying text and Appendix C for more information on deriving the proposed relationship.

3. Data on a quantity originally defined by Dillon et al. (2010) as "% demographic injury" as a function of Hg tissue burden was assembled and analyzed by PVA Team member M. Shibata, culminating in the derivation of a relationship between % injury and Hg burden for, among others, two primary demographic components of our *VORTEX* model: adult reproductive success, defined here as production of 97-day old offspring, and age-specific survivorship (see Appendix C for a detailed description of these relationships). It is important to note here that adult reproductive success, as modeled in *VORTEX*, combines the percentage of adult females that successfully spawn, the average number of larvae produced per successful female, and the survival of those larvae to the assigned date of 97 days. Based on the derived functional relationship between whole-body Hg burden and age shown in Figure 3, we transformed Shibata's analyses to an explicit relationship between % demographic injury and age for adult female fecundity (Figure 6) and age-specific survival (Figure 7).

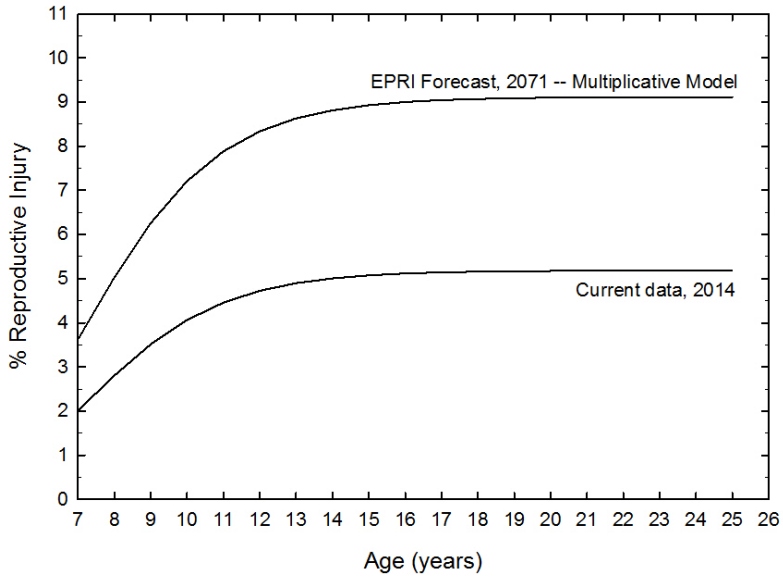

Figure 6. Percent reproductive injury as a function of adult age among Colorado pikeminnow in the San Juan River, assuming either constant environmental Hg burden through time (2014 dataset) or gradual increase in environmental Hg burden into the future (2071 dataset). See accompanying text and Appendix C for more information on definitions of terms and methods for deriving the proposed relationship.

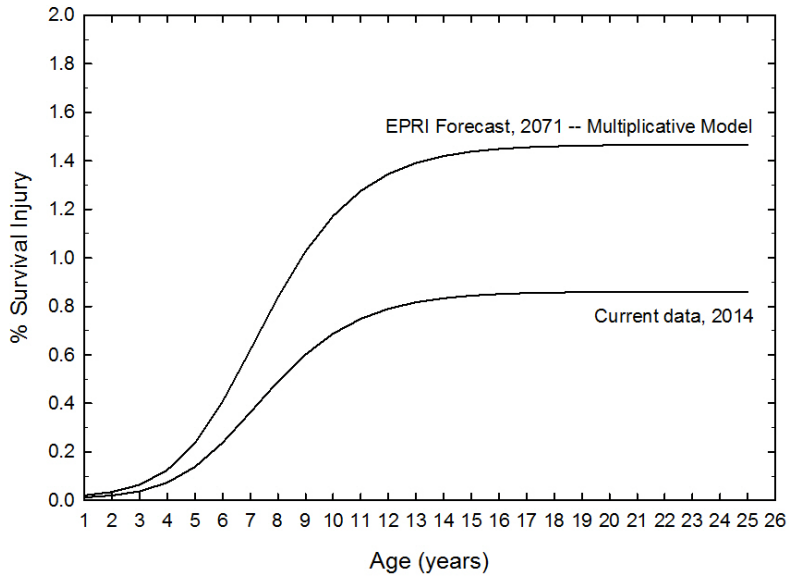

Figure 7. Percent survival injury as a function of age among Colorado pikeminnow in the San Juan River, assuming either constant environmental Hg burden through time (2014 dataset) or gradual increase in environmental Hg burden into the future (2071 dataset). See accompanying text and Appendix C for more information on definitions of terms and methods for deriving the proposed relationship.

Note that the multiplicative factor (1.82) identified in the estimation of current vs. future environmental Hg burden values carried forward in an identical fashion to the estimation of % injury curves. As the environmental Hg burden increases according to the EPRI projection, the % reproductive injury predicted by our analytical model ranges from 2 – 5% across the lifespan of adults recruited early in the simulation, through to 3.5 – 9% across the lifespan of adults recruited approximately 60 years into the simulation. Similarly, the % survival injury increased from a negligible level in the early life stages to about 0.8% among those cohorts born and recruiting early in the simulation, to a maximum of just less than 1.5% injury for those cohorts recruiting later in the simulation. It is clear from these curves that the absolute magnitude of survival impairment is markedly smaller than that for reproductive impairment.

4. With the % injury curve for reproductive success and age-specific survival in hand, we transformed these data to derive explicit functions for changes in offspring production and adult mortality – specific data used as input in *VORTEX* (Figures 7 and 8). When making these transformations, we assumed that a given % injury can be directly translated into an analogous reduction in the demographic parameter of interest. For example, since mean offspring production for an adult female in the absence of Hg-mediated impairment is 500 individuals in our "Lambda = 1" reference model, and Hg toxicity results in a 10% injury (equal to 90% of the reference value) to an adult female of a given age, then her rate of offspring production in the presence of Hg is (0.9*500) or 450 individuals. Each of the four curves in the figures below can be described by the following equations:

Offspring production, P

2014 dataset (static Hg burden): $P = 473.88 + 198.8e^{(-0.356*Age)}$
2071 dataset (increasing Hg burden): $P = 454.11 + 354.2e^{(-0.360*Age)}$

Adult survival, S

2014 dataset (static Hg burden): $S = 10.286 + [5.451(1-e^{(-0.360*Age)})]$
2071 dataset (increasing Hg burden): $S = 6.955 + [9.30(1-e^{(-0.360*Age)})]$

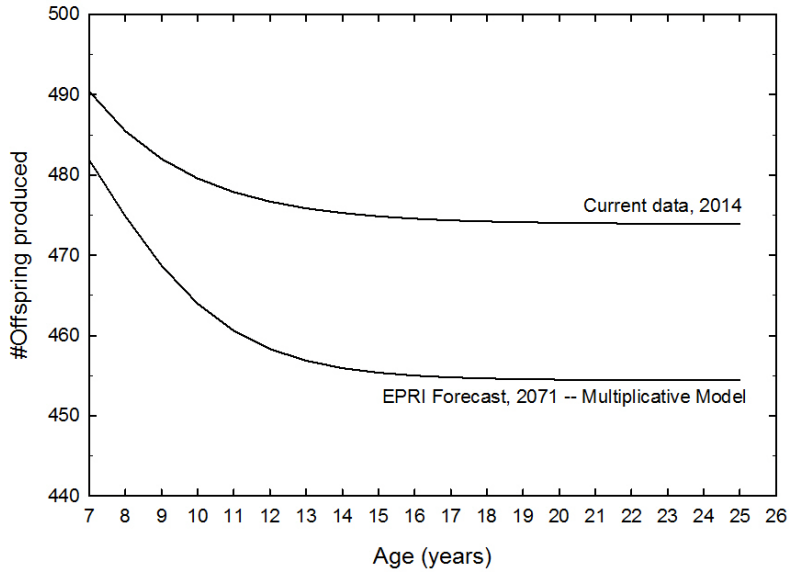

Figure 8. Offspring production per successfully spawning adult as a function of adult age among Colorado pikeminnow in the San Juan River, assuming either constant environmental Hg burden through time (2014 dataset) or gradual increase in environmental Hg burden into the future (2071 dataset). See accompanying text and Appendix C for more information on deriving the proposed relationship.

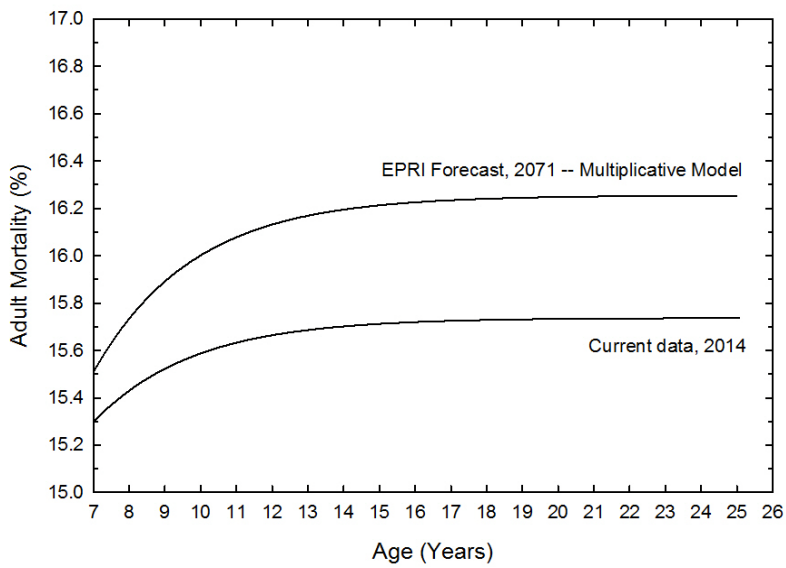

Figure 9. Adult mortality as a function of age among Colorado pikeminnow in the San Juan River, assuming either constant environmental Hg burden through time (2014 dataset) or gradual increase in environmental Hg burden into the future (2071 dataset). See accompanying text and Appendix C for more information on deriving the proposed relationship.

5. With the functional relationships derived in Step 4 above, we wrote equations within *VORTEX* to describe the gradual changes in offspring production and adult mortality as environmental Hg burdens increase according to EPRI projections. As a new cohort recruits into the adult stage each year of the simulation, the curve describing that cohort's mean offspring production rate (Figure 8) is shifted downwards by an additional factor of 1/58 between the initial curve assumed to be in place in the year 2014 (simulation timestep 1) and the year 2071 (simulation timestep 58). This cohort-specific fractional change in demographic rate is defined here as the "cohort increment", or CI_t. The equation describing age-specific offspring production at time t, designated $P_{A,t}$, is given by:

$$P_{A,t} = P_{A,2014} - [(CI_t)(\Delta P_A)] = P_{A,2014} - [(CI_t)(P_{A,2014} - P_{A,2071})]$$

where

$P_{A,2014}$ = Age-specific offspring production for adults recruited in 2014
$P_{A,2071}$ = Age-specific offspring production for adults recruited in 2071
CI_t = "Cohort Increment"
ΔP_A = Age-specific difference in offspring production for a given cohort

The following formula is used in *VORTEX* to represent the above equation:

$$P_{A,t} = (A>6)*(473.88+(198.8*EXP(-0.356*A))) - (((Y+7-A)/58)*((473.88+(198.8*EXP(-0.356*A)))-(454.11+(354.2*EXP(-0.360*A)))))$$

Where Y is simulation year (timestep) and A is the age of the fish in a given cohort. The quantity $(Y+7-A)/58$ represents the Cohort Increment.

In an identical manner, the equation for adult survival is written in *VORTEX* as:

$$S_{A,t} = (A>6)*(10.29+(5.45*(1-EXP(-0.36*A)))) - (((Y+7-A)/58)*((10.29+(5.45*(1-EXP(-0.36*A))))-(6.96+(9.3*(1-EXP(-0.360*A))))))$$

6. Impaired survival rates for pikeminnow ages 1 – 6 were coded in *VORTEX* in a slightly different manner, given that each rate applies only to a single age class. The data on survival rates for these age classes is given in Table 4. As noted earlier in this section, the unimpaired mortality rates were chosen to define "Lambda = 1" reference model (B), or a population with long-term population growth rate $\lambda \approx 1.0$. Note that the increases in mortality brought about by Hg-mediated impairment are quite small, in accordance with the small % injury values predicted from the relationships shown in Figure 7 above. We assumed a linear increase in mortality between simulation years 2014 and 2071 (timesteps 1 and 58), with a maximum mortality rate reached in 2071 and thereafter remaining constant in the absence of specific data indicating future Hg concentration changes from EPRI simulations. The MIN() function in *VORTEX* allowed us to maintain a constant mortality rate after the maximum value has been reached in timestep 58.

Table 4. Simulating Hg-mediated impairment of subadult survival in Colorado pikeminnow. Columns labeled "2014" and "2071" give predicted mortality rates under conditions of Hg-mediated demographic impairment in simulation years 2014 and 2071 (timesteps 1 and 58), respectively. Right-hand column gives the formula specifying the linear increase in mortality across the range defined in the previous two columns. Note that these subadult survival modifications are made at the same time that much larger changes are made to adult survival. See accompanying text for additional information.

	Mortality Rate, %			
Age (x)	Unimpaired	2014	2071	Mortality Formula
1	89.0	89.001	89.002	= 89.001+(MIN(0.0000165*Y;0.001))
2	78.0	78.004	78.008	= 78.004+(MIN(0.000055*Y;0.004))
3	67.0	67.012	67.021	= 67.012+(MIN(0.000153*Y;0.009))
4	45.0	45.040	45.069	= 45.040+(MIN(0.000494*Y;0.029))
5	30.0	30.097	30.166	= 30.097+(MIN(0.00119*Y;0.069))
6	18.0	18.195	18.334	= 18.195+(MIN(0.00239*Y;0.139))

Model Assumptions

The following is an attempt to identify the various assumptions regarding our understanding of Colorado pikeminnow biology, and how we incorporate that quantitative understanding into *VORTEX* models of population viability. The list is almost certainly incomplete, but covers the primary issues concerning structure and function of the PVA models discussed here, and the uncertainty regarding both process description and parameter estimation.

- The San Juan River population of Colorado pikeminnow experienced a rapid population decline before the initiation of a formal stocking program, due largely to very low levels of reproduction among adult females and, to a lesser extent, reduced adult survivorship.

  USFWS personnel conducting annual surveys inferred significant declines in abundance across all age classes. The current larval surveys find very small numbers of Age 0 fish, indicating very low levels of natural reproduction from one year to the next with uncertain or imperfect knowledge of their fate. The presence of these fish, however, does indicate that some capacity for natural reproduction exists within the San Juan River subbasin.

- The formal stocking program conducted by USFWS appears at the present time to be primarily responsible for maintaining Colorado pikeminnow in the San Juan River subbasin.

  The extremely low levels of documented natural reproduction among wild females contrasts with recapture rates of stocked fish, whose numbers typically exceed natural reproduction by 2 – 3 orders of magnitude annually (Furr 2012; Farrington et al. 2013).

- With the current stocking program in place, the adult pikeminnow population in the San Juan River has remained relatively constant in abundance over the past 20 years.

  Data summarized by Valdez (2014) in Appendix B indicates that adult population abundance remained relatively constant during the period 1990 – 2010. We may therefore be reasonably justified in developing a model, incorporating stocking, that shows a long-term population growth rate of $\lambda \approx 1.0$.

- The 180-mile stretch of the San Juan River defining the geographic scope of this analysis can be considered a single connected habitat inhabited by a single population of pikeminnow without metapopulation substructure.

  We are not concerning ourselves in this analysis with more complex substructuring of the San Juan River system. The river is not meaningfully subdivided into individual reaches that contain largely isolated pikeminnow subpopulations, so we can treat the full population as demographically contiguous. We acknowledge movement of fish downstream into Lake Powell and the impediment to returning fish by a natural waterfall in the San Juan arm, but because of the uncertainty and lack of quantified movement we restrict this analysis to the 180-mile stretch.

- In the absence of specific demographic data collected from pikeminnow in the San Juan River, we may justifiably adapt data collected from pikeminnow populations in the Green and Upper Colorado River Subbasins.

  If data on reproduction and survival are not available from San Juan River pikeminnow, we must use data on the same species from other river systems to gain insight into the processes occurring in the river system of primary interest.

- Colorado pikeminnow become adults at seven years of age, roughly corresponding to 450 mm TL.

  There is some level of uncertainty around this parameter, as discussed in some detail in the data summary of Valdez (2014) in Appendix B. We held this parameter constant in all scenarios comprising this PVA, thereby minimizing the impact of this uncertainty when comparing model output across scenarios.

- <u>All scenarios are initiated with approximately 65 – 70 adult Colorado pikeminnow, with equal number of males and females.</u>

  The actual number of adult pikeminnow in the San Juan River system is uncertain. Recent estimates put the adult abundance somewhere between 40 and 100 individuals. In order to maintain consistency across all model scenarios, we initiate our models with 68 adults under the assumption of an equal sex ratio (34 males, 34 females) and to approximate the abundance of adult fish in the system. While detailed estimates of long-term population viability would likely be influenced by the number of adults in a simulation of this type, the impact of this parameter value on our estimates of population growth rate is much reduced. As stated earlier in this document, the primary use of PVA is as a comparative analysis of Hg impairment and not as a definitive assessment of extinction risk. Furthermore, we are not explicitly concerned with generating detailed and accurate estimates of long-term extinction risk in this set of PVA models; an exploration of this risk can be conducted in a separate exercise.

- <u>We are not able to accurately measure the nature and extent of density dependence in recruitment from our data, and therefore cannot unequivocally parameterize the mode of density dependence in our models.</u>

  The detection and parameterization of density dependence in demographic rates is a very tricky business. We simply do not have the types and abundance of appropriate data on recruitment and population density to reliably estimate the mode and intensity of this process. The inclusion of density dependent processes in PVA models will often significantly impact long-term population viability (e.g., Ginzburg et al. 1990), so caution must be used in selecting the mode of density dependence and specifying the underlying parameters. Along those lines, the process of detecting and parameterizing density dependence in PVA models is a very complicated problem (e.g., Lande et al. 2006, 2002; Freckleton et al. 2006 discuss these issues in detail). If abundance estimates (or proxies thereof) are measured with error, this can lead to biased estimates of key density dependence parameters such as R_{max} in a Beverton-Holt mechanism of density dependence. Exploration of these processes outside of the *VORTEX* modeling environment on other species (results not reported here) indicates that long-term population growth rates and extinction risks are indeed strongly impacted by the strength of density dependence, even under very modest levels of R_{max}. In light of the high levels of uncertainty around this highly sensitive model parameter, the models discussed here included a simpler ceiling model of density dependence which is specified through the carrying capacity parameter, K.

- <u>The EPRI projection of environmental Hg burden, discussed among PVA Team members and used in this analysis, is a reasonable scenario to use as a basis for exploring demographic impairment of Colorado pikeminnow in the San Juan River.</u>

  We recognize that there are a number of different scenarios currently available that describe alternative assumptions regarding Hg deposition and transport rates in and around the San Juan River system. The specific scenario used here, shown in Figure 4, served as a foundation to develop the necessary methodology for incorporating demographic impairment through Hg accumulation. Uncertainty in the rate of Hg accumulation in the San Juan River system naturally leads to uncertainty in our estimates of the consequences of impairment resulting from this accumulation. Should the need present itself in the future, additional scenarios describing different rates of Hg deposition and environmental accumulation can be analyzed in a separate exercise to obtain new estimates of demographic impairment of Colorado pikeminnow.

- <u>The increase in age-specific Hg concentration for an individual fish is equivalent in proportional magnitude to the increase in environmental Hg burden as estimated in the EPRI projections.</u>

  In the absence of specific data to the contrary, we assumed that pikeminnow that reach seven years of age in the future will have tissue concentrations of Hg in proportion to the steady increase of environmental Hg predicted in the EPRI analysis shown in Figure 4.

- The fish ecotoxicity studies used by Shibata (2014) to determine % demographic injury as a function of Hg burden, summarized in Appendix C, are applicable to Colorado pikeminnow.

  None of the fish ecotoxicity studies used in this analysis directly examined effects to the Colorado pikeminnow. In order to use these data to derive estimates of % injury in the presence of Hg, we must assume that the physiological processes operating in the fish species examined in those ecotoxicity studies – including fathead minnow, mud minnow, brook trout walleye, Japanese medaka – are very similar to those operating in Colorado pikeminnow. Specifically, the PVA model assumes similar sensitivity among fish species — i.e., that effects (as a function of Hg concentrations in tissues) observed in species used in ecotoxicity studies are similar to those that would be observed for the Colorado pikeminnow (see Appendix C for additional discussions of uncertainty and assumptions used with respect to charactering % injury as function of Hg concentrations in fish tissue).

- % Injury can be used as a direct modifier of adult reproductive success (offspring production) and age-specific survival.

  The studies summarized by Shibata (2014) used different definitions of such demographic variables as reproductive success, thereby making it very difficult to easily and confidently combine data across studies into a single, cohesive analysis. By combining multiple studies of Hg-mediated injury to reproductive success into the single model variable describing offspring production, we are successfully incorporating nearly all of the various components included in these external analyses.

Other Processes Absent From the Reference Model

There are additional processes or factors that were not included as modifiers to overall Colorado pikeminnow demographic dynamics in the reference model.

- "Catastrophic" events in the San Juan River subbasin –Singular environmental events that are outside the bounds of normal environmental variation affecting reproduction and/or survival are typically referred to among conservation biologists as catastrophes. These events can originate naturally, as in the case of tornadoes, floods, droughts, disease, or similar events. Additionally, we can identify anthropogenic events that may act in a similar way, including chemical spills, man-made forest fires, etc. These events are modeled in *VORTEX* by assigning an annual probability of occurrence for each type of designated event and, once it is deemed to occur in a given year, by ascribing the type of impact the event may have in that year on one or more demographic rates specified in the model. The PVA Team was unable to reliably identify and quantitatively describe specific catastrophic events that could be included in the reference models. As the objectives of the modeling project did not explicitly include detailed examination of catastrophic events and their impacts to long-term viability of Colorado pikeminnow in the San Juan River, we chose to exclude this feature from our comparative model study. While we have not included any catastrophic events in our reference model, we could in the future explore options around including one or more events as considered appropriate.

- Genetic effects on population viability – Inbreeding depression (reduced viability of inbred offspring) and the gradual loss of genetic variability (heterozygosity) resulting from a small effective population size through time are often considered important factors to include in population viability analysis of endangered species (e.g., Reed et al. 2002). The current estimate of 40 – 100 breeding females in the San Juan River subbasin is rather small and could potentially result in some level of future inbreeding if recruitment of offspring were to increase over time. Moreover if the adult females show highly skewed levels of reproductive success, this could lead to a significant reduction in the effective population size, higher rates of inbreeding, and more rapid loss of population genetic diversity. We also do not know the effect of stocked fish, their likely future recruitment into the population, and

cross-breeding with the few remaining wild fish. While acknowledging these potential impacts, we do not have sufficient data to quantify these processes to any defensible extent; consequently, we have chosen to exclude genetic impacts from our current PVA.

Model Output Analysis and Interpretation

Performance of Alternative Reference Model Scenarios

This section describes an iterative process of reference model construction that explores the implications of our basic pikeminnow demographic dataset. This process facilitated the development of useful reference models, to which other scenarios could be compared. Our first model scenario used the data summarized by Valdez (2014), including data from hatchery studies on both fecundity and early life-stage survival. Moreover, this first scenario did not include any form of stocking, and did not incorporate Hg-mediated impairment of reproductive success and/or survival. Therefore, this scenario represented an attempt to simulate a Colorado pikeminnow population before stocking was initiated and with little impact from Hg input to the river system.

Under these conditions, a simulated population of Colorado pikeminnow in the San Juan River is expected to increase in abundance very rapidly. Specifically, the estimated stochastic population growth rate was $r_s = 0.522$ (Table 5). Under these favorable growth conditions, the adult population increased from its initial abundance of 68 individuals to the carrying capacity of 406 animals in just five years (Figure 10).

Table 5. Summary of results from reference model analysis. λ_{Ad}, stochastic growth rate of adults calculated from simulation; P(E), probability of population extinction during 70-year simulation; $N_{A,70}$, average adult abundance (standard deviation) at the end of the simulation; T(E), median time to extinction. See accompanying text for additional information on model structure and implementation.

Scenario	λ_{Ad}	P(E)	$N_{A,70}$ (SD)	T(E)
Base reference	1.430	0.000	406 (3)	
Rapid decline	0.845	1.000	0	22.0
Lambda = 1	1.004	0.005	93 (87)	

Recent study of Colorado pikeminnow in the San Juan River (e.g., Farrington et al. 2012) provides strong evidence over the past decade that, while some larval fish spawned 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. Furthermore, as documented in Durst (2013) and Valdez (2014), the number of adult pikeminnow appears to have remained rather small – on the order to 50 – 100 individuals – and rather constant over the period 1990 – 2010 (see Appendices). We may therefore surmise that recent and current growth of the San Juan River pikeminnow population through natural reproduction is quite limited, with any observed increase in abundance most likely due to survival of younger fish that were part of the stocking program started in 1996 and formalized in 2002. Taking all of the above information into account, and given that this version of the baseline demographic model does not explicitly include stocking, we concluded that this first iteration of our base reference model grossly overestimated the actual growth dynamics of the wild pikeminnow currently inhabiting the San Juan River.

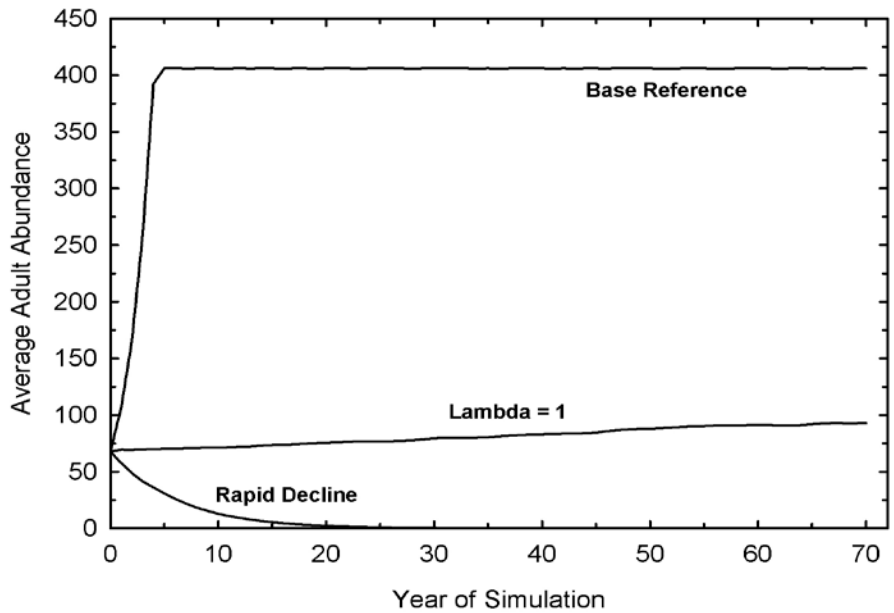

Figure 10. Trajectories of average adult abundance in reference scenario simulations of the San Juan River population of Colorado pikeminnow. See accompanying text for more information on reference scenario definitions and model structure.

In light of the results from this first iteration of our base reference model, it became necessary to adjust the model's demographic parameters in order to generate a population trajectory that more realistically tracked our estimates of actual population abundance over the recent past, in the absence of stocking. This logic formed the basis of creating our second reference model, referred to in the previous section on data input (page 11) as our "Rapid Decline" reference model (A). As seen in Table 5 and Figure 10, this scenario generated a rate of adult population decline of approximately 15% per year, leading to population extinction in about 20 years. This rate of adult population decline is very much in line with our expectations, given an adult mortality rate of 15% used in our model and very low levels of reproductive success. The PVA Team concluded that this is a much more reasonable simulation of pikeminnow population dynamics for the San Juan River over the past few decades in the absence of stocking, and may also be used to generate broad predictions of population performance if current levels of stocking were to cease and current threats were to remain unmanaged (for more information on these threats, see *Other Factors that Impact Colorado Pikeminnow Abundance*, p. 30).

Finally, we wanted to create a third reference model that described a population with a very low rate of increase in adult abundance. This model, described earlier (page 10) as the "Lambda = 1" reference model (B), was to be used as a base to explore the population-level impacts of Hg-mediated demographic impairment. Table 5 and Figure 10 show the results of projecting this model over 70 years. The simulated population shows a very low rate of increase in adult abundance under these input conditions, which over 70 years leads to an increase of about 30% in the number of adult pikeminnow. This scenario can provide some insight into the demographic conditions necessary to achieve minimal population stability, assuming that various factors that may compromise reproductive success and survival can be successfully managed. Specific discussions around alternative pikeminnow management strategies, however, are beyond the scope of this current analysis.

Demographic Sensitivity (Elasticity) Analysis

First, we conducted a relatively simple analysis designed to estimate the proportional sensitivity of a given demographic parameter to the derivation of population growth rate. This proportional sensitivity,

also known as elasticity (Caswell 2001), defines the comparative change in population growth rate given a unit change in one of a set of demographic parameters when the other parameters within that set are held constant at their baseline values. The elasticity values for a group of demographic input parameters provides a measure of the relative value of each parameter in driving population dynamics, or the contribution made by a given parameter to population growth.

We conducted our elasticity analysis on the reproductive parameters, both the % females spawning per year and the number of offspring produced by a successful adult female, and on each of the eight age-specific survival rates (after transforming mortality rates used as *VORTEX* input). The reference model used for this analysis was the "Lambda = 1" model. Each of these ten parameters was individually changed by ±5% of the original baseline value to create a new scenario, with a total of 20 separate scenarios being created in addition to the reference scenario. The deterministic growth rate, estimated in the absence of stochastic variation in demographic rates across years, was calculated in *VORTEX* for each scenario. Following Heppell et al. (1996), the elasticity for each parameter was calculated as:

$$E(x) = \frac{\lambda_{x+0.05x} - \lambda_{x-0.05x}}{0.1\lambda_x}$$

where $\lambda_{x+0.05x}$ is the deterministic growth rate of the model with parameter x increased by 5%. The difference in growth rates is divided by the reference model growth rate multiplied by the total perturbation. Elasticity analysis allows us to compare proportional changes in input parameters that may not be on the same scale, such as total offspring production and age-specific survival rates.

The results of the elasticity analysis are shown in Figure 11. Adult survival is clearly an important contributor to pikeminnow population growth dynamics, with an elasticity value that is approximately 5.5 times that of all other parameters governing reproduction and survival. This is typical of species with life histories featuring a long reproductive lifespan, even when fecundity is relatively high with associated low juvenile survival (Heppell 1998). If the underlying reference model were to change, e.g., to a higher growth rate ($\lambda > 1$), the absolute elasticity values would change but the relative value for adult survival would remain greater than those for the other parameters.

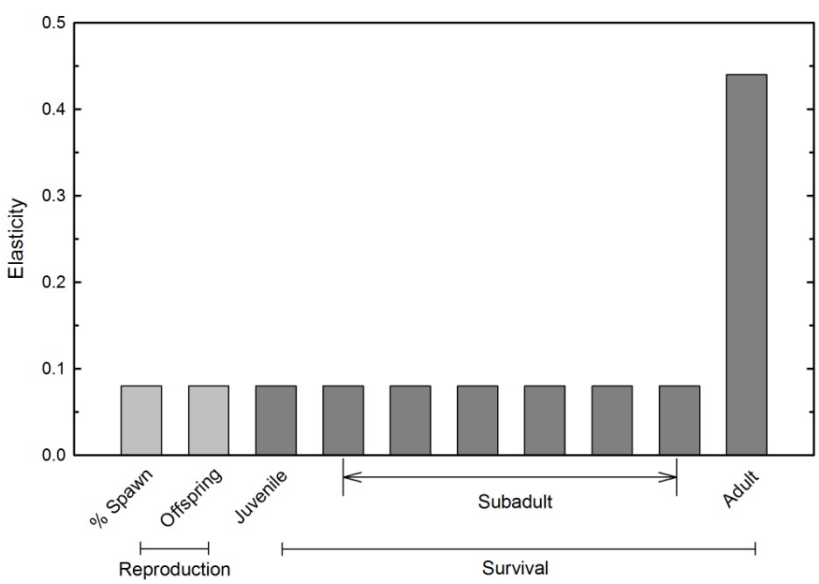

Figure 11. Results of elasticity analysis on demographic rates. Reproduction parameters (light gray bars) include % females successfully spawning and number of offspring produced per year, while survival parameters (dark gray bars) include annual survival rate of juvenile (age 0-1), subadult (ages 1-7), and adult (7+) age classes. See accompanying text for additional information on model structure and implementation.

As a complement to the elasticity analysis, we conducted a sensitivity analysis in *Vortex* using logistic regression to explore the importance of these same ten parameters on estimates of extinction risk (McCarthy et al. 1995). Using the sensitivity testing module in *Vortex*, we created 500 parameter sets by randomly choosing input values from uniform distributions within reasonable ranges for each parameter using a Latin Hypercube sampling scheme (Table 5). We ran 100 iterations in *Vortex* for each parameter set, resulting in 50,000 binary observations of population persistence or extinction by year 70. Using parameter set values as independent variables and whether the population goes extinct or not by year 70 as the binary dependent variable, we conducted logistic regression in R (R Development Core Team 2011) and compared the standardized regression coefficients to rank each independent variable's importance in relation to extinction risk. The standardized regression coefficient is scaled by parameter uncertainty and expresses the contribution of each independent variable to changes in the dependent variable (Cross & Beissinger 2001).

As seen in Table 6, the logistic regression method also shows that the reference model is highly sensitive to adult survival, with all other parameters showing similar levels of sensitivity. The percentage of adult females that successfully spawn shows a relatively higher level of sensitivity that is not apparent from the elasticity analysis discussed above. This parameter is of course closely related to the number of adults in the population, which is governed by adult survival. Therefore, it seems reasonable that this parameter may show some heightened sensitivity with respect to population extinction risk, which is itself a more volatile parameter than the more stable deterministic growth rate.

Table 6. Results of sensitivity analysis for parameters used in the "Lambda = 1" reference model of Colorado pikeminnow population dynamics. The standardized coefficient reflects the *z-value* resulting from logistic regression (see McCarthy et al. 1995 for a more detailed discussion of this methodology).

Parameter	Base Value	Min Value	Max Value	Standardized Coefficient
% females spawning	50.0	40.0	60.0	116.94
Number of offspring	500	450	550	59.09
0 – 1 survival	50.0	45.0	55.0	62.41
1 – 2 survival	11.0	9.9	12.1	75.16
2 – 3 survival	22.0	19.8	24.2	78.45
3 – 4 survival	33.0	29.7	36.3	75.76
4 – 5 survival	55.0	49.5	60.5	76.53
5 – 6 survival	70.0	63.0	77.0	77.48
6 – 7 survival	82.0	73.8	90.2	75.90
Adult survival	85.0	76.5	93.5	203.69

Overall, these two methods for investigating model sensitivity each converge on the identification of adult survival as a major factor that influences the long-term growth dynamics of pikeminnow in the San Juan River. With this information in hand, one may conclude that manipulating adult survival through active population management may be the most effective means for improving long-term population growth and, by extension, population viability. This conclusion may be inappropriate, however, because it (and the underlying analysis of population sensitivity/elasticity) does not consider the various factors that may actually be compromising other demographic processes and putting the population at risk of decline, but which may otherwise show relatively low sensitivity. The Colorado pikeminnow in the San Juan River appears to be a clear example of this complexity. The elasticity results presented here are to be interpreted in an ideal sense – that is, in a population that is not destabilized by external threatening processes. Under these conditions, changes to adult survival produce comparatively larger changes to population growth. However, in the real world of the San Juan River, the population appears to be most gravely threatened by

factors such as restricted nursery habitat availability, predation by and competition with non-native species, and entrainment into undesirable components of the river system – each of these impacting the earliest life stages much more severely than adults. Therefore, active management of adult survival while largely ignoring threats to early life-stage fish is not likely to significantly improve the long-term viability of the population in the San Juan River. A more detailed examination of these issues, while important for management of the species, is outside the scope of the current project.

Treatment of Simulated Stocking In the Presence of Rapid Population Decline

Using the "Rapid Decline" (A) model as a reference, we can explore the mechanisms by which we can simulate stocking of 6-month-old Colorado pikeminnow. Remember that while these individuals are not technically 12 months old at the time of stocking, they are stocked as new one-year-olds in *VORTEX*, as if they are added to the population immediately before their first birthday. The stocking process is therefore simulated as an "effective" stocking rate which takes into account the mortality of these fish from the day of stocking to the next census just before spawning in early July.

Our goal here was to generate a population that has an adult population growth rate very similar to the "Lambda = 1" reference model as a means to simulate a San Juan River pikeminnow population that, despite very low levels of natural reproduction, maintains a roughly constant abundance of adults through time. Furthermore, because of annual variability in survival of stocked individuals, we wanted to implement stocking by creating a statistical distribution from which *VORTEX* would draw the effective number of individuals that were stocked in November and survived to the next census in early July. Evaluation of model behavior led to choosing an effective mean stocking rate of 6,000±1,000 individuals added to the population on an annual basis. This was implemented in *VORTEX* by specifying the following equation separately for males and females, assuming that the actual population available for stocking each year has an approximately equal sex ratio:

Effective Stocking Rate = 3000+(1000*SNRAND(Y+(R*100)))

Using this equation, *VORTEX* draws a random normal deviate (mean =0, standard deviation = 1) to generate the specified variability around the mean of 3,000 for each sex. The expression (Y+(R*100)), where Y is year (timestep) and R is the run (iteration) number, assures that the random numbers drawn from the distribution using the SNRAND function will be different each year and each iteration, as desired. For purposes of illustration here, the stocking event was set to occur each year of the simulation to year 40, at which time the stocking ceases and the population is then left to rely on natural reproduction to maintain adult abundance.

The resulting trajectory in the presence of this stocking scenario is shown in Figure 12, with the no-stocking "Rapid Decline" reference model trajectory included for comparison. In the presence of stocking at the specified rate, the adult population abundance was maintained close to its initial value throughout the stocking period, with variability in annual abundance according to an annual coefficient of variation (CV, defined as standard deviation divided by the mean) of approximately 35%. Under these conditions, the population was being maintained solely by continued addition of young fish to the population, with a sufficiently large cohort abundance to facilitate recruitment of some individuals into adults at a rate that offsets natural adult mortality. As soon as stocking is terminated after year 40, the population returned to the simple demographics described by the underlying reference scenario and drops rapidly to extinction by the end of the simulation. This results from the fact that stocking by itself does not impact the underlying negligible levels of natural reproduction in this population that severely limits natural recruitment. This analysis suggests that stocking may be an effective mechanism for maintaining pikeminnow in the San Juan River, but likely cannot be terminated unless specific measures are implemented that reduce or eliminate threats to natural reproduction by wild adults.

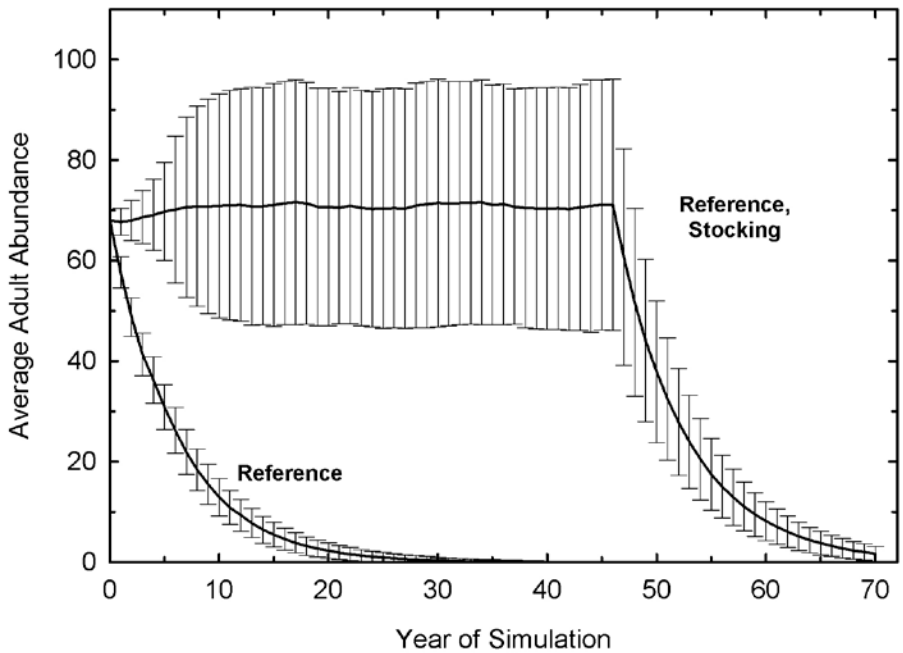

Figure 12. Projections of average adult abundance of Colorado pikeminnow under alternative models of stocking in the presence of a "rapid decline" reference model. Stocking is absent in the Reference model, and is present for the first 40 years of the simulation in the "Reference, Stocking" scenario. Variability in annual adult abundance is given by the standard deviation. See accompanying text for more information on model structure and implementation.

Population-Level Impacts of Hg-Mediated Demographic Impairment

I. Static vs. increasing environmental Hg burden

Initially we considered a simple model of demographic impairment, assuming a static Hg burden and assuming only reproductive impairment as defined by the number of offspring produced per successfully spawning female. Under these conditions, we simulated reduced reproductive success with increasing adult age according to Hg accumulation defined by current year 2014 conditions (see Figures 5, 6 and 8). Under these simple conditions, the adult population growth rate with reproductive impairment was reduced from the reference value of λ == 1.004 (using the "Lambda = 1" reference model) to λ = 1.001 (Figure 13). This is a rather small difference in overall magnitude, but this difference manifests itself in a gradual reduction in the number of adult pikeminnow in the population – by year 30 there are five fewer adults in the population and 14 fewer adults at year 70. [Note that this difference between scenarios is not statistically significant, as the amount of within-scenario variation is quite large. Variation in abundance within a given scenario is not shown here for purposes of clarity.]

Alternatively, if we assume an increasing Hg burden according to EPRI projections, the long-term adult population growth rate was reduced further to λ = 1.000 (Figure 13). This very small difference in growth rate ultimately translates into a reduction of six adults in the simulated population after 70 years. Most notable, perhaps, is the observation that the increasing Hg burden apparently leads to an accumulation of reproductive impairment such that the adult population growth rate becomes negative about midway through the simulation, i.e., after about 35 years. This implies that, under a reference condition where long-term $\lambda \approx 1.0$, a relatively modest amount of Hg-mediated reproductive impairment resulting from a relatively small demographic injury can reduce offspring production and, later, recruitment of new adults to a level that cannot keep pace with annual adult mortality. While this is a specific case that may not be replicated across a suite of potential starting conditions, it nevertheless indicates a "tipping point" for the population at which Hg impairment exceeds annual survival.

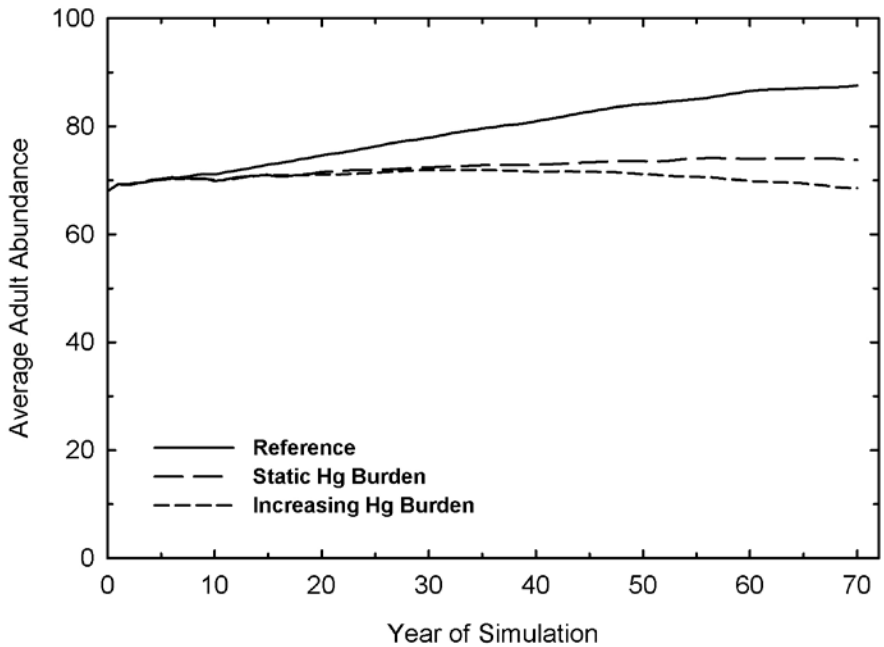

Figure 13. Projections of average adult abundance of Colorado pikeminnow under alternative models of Hg-mediated reproductive impairment. Reference model assumes no reproductive impairment. The "Static Hg Burden" scenario assumes current levels of Hg burden in effect throughout the duration of the simulation, and the "Increasing Hg Burden" scenario assumes gradual increases in Hg burden according to the EPRI projection discussed in the presentation of model input. See accompanying text for more information on model structure and implementation.

II. Demographic impairment under increasing Hg burden and low reference growth rate

Separate scenarios were constructed and run with the inclusion of only reproductive impairment or only survival impairment, using the "Lambda = 1.0" reference model as a base. This was done to evaluate the relative contributions of these two impairment processes to overall Colorado pikeminnow population growth dynamics. As seen in Figure 14, each of the two sources of impairment contributed nearly equally to reducing the long-term adult population growth rate relative to the reference model: reference, λ = 1.004; reproductive impairment, λ = 1.000; survival impairment, λ = 0.999. It is important to remember, however, that these nearly equivalent results are the product of survival impairment that is only about 15 – 20% of the magnitude of reproductive impairment emerging from the % injury analysis. This outcome reaffirms the results of the demographic sensitivity analysis discussed in the previous pages – the observation that, all else being equal, adult survival is a very important driver of Colorado pikeminnow population dynamics. While all age classes were subject to Hg-mediated impairment using the equations described previously, the extremely low levels of impairment in the early life stages, coupled with the high elasticity seen for adult survival, suggests that impairment of adult survival is the main contributor to survival impairment (this conclusion confirmed through separate simulation modeling, results not shown here for clarity of presentation).

Given that reproductive and survival impairment operate essentially independently in our *VORTEX* model, we might expect that the population-level impact of these two processes acting together would be nearly additive. This expectation is confirmed in Figure 14, where the long-term adult population growth rate λ = 0.996. Over a simulation duration of 70 years, the difference between this growth rate and that of the reference model yields a reduction in adult abundance of 38 individuals, or about 43% of the reference model final adult abundance. While this difference in abundance may not be labeled significant by standard statistical methods due to the large amount of variation across iterations within any given scenario, the mean trajectories described by these different scenarios are robust (10,000 iterations for each Hg impairment scenario).

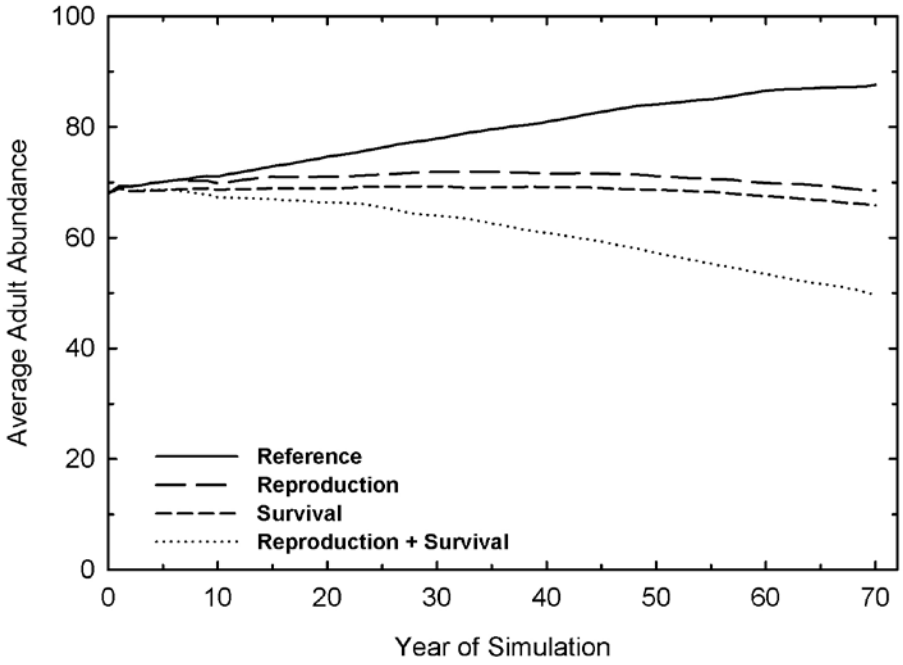

Figure 14. Projections of average adult abundance of Colorado pikeminnow under alternative models of Hg-mediated demographic impairment with increasing Hg burden. Reference model assumes no reproductive impairment. See accompanying text for more information on model structure and implementation.

III. Demographic impairment under increasing Hg burden and high reference growth rate

We cannot draw broad conclusions about the population-level impacts of Hg-mediated demographic impairment with only a single set of comparisons to a given reference model. It is valuable to repeat the above scenarios in comparison with a reference model that shows a considerable difference in underlying growth rate. Specifically, we should develop a reference model that displays the capacity for significant positive growth and then explore how Hg-mediated demographic impairment affects growth.

We created this alternative reference model by reducing the mortality of juveniles (Age 0) from 50% to 25%, yielding a reference model population growth rate of $\lambda = 1.023$. This reduction in juvenile mortality may be thought to result from an unspecified reduction in predation by non-native fish, increases in quality and/or quantity of low-velocity nursery habitat, etc. Under this assumption, scenarios depicting reproductive impairment only, survival impairment only, and combined impairment demonstrate comparative growth dynamics that are very similar to those where reference model growth conditions are less favorable (Figure 15). With the reference model growth rate of $\lambda = 1.023$, each of the single-impairment scenarios yield growth rates of $\lambda = 1.022$ and the combined impairment model gives an adult population growth rate of $\lambda = 1.020$. This smaller absolute difference in adult population growth rate leads to a smaller reduction in final adult abundance: 56 individuals, or approximately 17% of the reference population final abundance of 329 individuals. This difference in final adult population abundance is less than half the difference in abundance when the reference model population growth rate was just above $\lambda = 1.000$. While still not an exhaustive examination of the relationship between Hg impairment and population growth, the analysis described here provides important evidence that the population-level impact of impairment may be smaller when the underlying growth dynamics of the affected pikeminnow population are more robust.

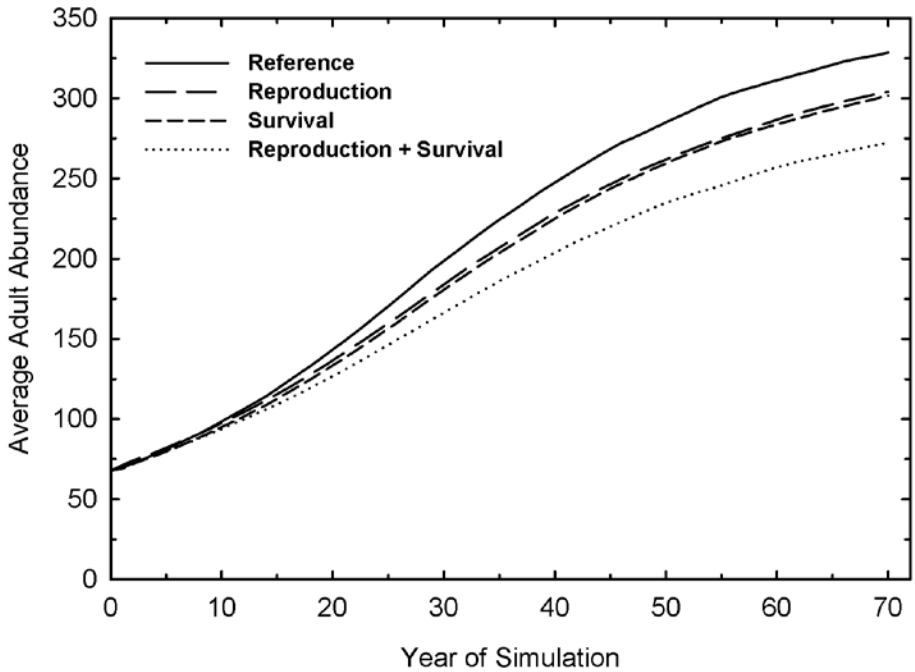

Figure 15. Projections of average adult abundance of Colorado pikeminnow under alternative models of Hg-mediated demographic impairment with increasing Hg burden, and under conditions of high reference population growth. Reference model assumes no reproductive impairment. See accompanying text for more information on model structure and implementation.

Other Factors that Impact Colorado Pikeminnow Abundance

As presented in Figure 1 and discussed in this report, there are other processes besides Hg-mediated demographic impairment that are considered to impact reproduction and/or survival of Colorado pikeminnow in the San Juan River (USFWS 2002). These factors may be targeted for future management activity with the goal of reducing their impact in order to improve the long-term viability of the pikeminnow population in the presence of continued future Hg deposition in the river, with associated impacts as analyzed in the previous section. These factors have not yet been incorporated into the current PVA model, but they can be added to the appropriate reference model at a future date.

These factors are discussed briefly below, with reference made to the way in which they affect pikeminnow demography and the mechanism by which they would be included in future *VORTEX*-based PVA models. These factors are discussed in greater detail in Valdez (2014, Appendix B).

Nursery (Backwater) Habitat Availability

Soon after hatching, larval Colorado pikeminnow are transported downstream and move into low-gradient reaches containing low-velocity nursery habitats (Bestgen et al. 2006). These areas are vitally important for larval fish development, growth, and survival. Therefore, reduced nursery habitat availability can significantly decrease offspring production and first-year survival.

Changes to nursery habitat availability, and resulting pikeminnow demographic impacts, would be simulated within *VORTEX* through changes in the number of offspring produced per successfully spawning adult female, and likely also in the survival of those offspring to one year of age (0-1 survival). Ideally, data on the quantitative relationship between nursery habitat area and larval pikeminnow production would be used to incorporate this factor into our PVA models. At this time, most of the relevant data on this relationship come from the Green and Upper Colorado River basins, with about 20 years of information available for analysis. There are ample data available on the amount and distribution of

backwater habitats in the San Juan River system, but no data on pikeminnow larval fish abundance since effectively all of the pikeminnow currently inhabiting the San Juan River were stocked at about six months of age. There are approximately 15 years of data from the San Juan on larval abundance of other fish species; the PVA Team would need to make a decision on the applicability of those data to understanding nursery habitat use by larval Colorado pikeminnow. In light of this, we would therefore rely on data from the upper basin to come up with a quantitative relationship characterizing the amount of backwater area to the number of offspring produced and that survive to one year of age. However, data from Bill Miller that was discussed during PVA Team meetings indicates that the average area of backwater habitats in the San Juan is just 32 m^2 – much smaller than similar types of habitat in the upper basins. Therefore, it is unclear if and how the data from the upper basins can be adapted to the San Juan River system.

Non-Native Fish Species: Predation and Competition

Channel catfish (*Ictalurus punctatus*) and red shiner (*Cyprinella lutrensis*) likely pose the greatest threats to Colorado pikeminnow larvae and juveniles (USFWS 2002). [Consumption of young pikeminnow by older pikeminnow is also recognized as a contributing factor to overall mortality, but is not considered as a separate factor in this analysis.] Individuals up to about 300 mm (approximately age 2) can be consumed by catfish, although the rate of predation on these life stages is uncertain. Clearly, however, the survival rate of larval and juvenile pikeminnow can be significantly impacted by these fish.

A realistic quantitative relationship describing the density of predators and the resultant predation rate on young Colorado pikeminnow may be possible, but the data are not yet available to perform the analysis. Yard et al. (2011) and Yackulic et al. (2014) developed such a relationship for predation of humpback chub (*Gila cypha*) by rainbow trout (*Oncorhynchus mykiss*), ultimately identifying the proportion of trout that consumed humpback chub and the number of chub of a vulnerable size that were consumed over a given period of time. This intensive study could be used as a model deriving a similar relationship for the rate of pikeminnow consumption by catfish and/or shiner as a proportion of the total crop of vulnerable pikeminnow. With this information in hand, we could set up a relatively simple function in *VORTEX* that describes changes in mortality in first- or second-year pikeminnow as other aquatic predators are removed from the system. The actual population abundance of catfish or shiner would not be simulated directly within the pikeminnow demographic model, but would instead be estimated externally. The change in abundance of these species through management would then be used to estimate changes in total numbers of pikeminnow consumed.

Entrainment into Unsuitable Habitat or Outside the Model System

The process of entrainment involves two primary components: loss of individuals into unsuitable habitat (e.g., agricultural facilities) through diversion canals and similar structures; and drift of individuals downstream to Lake Powell, which in this model is considered outside the geographic boundaries of the simulated population. The age of individuals lost through diversion structures depends on the type of structure; adults are typically not lost in this process, so we could confine our study of this threat factor to survival of juvenile and subadult fish. It is feasible within *VORTEX* to modify the rate of juvenile and subadult mortality as a way to simulate changes made to diversionary structures – addition of screens, changes to structure geometry, etc. -- through management. Very little data are available on the number and ages of fish lost to diversion structures. Since no major diversion structures are present below River Mile 158, we may surmise that the total loss of individuals from the population is relatively small on a proportional basis; however, a detailed analysis of this process is required to determine if this is a valid hypothesis.

The San Juan River has a markedly steeper downstream gradient than the Green or Upper Colorado Rivers. Consequently, we may expect a fairly large proportion of larval and young Colorado pikeminnow

to drift long distances toward Lake Powell, especially if low-velocity backwater habitats are unavailable. In fact, we may consider offspring production and larval survival to be significantly impacted by this process. While it may be easy in practice to manipulate these parameters in *VORTEX*, the underlying evidence we would use to justify a specific scenario featuring such a manipulation would be challenging to generate. Data on larval pikeminnow retention are available (Archer et al. 2000), and in fact have been used by Miller and Lamarra (2006) to estimate larval downstream movement. Other data on drift rates may be available, including some information on travel times using bead studies or other hydrologic modeling efforts.

Habitat Access

In addition to increasing the quality of existing habitat to boost offspring production and survival, it may be possible to increase the quantity and quality of habitat by opening up new areas for Colorado pikeminnow to spawn and develop. For example, stretches of the San Juan River upstream of River Mile 180 could be made available, or access to the Animas River at Farmington could be re-established by manipulating current barriers to upstream movement in that system. Our *VORTEX*-based PVA model can simulate these proposed activities by increasing the total carrying capacity of the habitat, and perhaps by increasing overall levels of reproduction and/or survival of fish within the full extent of the river system as potentially higher-quality habitat is made available. However, as with all the factors discussed within this section, a responsible approach to incorporating this factor into the model would require considerable thought and careful analysis of relevant data on demographic responses to increased habitat availability. It is currently unclear how much quality spawning habitat is available in the upper reaches of the San Juan River and within the Animas River, or how favorably adult pikeminnow would respond to the increased availability of spawning habitat.

To be treated most effectively within the context of the present PVA model, each of these factors should be simulated using the same type of functional relationship constructed for Hg-mediated demographic impairment as described earlier in this report. Unfortunately, the data required to develop such relationships for all of these factors are not yet available. We are therefore restricted at present to using a different approach to exploring the impact of these other factors. Specifically, we can use a more "generic" method of manipulating those parameters we believe are impacted by the factors discussed here across a range of plausible values, and taking note of how much change is required in that parameter to achieve a desired change in population growth rate. This may offer some insight into how much management activity is required to observe that desired change, and could lead to an informed mode of prioritization around which management activities to adopt more rapidly than others.

Conclusions

This report describes in detail a population viability analysis for the San Juan River population of the Colorado pikeminnow. Concluding remarks are outlined below in the context of the objectives of the analysis, first presented in the Introduction.

- Develop a realistic and credible model of current Colorado pikeminnow population dynamics in the San Juan River

  The model described in this report utilized the full range of relevant demographic and ecological information and data currently available on the Colorado pikeminnow populations of the Colorado River Basin. Where necessary, data on pikeminnow populations from the Green and Upper Colorado River subbasins were adapted for use in our model of the San Juan River subbasin population. Furthermore, when data from other species were used to develop specific parameter values, assumptions were clearly stated and limitations of their use were explained.

We developed two model scenarios that attempt to describe with some realism the demographic dynamics of the San Juan River population of the Colorado pikeminnow: first, a population in rapid decline in the presence of multiple threat factors (proportional threat severity not quantitatively specified), and second, a population threatened by these same factors but maintained with relatively constant abundance through dedicated annual stocking of Age-0 pikeminnow in accord with actual practice. Both of these scenarios yield projections of future population abundance that are in general agreement with expectations based on past and present observations of pikeminnow population dynamics. Consequently, the PVA Team declared their acceptance of these scenarios as building blocks for future viability analysis.

As explained in the Introduction to this report, the models used here are not of sufficient realism and accuracy to allow us to confidently predict future pikeminnow population abundance. In fact, almost no PVA models can realistically make such a claim. Significant levels of measurement uncertainty around specific demographic / ecological parameters and processes preclude the use of PVA models for this purpose. Instead, we use these models to generate predictions of relative change in population growth and abundance when specific input parameters are changed according to our definitions of specific scenarios. These relative changes are much more robust in the face of this uncertainty, and can be used to gain important insight into how pikeminnow populations respond to proposed manipulations.

- <u>Identify specific demographic parameters – reproductive success, age-specific mortality, etc. – that are important drivers of population growth or decline</u>

  The sensitivity analyses presented here – including both elasticity analysis with respect to deterministic growth rate across the full suite of reproduction and survival parameters making up our model, and logistic regression of changes in population extinction risk in response to variation in these same rates – indicated that adult survival is an important driver of growth in Colorado pikeminnow populations. Care must be used, however, when interpreting these results in the context of future population management as the highly sensitive parameter may not be the target of threat factors that lead to population decline and risk of local extinction. This appears to be the case for Colorado pikeminnow, where recent declines in population abundance appear to be caused by very low levels of reproductive success among adult females, including survival of the earliest life stages. Management activities must first be directed at the major threats to long-term population growth; only when this condition is satisfied can managers begin to freely exploit parameter sensitivity to achieve specific population conservation outcomes.

- <u>Study in detail the impacts of specific anthropogenic processes – namely, deposition of mercury (Hg) in the river and resulting bio-accumulation in individual fish – on long-term pikeminnow population persistence</u>

  We implemented a detailed analysis of the rate of Hg accumulation in Colorado pikeminnow, the demographic impacts (% injury) of that accumulated burden, and the projected future increase in environmental Hg concentration in the San Juan River subbasin from local, regional and global industrial and other activities. We defined the demographic impacts in terms of fecundity among spawning females (offspring production), and age-specific survival across the full lifespan of the species.

  Under the assumptions built into our models, the analysis suggested that if we assume a constant environmental Hg burden into the future, we may expect reproductive success to be reduced by about 2% among newly-recruited adult females compared to those adults in an environment free of this type of Hg burden. As these females age, the % injury was expected to increase to an asymptotic maximum of about 5%. Under a reasonable model of future increase in environmental

Hg concentration in the San Juan River, these injury estimates may increase to approximately 3.5% to 9%, respectively. Injury to adult survival increases from approximately 0.35% to 0.85% under a static Hg burden, and from approximately 0.65% to 1.5% if environmental Hg concentrations are assumed to increase over time.

Under the assumption of an increasing environmental Hg burden in the San Juan River, the estimated injuries to both reproductive success and age-specific survival led to observable decreases in simulated pikeminnow population growth. The intensity of this population-level effect is itself likely to be a function of the underlying growth rate assuming no Hg-mediated impact. For example, if a population is already compromised by other threatening factors so that growth is very limited, the addition of demographic injury through Hg accumulation may result in a transition to population decline (i.e., negative growth rate). On the other hand, if a population is growing relatively strongly, the consequence of Hg-mediated impairment may be smaller. It is important to note that, while the absolute magnitude of injury to adult survival is less than that for adult reproductive success, the population-level impact is nearly equal. This is a result of the large sensitivity (elasticity) of our model to changes in adult survival described above.

We chose to focus on only two targets of Hg-mediated impairment: adult reproductive success and age-specific survival. Another potentially important target is impairment of individual fish behavior, which may lead to higher rates of demographic impairment than those used in this analysis (see Appendix C for more information on this issue). Consequently, we may be under-estimating the total extent of impairment from Hg accumulation in pikeminnow in the San Juan River. While acknowledging this simplification, we also recognize the difficulty in extrapolating data on behavioral impairment to specific estimates of reductions in reproduction and/or survival that may emerge from this process. Because of these significant uncertainties, the PVA Team elected to not include Hg-mediated behavioral impairment of pikeminnow in this analysis. More information and analysis is required before we can include this process more responsibly in our current analysis.

- <u>Identify other threatening factors that may be the target of future management activity designed to improve long-term chances of species persistence of pikeminnow in the San Juan River.</u>

  We discussed four factors that may also contribute to long-term changes in Colorado pikeminnow population abundance in the San Juan River: availability of nursery (backwater) habitat, predation by and competition with non-native fish species, entrainment of pikeminnow into unsuitable habitat or to regions outside of the model system, and reduced access to the full range of available habitat in the river system. We identified specific mechanisms for incorporating these factors into our *VORTEX*-based demographic model, and have briefly summarized the available data we could use to estimate relevant demographic parameters for appropriate model scenarios.

  With this information at our disposal, and given the informative model structure currently available, it is now possible to construct additional scenarios that explore management options that target these factors. The goal of these models would be to identify the extent of management necessary to achieve a specific desired future population state, whether defined by long-term population growth rate, mean long-term population abundance, etc. While the details of this future population state are at present unspecified, this state would include continued Hg deposition from a variety of sources, and may feature continued stocking of Age 0 individuals at some required rate if other threatening factors are not sufficiently managed.

Taken as a whole, it is the opinion of this report author that the general model described in these pages is of sufficient depth and realism to be regarded as a valuable tool for evaluating the relative response of a population of Colorado pikeminnow inhabiting the San Juan River to alternative future management scenarios. The extent of uncertainty present in these models makes it very difficult at best to generate an accurate prediction of future population abundance or extinction risk under any given threat scenario. In this sense, our imperfect understanding of pikeminnow biology and ecological processes leads to difficulties in deriving specific population performance targets, such as abundance, growth rate, extent of habitat occupied, etc., as long-term measures of recovery. Greater clarity on these issues will come with the collection of additional data on pikeminnow demography and ecology, hopefully guided by the insights gained by this first round of population viability analysis.

Acknowledgements

The information in this report represents the collective deliberation and analysis of information by the Colorado Pikeminnow PVA Team. The author wishes to express his sincere thanks to all Team members and associated participants for their dedication to the project and their professional approach to shaping and informing the process. Special thanks go to those experts formally constituting the Team: Dave Campbell, Scott Durst, Joel Lusk, Bill Miller, Mark Shibata, Rich Valdez, and Sharon Whitmore. Additional thanks to Robert Lacy (Chicago Zoological Society) for advice on *VORTEX* model development, and to Sara Zeigler (Virginia Tech) for assistance with conducting the logistic regression methods as part of the sensitivity analysis.

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Appendix A

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- Assesses progress of Colorado pikeminnow population toward recovery
- Evaluates SJRIP management activities to inform adaptive management

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- Senior Fish and Wildlife Biologist
- Employed with the Service for 20 years
- Works predominantly on pollution-related issues affecting fish and wildlife resources working with federal, state and tribal agencies, universities, and consultant and other environmental groups

Phil Miller, PhD – Conservation Breeding Specialist Group
- Senior Program Officer
- 20 years of experience in the development and implementation of population viability analysis (PVA) tools and processes across a broad diversity of species and human cultural backgrounds around the world
- Expert in design and facilitation of stakeholder-based species conservation planning workshops

William Miller, PhD – Miller Ecological Consultants, Inc.
- President and Senior Aquatic Ecologist
- Expertise in fishery, aquatic, instream flow, and ecological modeling studies

Mark Shibata, MS – Environmental Resources Management, Inc.
- Technical Director
- Expertise in risk assessment, communication and management

Rich Valdez, PhD – SWCA, Inc.
- Fisheries biologist
- 40+ years experience with the Colorado pikeminnow (1968-present); author or co-author of 30+ papers and reports on Colorado pikeminnow
- Co-author of 2002 Recovery Goals for Colorado Pikeminnow (2002)
- Member of Science Panel to evaluate predation by non-native fish on native fishes, including Colorado pikeminnow in the San Juan River (2010)
- Current Writing Team Coordinator for USFWS for revised Colorado Pikeminnow Recovery Plan (2013-14)

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Appendix B

Life History and Demographic Parameters of the Colorado Pikeminnow
R. Valdez

Life History and Demographic Parameters Of the Colorado Pikeminnow

For Population Viability Analysis

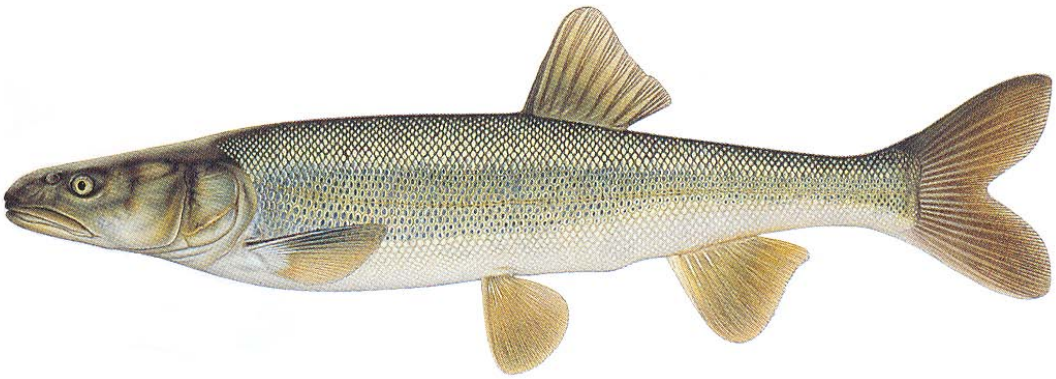

Illustration © Joseph R. Tomelleri

Life History and Demographic Parameters Of the Colorado Pikeminnow

For Population Viability Analysis

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Final Report
July 3, 2014

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Preface

The U.S. Fish and Wildlife Service is coordinating the development of a Population Viability Analysis (PVA) for the endangered Colorado pikeminnow (*Ptychocheilus lucius*). This PVA is intended to help inform the formal Section 7 consultation process for the Four Corners Power Plant and Navajo Mine Energy Project (FCPP & NMEP) in San Juan County, New Mexico. The PVA was developed and conducted by the Conservation Breeding Specialty Group (CBSG) using the Vortex 10 Population Viability Analysis software. This document is a synthesis of the life history and demographic parameters of the Colorado pikeminnow that helped to inform the structure of the demographic model for the PVA and provided first approximations of state and rate variables.

The wild population of Colorado pikeminnow in the San Juan River subbasin is small and there is little demographic and life history information available for the species from that subbasin. Wild populations in the Green River and Upper Colorado River subbasins are self-sustaining and represent the current understanding of demography and life history for the species in the wild. The information from these subbasins is used to better understand the likely life history strategies of the Colorado pikeminnow in the San Juan River, given the different geomorphic and biological settings of the subbasin.

This document is not intended to be an exhaustive treatise of the demographics and life history of the Colorado pikeminnow; rather, it is an assimilation of information pertinent to the PVA. Additional and more comprehensive information on the species can be found at the web sites of the Upper Colorado River Endangered Fish Recovery Program and the San Juan River Basin Recovery Implementation Program: http://www.coloradoriverrecovery.org/ and http://www.fws.gov/southwest/sjrip/.

The Colorado Pikeminnow is listed as “endangered” throughout its historic range in the states of Arizona, California, Colorado, New Mexico, Nevada, Utah, and Wyoming (and Mexico) in the List of Endangered and Threatened Wildlife and Plants (50 CFR 17.11 & 17.12) and is protected under provisions of the Endangered Species Act of 1973, as amended (ESA; 16 U.S.C. 1531 *et seq.*). A “nonessential experimental population” was designated in 1985 for the Salt and Verde rivers, Arizona (50 FR 30194), under Section 10(j) of the ESA.

Critical habitat was designated as 1,848 km of the Colorado River System on March 21, 1994 (59 FR 13374). Recovery plans for the Colorado Pikeminnow were approved March 16, 1978, and revised August 6, 1991; and recovery goals that amended and supplemented the 1991 plan were approved August 1, 2002. The Colorado Pikeminnow Recovery Plan is being revised during 2014.

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Much of the information contained in this document was assimilated and provided by members of the PVA Technical Team that served as principal technical experts on various aspects of the Colorado pikeminnow life history, the impact of mercury on fishes, and the San Juan River ecosystem. Specific contributions from members of the Technical Team are acknowledged in the body of this report. Additional thanks is extended to Dave Campbell, Scott Durst, Joel Lusk, Dr. Bill Miller, Dr. Phil Miller, Mark Shibata, Larry Wise, Alex Birchfield, Sharon Whitmore, Patty Corbetta, Brent Musslewhite, Kent Applegate, Richard Grimes, and Maria O'Brien for professional exchange of information and discussions, and for materials provided.

1.0 Range and Distribution

Wild populations of the Colorado pikeminnow remain in about 2,101 km (1,311 mi) of three subbasins of the Upper Colorado River Basin (Figure B1), as:

1. 1,278 km (798 mi) of the Green River subbasin, including the Green River and its tributaries (Yampa, White, Duchesne, Price, and Little Snake rivers) from Lodore Canyon, CO downstream to the confluence of the Colorado River, (Bestgen et al. 2010). Critical habitat in the Green River subbasin includes 984 km (614 mi).
2. 476 km (296 mi) of the Upper Colorado River subbasin, including the Colorado River and its tributaries (Gunnison and Dolores rivers) from Palisade, CO downstream to the Lake Powell inflow (Osmundson and White 2009). Critical habitat in the Upper Colorado River subbasin includes 574 km (358 mi).
3. 347 km (217 mi) of the San Juan River subbasin, including the San Juan River and its tributaries (Animas River, McElmo and Yellow Jacket creeks) from Farmington, NM downstream to Lake Powell, UT (Holden 1999). Critical habitat in the San Juan River subbasin includes 290 km (180 mi) of the San Juan River from the State Route 371 bridge at Farmington to Neskahai Canyon in the San Juan arm of Lake Powell (59 FR 13374).

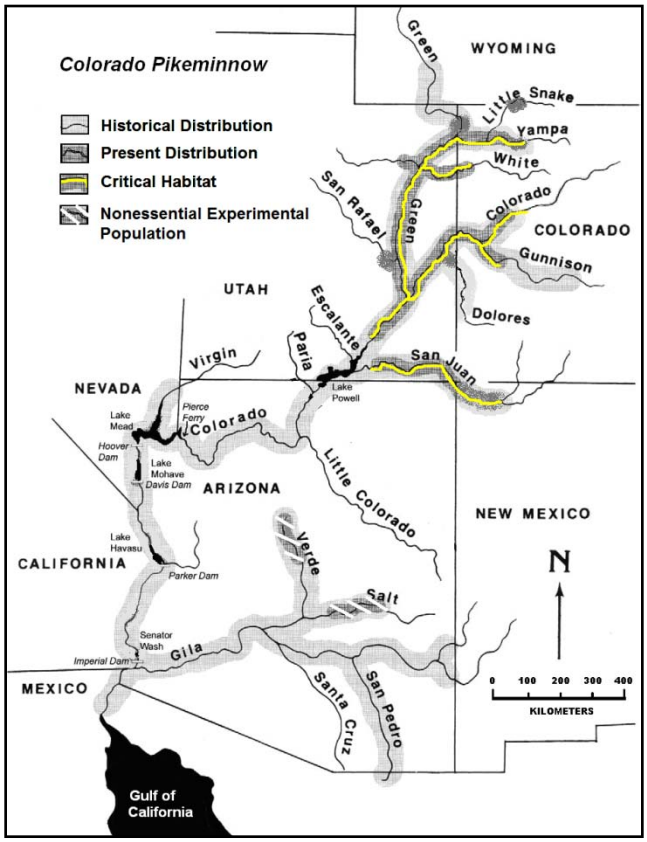


Figure B1. Distribution and critical habitat of the Colorado pikeminnow in the Colorado River System (U.S. Fish and Wildlife Service [USFWS] 2014).

2.0 Population Size

2.1 Green River Subbasin

The Green River population ranged from a low of 2,142 adults (age 7+, ≥ 450 mm total length [TL]) in 2003 to a high of 4,084 adults in 2000 (Table B-1, Figure B-2), with an overall average for the seven estimates of 3,020 adults, or about 4.0 fish/mi, although the fish are not evenly distributed (see also section 3.0, *Carrying Capacity*). Preliminary estimates for 2011–2013 range from 1,795 to 1,877 adults and are lower than all prior estimates.

2.2 Upper Colorado River Subbasin

The Upper Colorado River population ranged from a low of 440 adults in 1992 to a high of 889 in 2005 (Table B-1, Figure B-2), with an overall average for the 12 estimates of 658 adults, or about 2.2 fish/mi, although the fish are not evenly distributed. The sum of concurrent estimates for the Green River and Upper Colorado River subbasins was 4,857 adults in 2000; 2,803 adults in 2003; and 4,527 adults in 2008.

2.3 San Juan River Subbasin

The number of adult Colorado pikeminnow in the San Juan River is small and estimates of adults are not available as for the Green River and Upper Colorado River subbasins. Only 17 wild adults were captured in the entire San Juan River between 1991 and 1995, and it was surmised that there were probably 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 (*p*-hat).

Colorado pikeminnow in the San Juan River are currently being stocked as hatchery fish to reestablish the population; between 1996 and 2006, over 2.7 million fish were stocked (Ryden 2003b, 2004; personal communication, Dale Ryden, USFWS). About 8,400 stocked fish were recaptured during 2004–2006, with many fish having reached sexual maturity. The estimated number of age 2+ fish (> 150 mm TL) was 4,666 in 2009 and over 5,400 in 2010 (Elverud and Davis 2011).

2.4 Other Regions of the Colorado River System

Efforts to reestablish the Colorado pikeminnow have also taken place in the Lower Colorado River Basin. Over 623,000 Colorado pikeminnow were introduced into historic habitat in the Salt and Verde rivers, tributaries of the Gila River in Arizona, during 1981–1990 (Hendrickson 1994). These reintroductions were part of conservation efforts and the fish were classified as a “nonessential experimental” population in 1985 (50 CFR 17.11) under Section 10(j) of the Endangered Species Act of 1973, as amended (ESA, 16 U.S.C. 1531 *et seq.*). Colorado pikeminnow continue to be stocked annually into the Verde River by Arizona Game and Fish Department (Hyatt 2004) where small numbers persist, but with low survival and no evidence of natural reproduction (Robinson 2007).

Table B-1. Annual mark-recapture population estimates for adult Colorado pikeminnow (age 7+, **≥ 450 mm** TL) in the Green River subbasin and Upper Colorado River subbasin. N = population estimate, Low CI = lower 95% confidence interval, High CI = upper 95% confidence interval. Green River estimates are the sum of estimates for the Middle Green, Lower Green, Yampa, and White rivers, as well as the Desolation/Gray Canyon reach. Upper Colorado River estimates are for the Upper Colorado River and the lower 5 km (3 mi) of the Gunnison River below the Redlands Diversion.

Year	Green River Subbasin[a]			Upper Colorado River Subbasin[b]		
	Estimate	Low 95% C.I.	High 95% C.I.	Estimate	Low 95% C.I.	High 95% C.I.
1992	--	--	--	440	251	832
1993	--	--	--	705	448	1,181
1994	--	--	--	687	508	955
1995	--	--	--	--	--	--
1996	--	--	--	--	--	--
1997	--	--	--	--	--	--
1998	--	--	--	583	462	758
1999	--	--	--	589	466	764
2000	4084[c]			773	562	1,095
2001	3303	2900	3707	--	--	--
2002	2771	2216	3325	--	--	--
2003	2142	1686	2598	661	452	990
2004	--	--	--	688	511	946
2005	--	--	--	889	746	1,075
2006	2454	1920	3185	--	--	--
2007	2714	2055	3656	--	--	--
2008	3672	2397	5715	710	511	1535
2009	--	--	--	511	396	685
2010	--	--	--	493	393	692
2011	1813	--	--	--	--	--
2012	1795	--	--	--	--	--
2013	1877	--	--	--	--	--

[a] Estimates for 2000-2003 (Bestgen et al. 2005); estimates for 2006-2008 (Bestgen et al. 2010); estimates for 2011−2013 are preliminary (Bestgen 2014, pers. comm.).
[b] Estimates for 1992-2005 (Osmundson and White 2009); estimates for 2008-2010 (Osmundson and White 2014).
[c] Estimate of 4084 expanded from 3030 that did not include Desolation-Gray Canyon and Lower Green River to be comparable with estimates in other years for all regions of the Green River subbasin; estimates after 2000 included all reaches.

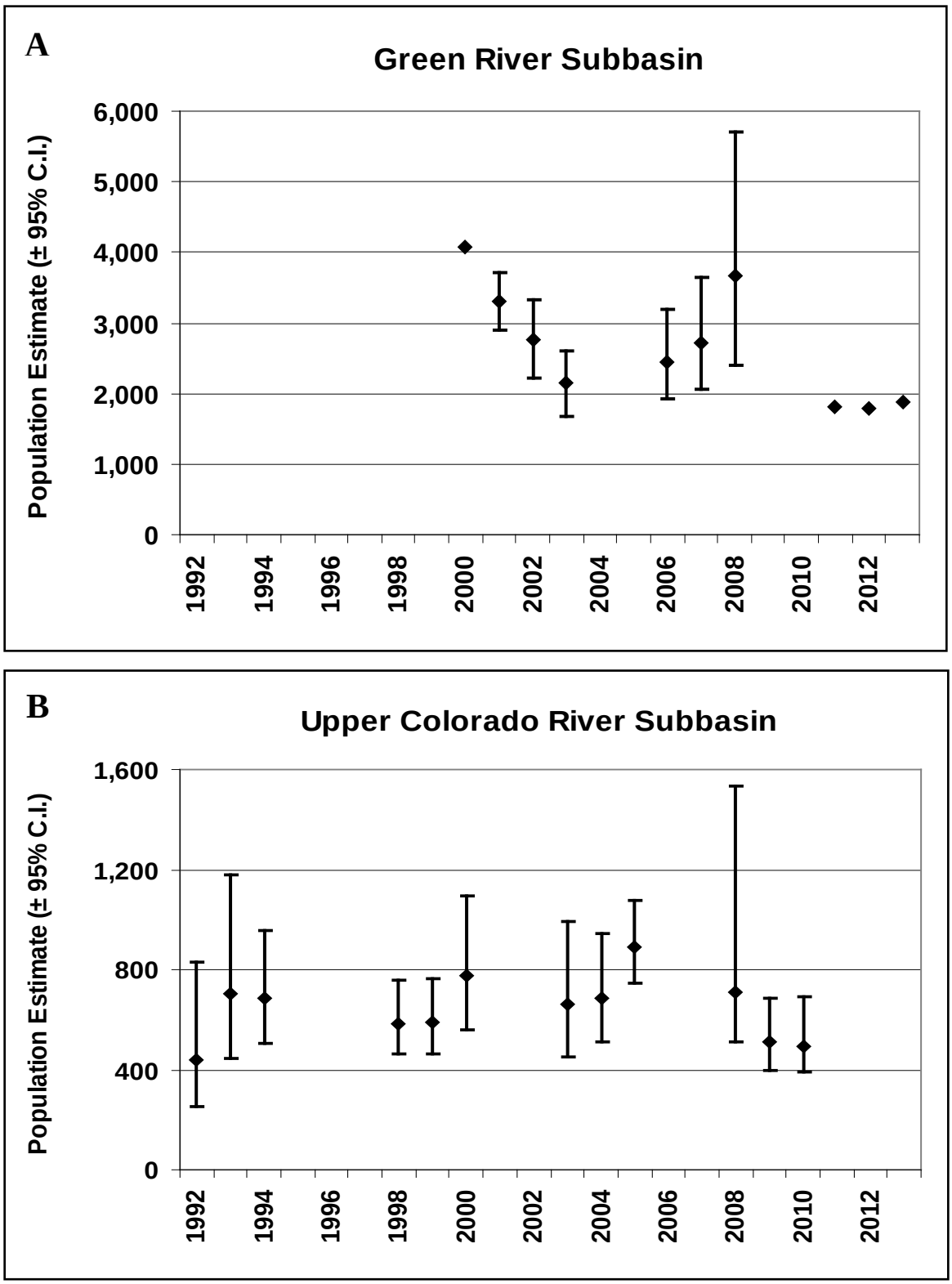


Figure B-2. Annual mark-recapture population estimates for adult Colorado pikeminnow (age 7+, **≥ 450 mm** TL) in the (A) Green River subbasin and (B) Upper Colorado River subbasin. See Table B-1 for estimates, 95% confidence intervals, and sources of data.

2.5 Intrinsic Population Growth Rate—Lambda

Based on annual population estimates provided in Table B-1, the intrinsic growth rates of Colorado pikeminnow for the Green River (2000–2008) and the Upper Colorado River (1992–2010) are 0.5% and 0.4%, respectively (Figure B-3). This indicates that for the periods examined the populations increased by 0.4% and 0.5% annually.

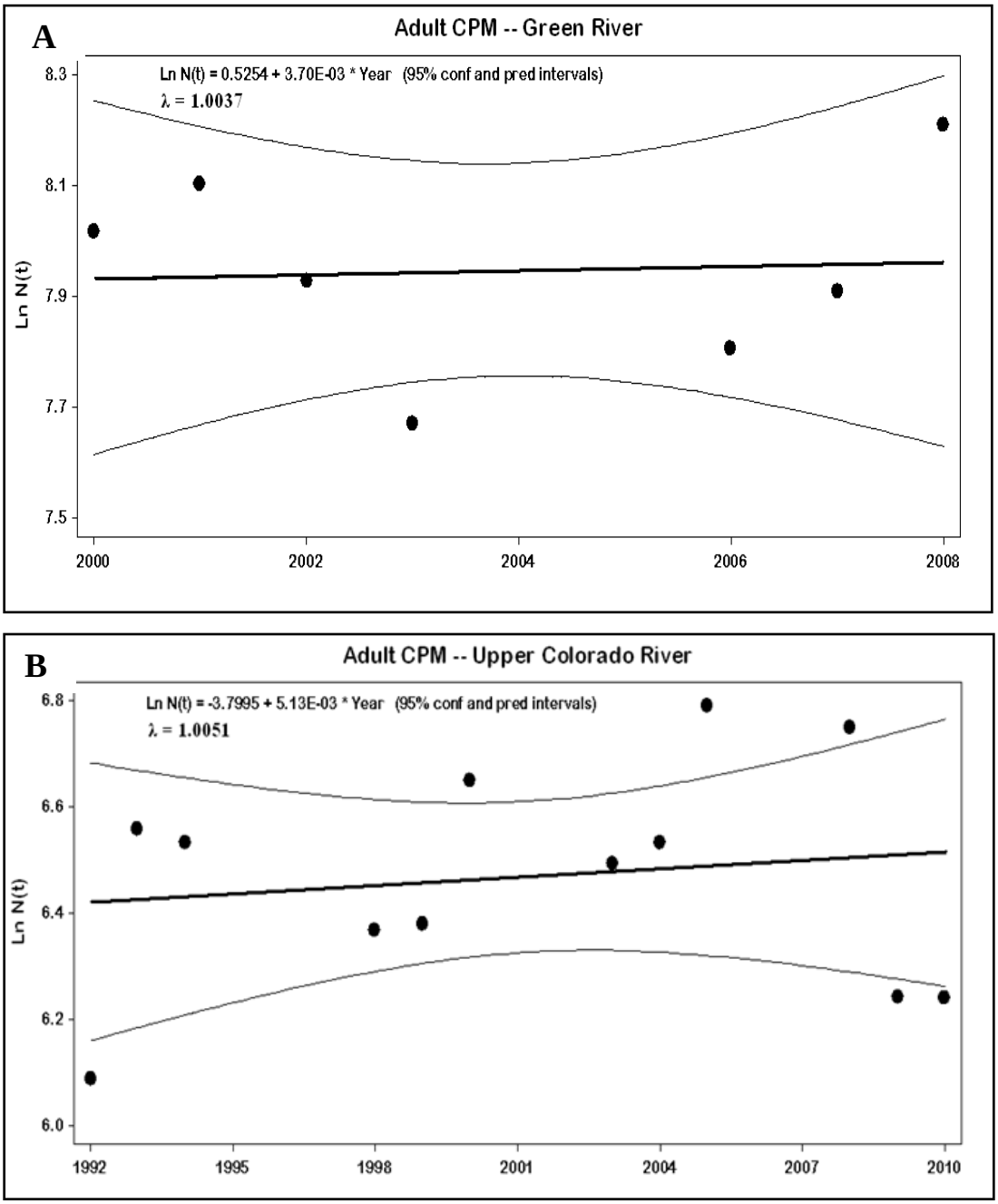


Figure B-3. Intrinsic growth rate for the Colorado pikeminnow (CPM) population, based on annual **population estimates and denoted as lambda (λ), for the (A) Green River subbasin and (B) Upper Colorado** River subbasin. See Table B-1 for population estimates.

3.0 Carrying Capacity

3.1 Green River Subbasin

Carrying capacity of Colorado pikeminnow populations is unknown but some inference is provided by estimates of catch rates and abundance and changes in body condition. During 1986–2000, the mean electrofishing catch rate of subadults and adults in the Green River steadily increased by four times from 0.9 fish/hr to 3.6 fish/hr (McAda et al. 1997), and the relative condition of adults declined, suggesting that the population was approaching carrying capacity. The population at maximum density was estimated at 4,084 adults in 2000 (Bestgen et al, 2005), or about 3.4 adults/km (4,084 adults/1,209 km), or 5.4 adults/mi (Table B-2). This is average density for the Green River subbasin where individual reaches likely have lower or higher densities of fish.

Table B-2. Estimated carrying capacity of adult Colorado pikeminnow for reaches included in abundance estimates. Estimate for the San Juan River is based on a bioenergetics model and not on number of fish currently in the system.

Subbasin	River Length (km)	Highest Estimate	No./km	No./mi
Green River	1,209	4,084	3.4	5.4
Upper Colorado River	286	1,051	3.7	5.9
San Juan River	290	406	1.4	2.3

3.2 Upper Colorado River Subbasin

Osmundson and White (2013) suggested that carrying capacity of the Upper Colorado River differs for the upper reach (106 km, 66 mi) and lower reach (180 km, 112 mi), primarily as a function of food availability (i.e., small-bodied forage fish), which is 4.5 times higher in the upper reach. The greatest abundance of adult Colorado pikeminnow (≥ 450 mm TL) in the upper reach was an estimated 477 adults in 2005, for a density of 4.5 fish/km (477 fish/106 km), or 7.3 fish/mi. The mean estimated number of fish in the lower reach ranged from 0.85 to 2.7 fish/km (1.4 to 4.4 fish/mi) with an annual mean of 1.6 fish/km (2.7 fish/mi). Assuming that carrying capacity of the lower reach is an annual average density of 1.6 adults/km and the upper-reach is a density of 7.2 fish/km, the two reaches combined might support an estimated 1,051 adults (2.7 fish/mi in the lower reach and 11.6 fish/mi in the upper reach, or 5.9 fish/mi combined), not counting the Gunnison River upstream of the Redlands Diversion. Osmundson and White (2013) concluded that population abundance in the Upper Colorado River is not currently limited by carrying capacity but rather by insufficient recruitment due to a low frequency of strong or moderately-strong year classes.

3.3 San Juan River Subbasin

Miller and Lamarra (2006) developed a population model for the San Juan River through the use of bioenergetics which included an estimate of the carrying capacity of Colorado pikeminnow. Using this model, they estimated that 800 adults (> 450mm TL) could be sustained in the San Juan River. This preliminary estimate was based on prey availability data collected only in the upper-most reach of critical habitat (geomorphic reach 6; Bliesner and Lamarra 2000). This estimate was based on the assumption that ongoing removal of channel catfish and common carp would allow small-bodied prey species to increase in numbers to densities similar to those found in reach 6, where common carp and channel catfish were absent and/or rare at the time. However, after 15 years of non-native fish removal, this

assumption has not proven to be true and densities of small-bodied fishes continue to be low downstream of reach 6.

Carrying capacity of Colorado pikeminnow for the San Juan River was recalculated in 2013 using the estimated densities of prey for each of the six reaches (Figure B-4). Based on these data, it was surmised that carrying capacity of Colorado pikeminnow would decrease similar to prey availability among reaches. The revised carrying capacity for the 180 mi (290 km) of river is 406 adults, or about 2.3 fish/mi (1.4 fish/km; Table B-3; Miller 2013). Key uncertainties for this estimate are densities of small-bodied fishes and the ability of Colorado pikeminnow to utilize these as a forage base.

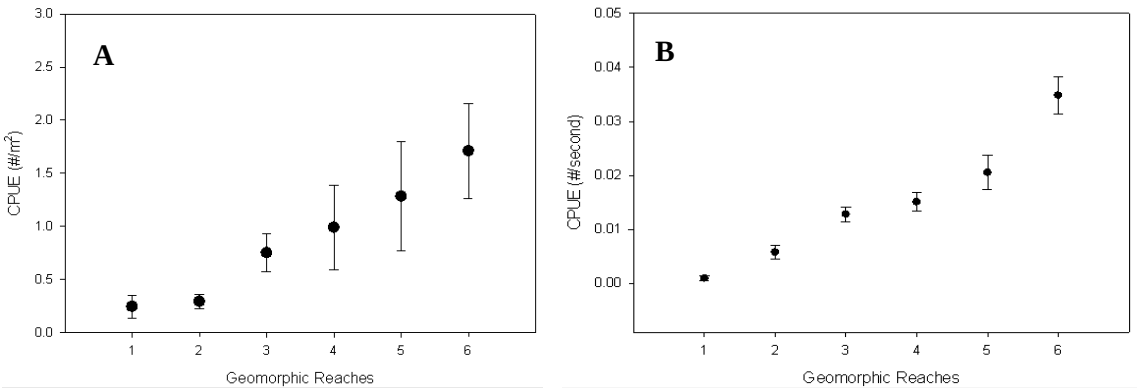


Figure B-4. Catch rate (CPUE) of forage fishes in six reaches of the San Juan River: (A) small-bodied fishes caught by seining of backwaters, secondary channels, and the primary channels, 2003-2011, and (B) juvenile fishes caught by electrofishing, 2003-2012. Mean +/-1 standard error (SE). Figures provided by the San Juan River Basin Recovery Implementation Program.

Table B-3. Estimated carrying capacity of adult Colorado pikeminnow in six geomorphic reaches of the San Juan River (Miller 2013). River miles are measured from Piute Farms (RM 0.0) upstream to about the confluence of the Animas River (RM 180.0).

Reach	Length (miles)	Total Adults	Number of adults/mile
1	0-16 (16)	16	1
2	17-67 (51)	51	1
3	68-105 (38)	38	1
4	106-130 (25)	75	3
5	131-154 (24)	96	4
6	155-180 (26)	130	5
Totals:	180	406	2.3

4.0 Stock-Recruitment

The relationships of spawners to recruits in the Green River and the Upper Colorado River were derived with Beverton-Holt and Ricker models to investigate the possibility of a density-regulated carrying capacity for the Colorado pikeminnow. These stock-recruitment relationships are determined by two parameters: α is the slope of the relationship from its origin, and β is the parameter that approximates carrying capacity.

4.1 Green River Subbasin

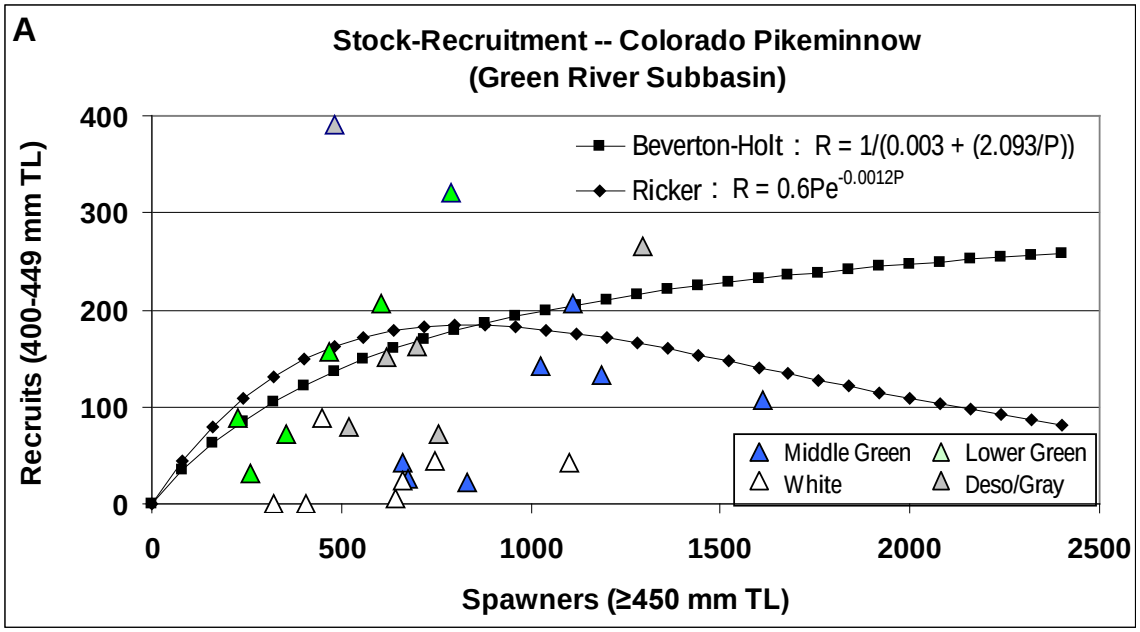
The Green River relationships were computed for the combined data from four reaches (middle Green, lower Green, and White rivers; and Desolation/Gray canyons). The pattern of data points for each reach clearly show different spawner-recruit relationships (Figure B-5, Table B-4). These relationships likely reflect the role of different river reaches in the life history of the species; i.e., the White River is used by adults for resting and feeding and has a low number of recruits, whereas the middle Green and lower Green rivers contain nursery areas with high numbers of young and recruits. These reach-specific relationships and the paucity of data for each reach (i.e., 7 years, 2000-2003, 2006-2008) precludes confident determination of density-dependence with these models.

4.2 Upper Colorado River Subbasin

The Upper Colorado River relationships are for the combined data from the lower and upper reaches, also with clearly different spawner-recruit relationships (Figure B-5, Table B-5). The upper reach is used primarily by adults for spawning and feeding and there are low numbers of recruits; whereas the lower reach is used primarily as a nursery area with high numbers of young and recruits. As with the Green River subbasin, these reach-specific relationships and the paucity of data for each reach (i.e., 9 years, 1992-1994, 1998-2000, 2003-2005) precludes confident determination of density-dependence with these models.

4.3 San Juan River Subbasin

There are currently insufficient data for spawners and recruits in the San Juan River to attempt any stock-recruitment relationships for that river system. The spawner-recruit relationships for the Green River and Upper Colorado River subbasins show that different river reaches probably have different stock-recruitment relationships and different carrying capacities. The different forages bases reported for the San Juan River (see section 3.3) indicate a similar phenomenon linked to the life history of the species. More data will be needed before stock-recruitment relationships can be reconciled for the Colorado pikeminnow.



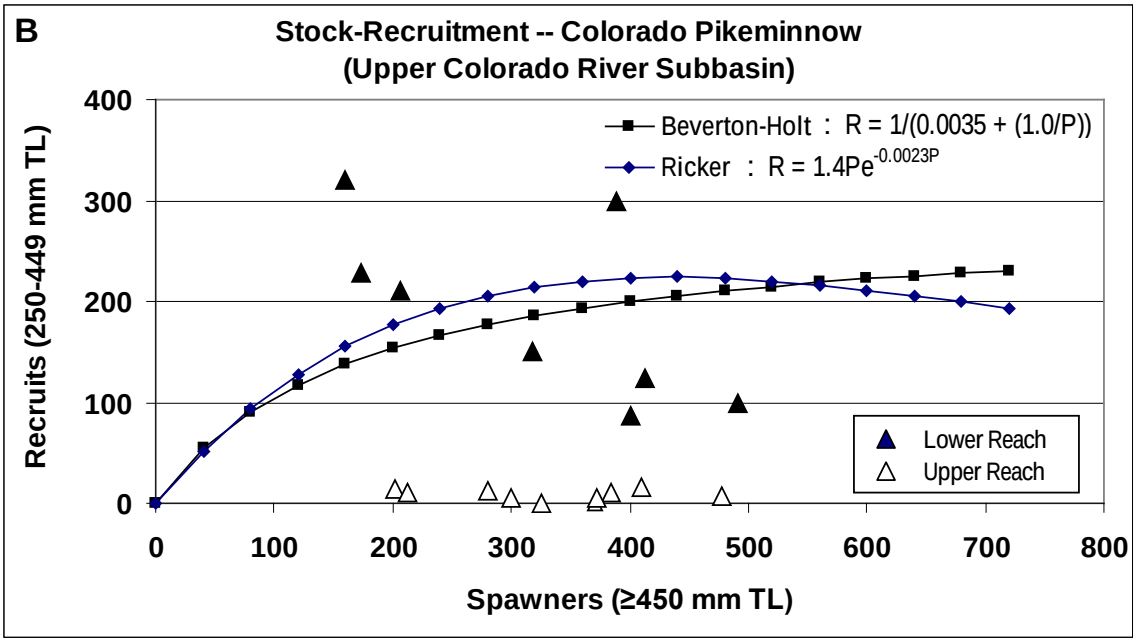


Figure B-5. Combined Beverton-Holt and Ricker stock recruitment curves predicting average recruitment rates at different stock sizes for Colorado pikeminnow in the (A) Green River subbasin, and (B) Upper Colorado River subbasin. Data for the middle Green, lower Green, and White rivers and Desolation/Gray canyons (n = 26) from Bestgen et al. (2005, 2010), and data for the lower and upper reaches (n = 19) of the Colorado River from Osmundson and White (2009), as presented in Tables 4 and 5, respectively.

Table B-4. Annual mark-recapture population estimates (2000-2008) for Colorado pikeminnow in portions of the Green River for adults (**≥ 450 mm TL), recruits (400**-449 mm TL), and juveniles (< 400 mm TL) used to generate the Beverton-Holt and Ricker curves shown in Figure B-5A. Data from Bestgen et al. (2005, 2010).

River/Reach	Life Stage	2000	2001	2002	2003	2006	2007	2008
White River	Adults	1100	746	643	407	321	451	660
	Recruits	43	45	5	0	0	88	24
	Juveniles	--	--	--	--	0	13	83
Middle Green River	Adults	1613	1184	834	663	674	1026	1109
	Recruits	107	133	22	43	25	142	207
	Juveniles	--	--	--	--	6	97	124
Deso/Gray Canyon	Adults	--	699	757	621	519	484	1296
	Recruits	--	163	72	152	79	391	265
	Juveniles	--	--	--	--	182	87	105
Lower Green River	Adults		355	261	227	791	604	467
	Recruits	--	71	31	89	321	207	157
	Juveniles	--	--	--	--	987	212	163
Combined[1]	Adults	3030[2]	3303	2771	2142	2454	2714	3672
	Recruits	150	412	130	284	425	828	653
	Juveniles	--	--	--	--	1175	409	475

[1]Combined totals are sums of independent estimates and do not correspond to estimates in Table B-1 which are based on the total of fish marked and recaptured

[2]Estimate of 3030 did not include Desolation/Gray Canyon and Lower Green River; estimate of 4084 in Table B-1 was expanded for entire Green River subbasin to be comparable with other years

Table B-5. Annual mark-recapture population estimates (1991-2005) for Colorado pikeminnow in two reaches of the Upper Colorado River for adults (**≥ 450 mm TL) and recruits (250**-449 mm TL) used to generate the Beverton-Holt and Ricker curves shown in Figure B-5B. Data from Osmundson and White (2009).

Reach	Life Stage	1991	1992	1993	1994	1998	1999	2000	2003	2004	2005
Lower	Adults	--	160	492	317	174	206	400	337	388	412
	Recruits	--	320	98	150	229	210	88	856	299	124
Upper	Adults	202	280	213	370	410	384	373	325	299	477
	Recruits	15	12	11	0	16	11	5	0	6	7
Combined	Adults	--	440	705	687	584	590	773	662	687	889
	Recruits	--	332	110	150	245	221	93	856	305	131

5.0 Survival

5.1 Green River Subbasin

Bestgen et al. (2005, 2010) estimated average annual survival for adult males and females (≥ 450 mm TL) from the Green River subbasin as 82% during 1991–1999, 65% during 2001–2003, and 80% during 2006–2008. From 2000 to 2003, the population declined from 4,084 to 2,142 adults for an apparent decline of 48%. Recruitment was low during that period, with the proportion of recruits (400–449 mm TL) < 10% of the adult population, far less than the estimated average annual adult mortality of 35%. Reasons for this decline are not understood, but the low recruitment was concurrent with drought conditions leading to low streamflows and increases in numbers and distributions of non-native fishes, such as smallmouth bass (*Micropterus dolomieu*), particularly in the Yampa River, the principal spawning area for this population. For the period 2003 to 2008, the population of Colorado pikeminnow increased from 2,142 to 3,672 adults, an apparent increase of 71%, and overall the population increased slightly (see Table B-1). Abundance of recruits during 2006–2008 averaged 22% (17.4% to 30.4%) of estimated adult abundance, which was more than sufficient to offset overall estimated adult mortality (20%). Preliminary estimates of adults in the Green River indicate a decline for the period 2011–2013 compared to previous estimates (see Table B-1).

Overwinter survival of age-0 fish showed a significant relationship between densities in the fall and spring, suggesting that high spawning success and egg and larval survival by fall (i.e., 3–4 months of age) largely determine cohort strength (Valdez et al. 1999; Converse et al. 1999; McAda and Ryel 1999). Overwinter survival also influences cohort strength, but the linkage to environmental correlates (e.g., flow variability, river temperature and ice formation, average backwater depth, and non-native fish density) was unclear. Overwinter survival (October–March) of age-0 fish in backwaters of the upper Green River, based on the difference between fall and spring seine catch rates for 1989, 1990, 1991, 1992, and 1993 was 96, 29, 31, 38, and 62% (mean, 51%), respectively (Valdez et al. 1999). Survival was highest (85%) in backwaters deeper than 120 cm and lowest survival (18%) in backwaters less than 30 cm deep.

5.2 Upper Colorado River Subbasin

Osmundson and White (2009) estimated survival of adults ≥ 500 mm TL as 88.2% (95% CI = 85–91%) during 1991–1994, 85.9% (95% CI = 81–89%) during 1998–2000, and 80.4% (95% CI = 66–90%) during 2003–2005. The Upper Colorado River population ranged from a low of 440 adults in 1992 to a high of 889 in 2005 (Osmundson and White 2009). During 2003–2005, the estimated number of adults was 661 in 2003, 688 in 2004, and 889 in 2005, with a 3-year average of 746. The average annual survival of adults over the three sample periods was 85%, and annual abundance of recruits (400–449 mm TL) exceeded annual adult mortality in 6 of the 9 years. When annual gains and loses were summed for 1992–2005, there was an estimated net gain of 332 adults in the Upper Colorado River population. The overall average of the six adult survival estimates for the two populations (Green and Colorado rivers) was 80%, which is similar to the estimated annual survival rate of adults computed by Gilpin (1993) from length distribution.

Overwinter survival of age-0 fish in the Upper Colorado River ranged 7–77% (mean, 49%; McAda and Ryel 1999). Overwinter survival of age-0 Colorado pikeminnow in Green River backwaters, based on mark-recapture population estimates, ranged 6–62% (mean, 45%), compared to catch rate estimates for the same period of 11–49% (mean, 34%; Haines et al. 1998).

5.3 San Juan River Subbasin

Estimated survival of Colorado pikeminnow for ages 1−3 were determined from changes in mark-recapture abundance estimates of stocked fish (Figure B-6, Table B-6). These survival estimates are based on the time interval from stocking in late summer/fall to the next census 1 year later; whereas survival rates presented in Table B-7 are for a different interval of time for wild fish of the Green and Upper Colorado rivers.

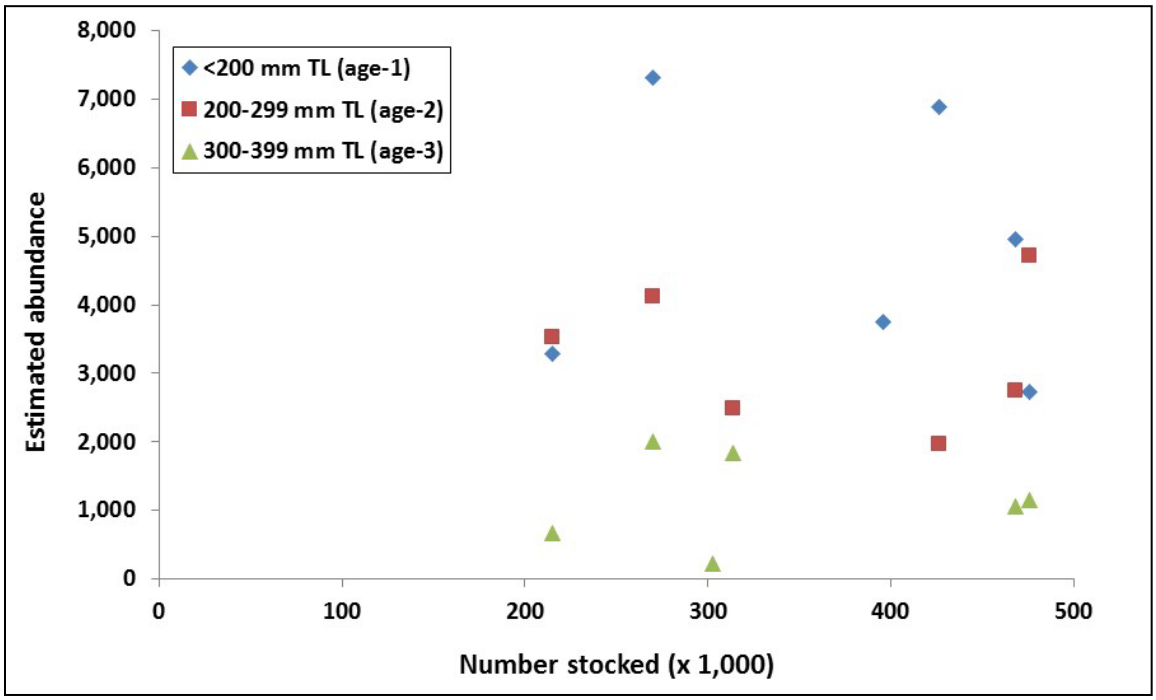


Figure B-6. Estimated abundance of age-1, age-2, and age-3 Colorado pikeminnow after having been stocked in the San Juan River at age-0. Figure provided by Scott Durst (USFWS).

Table B-6. Estimated survival of Colorado pikeminnow in the San Juan River based on mark-recapture abundance estimates from stocking at age-0 to ages 1−**3. Data and analysis provided by Scott Durst** (USFWS).

Statistic	Age-0 to Age-1	Age-1 to Age-2	Age-1 to Age-2	Age-2 to Age-3
Mean	0.014	0.841	0.467	0.409
SD	0.007	0.573	0.157	0.217
CV	0.531	0.682	0.336	0.53

5.4 Summary of Survival Estimates

A considerable amount of literature was reviewed and evaluated in deriving survival estimates for the Colorado pikeminnow. A summary of preliminary survival estimates used in the PVA by life stage and time step is provided in Table B-7. Survival estimates are provided for eggs and ages 0 through 7+.

Eggs and Age 0.—Estimates of egg survival were determined from Hamman (1986) in which he injected and manually striped hatchery-reared 9 and 10-year old fish at Willow Beach National Fish Hatchery. The eggs were held at 22ºC in Heath trays or jars, and the number of viable eggs enumerated after 48 hr of the stated 100-hr incubation period. Estimates of egg survival were computed for Table B-7 by expanding the 48-hr viability counts to estimated viability after 100 hr of incubation (to hatching).

Age 0, Phase a (7 d hatch to swim-up).—Survival was estimated as the numbers of larvae counted by Hamman (1986) 5-7 days after hatching, or at the time of swim-up, compared to the number of viable eggs after 100 hr of incubation.

Age 0, Phase b (50 d post-swim-up).—Survival was estimated as the numbers of larvae surviving in outdoor earthen ponds 50 days after swim-up (Hamman 1989). These fish were 57 days of age (i.e., 7 days from hatch to swim-up + 50 days in the ponds). Daily survival was computed for fish held in each of three separate ponds (48, 49, and 51 days), and average survival was computed for a standardized period of 50 days.

Age 0, Phase c (90 d post-swim-up).—Survival was estimated as the numbers of larvae surviving in outdoor earthen ponds from day 51 to day 90 following swim-up (Hamman 1989). These fish were 58-97 days of age (i.e., 57 days from hatching + 40 days in the ponds). Daily survival was computed for fish held in each of two separate ponds (36 and 40 days), and average survival was computed for a standardized period of 40 days.

Age 0, Phase d (6 mo overwinter survival).—Survival was estimated as the numbers of young surviving in natural backwaters of the Green and Upper Colorado rivers from October 1 to March 31 (Valdez and Cowdell 1996). These fish were 98-278 days of age. Survival for the period between collections was computed from catch-per-effort (CPE) of fish seined in backwaters in fall and in the following spring (backwaters remained open to the river without confinement to fish movement). Daily survival was computed for each of 7–9 years, standardized for 6 months and averaged.

Age 0, Phase e (3 mo post-winter survival).—Survival was estimated from the monthly survival computed from catch rates of young in natural backwaters of the Green and Upper Colorado rivers (Valdez and Cowdell 1996) and applied to the period April 1 to June 3. This may be an underestimate of survival because it is based on the winter period when survival is believed to be low; nevertheless, this period encompasses the spring runoff, when flows are high and fish are being displaced from habitats and exposed to predators and possibly food shortages. These fish were 279 – 365 days old.

Age 1.— Survival was estimated as the numbers of young surviving in natural backwaters of the Green and Upper Colorado rivers from October of one year to the following October (Valdez and Cowdell 1996).

Age 2.—Survival was estimated as the proportions of fish surviving from one age to the next, based on mark-recapture population estimates of stocked fish in the San Juan River (Data provided by S. Durst, USFWS 2014).

Age 3.—Survival was computed from a survival relationship provided by Bestgen et al. (2007). The relationship is for fish 340−900 mm TL (ages 5−20+) and was applied to fish 200 mm TL as age 3. The conversion of length to age was determined from a von Bertalanffy relationship by Hawkins (1992) (see section 7.0 Age and Growth).

Ages 4–7+.—Survival was computed from survival curves of wild fish from the Upper Colorado River (Osmundson and White 2009). The average of survival for the "upper reach" and the "lower reach" were used for a specified fish length that corresponded to age from a von Bertalanffy relationship by Hawkins (1992).

Table B-7. Summary of survival estimates by age for the Colorado pikeminnow PVA. Age-specific survival is in bold numbers.

Age	Life Stage (Phase a – d)	Time Step	Average Fish Size (mm TL)	Measured at End of Time Step		Citation
				Proportion Surviving	Cumulative Survival by Age	
Egg	100 h egg hatching (Heath trays, jars)	0 – 4 d (pre-hatch)	--	0.3145	0.3145	Hamman (1986)
Age 0	a. 7 d hatch to swim-up (Heath trays, jars)	0 – 7 d (July 1 hatch)	10	0.5651	0.5651	Hamman (1986)
	b. 50 d post-swim-up (outdoor earthen ponds)	7 – 57 d	20	0.3237	0.1829	Hamman (1989)
	c. 90 d post-swim-up (outdoor earthen ponds)	58 – 97 d	40	0.9633	0.1762	Hamman (1989)
	d. 6 mo overwinter survival (natural backwaters)	98 – 278 d (Oct 1 – Mar 30)	60	0.3867	0.0681	Valdez and Cowdell (1996)
	e. ~3 mo from spring to first birthday	279 – 365 d (Apr 1 – Jun 30)	70	0.4614	0.0314	Valdez and Cowdell (1996)
Age 1	2nd full year of life	366 – 730 d (Jul 1 – Jun 30)	90	0.5472	**0.5472**	Valdez and Cowdell (1996)
Age 2	3rd full year of life	721 – 1095 d (Jul 1 – Jun 30)	140	0.7294	**0.7294**	Durst (2014)
Age 3	4th full year of life	1096 – 1460 d (Jul 1 – Jun 30)	195	0.8470	**0.8287**	Bestgen et al. (2007)
Age 4	5th full year of life (computed from mark-recapture of wild fish)	1461 – 1825 d (Jul 1 – Jun 30)	260	0.7250	**0.7250**	Osmundson and White (2009)
Age 5	6th full year of life (computed from mark-recapture of wild fish)	1826 – 2190 d (Jul 1 – Jun 30)	335	0.7700	**0.7700**	Osmundson and White (2009)
Age 6	7th full year of life (computed from mark-recapture of wild fish)	2191 – 2555 d (Jul 1 – Jun 30)	400	0.8200	**0.8200**	Osmundson and White (2009)
Age 7+	8th full year of life (computed from mark-recapture of wild fish)	2556 – 2920 d (Jul 1 – Jun 30)	≥ 450	0.8500	**0.8500**	Osmundson and White (2009)

6.0 Reproduction

6.1 Maternity

Maternity is defined in this document as the number of eggs produced by a female as indicated by the number of eggs manually stripped from a fish. The number of eggs per female Colorado pikeminnow varies considerably as reported. An estimated 55,000 eggs were manually stripped from five injected wild fish for an average of 11,000 eggs/fish; at an average fish size of 681 mm TL and 2,824 g, maternity was 3,895 eggs/kg (Table B-8; Hamman 1981). Maternity of 10 injected hatchery-reared females was 78,540 eggs for an average of 10,542 eggs/kg.

Hamman (1986) later induced spawning of hatchery-reared Colorado pikeminnow that were 9 and 10 years old. Average maternity of injected hatchery-reared 9-year old females (n = 24) was 77,400 eggs (range, 57,766–113,341) or 55,533 eggs/kg, and average maternity of 10-year old females (n = 9) was 66,185 eggs (range, 11,977–91,040) or 45,451 eggs/kg (Table B-9; Hamman 1986).

Table B-8. Summary of spawning data for Colorado squawfish at Dexter National Fish Hatchery, New Mexico. Table from Hamman (1981).

Locale: Fish	Fish Age	Fish Size	Average Eggs/Fish	Eggs/kg	Citation
WBNFH[a]: 5 injected wild females	unknown	681 mm TL 2,824 g	55,000 / 5 = 11,000	3,895	Hamman (1981)
WBNFH: 10 injected hatchery-reared females	6	429 mm TL 681 g	78,540 / 10 = 7,854	10,542	Hamman (1981)
DNFH[b]: 24 injected hatchery-reared females	9	1,403 g (572 mm TL)[c]	77,400 (57,766–113,341)	55,533	Hamman (1986)
DNFH: 9 injected hatchery-reared females	10	1,464 g (579 mm TL)[c]	66,185 (11,977–91,040)	45,451	Hamman (1986)

[a] WBNFH = Willow Beach National Fish Hatchery, Willow Beach, AZ.
[b] DNFH = Willow Beach National Fish Hatchery, Willow Beach, AZ.
[c] Derived from length-weight relationship for Green River: $Log_{10}W = -5.692 + 3.206 * Log_{10}L$ (Hawkins 1992).

Table B-9. Summary of spawning data for Colorado squawfish during May-Jun 1983 and 1984 at Dexter National Fish Hatchery, New Mexico. Table from Hamman (1986).

Value	Weight of fish (g)	Eggs per female	Eggs per kg body weight
1983: 24, 9-year-old females			
Minimum	1,045	57,766	37,695
Maximum	2,045	113,341	66,452
Mean	1,403	77,400	55,533
1984: nine, 10-year-old females			
Minimum	1,182	11,977	7,984
Maximum	1,727	91,040	61,135
Mean	1,464	66,185	45,451

6.2 Temperature Requirements

The Colorado pikeminnow is an obligate warm-water species that requires relatively warm temperatures for spawning, egg incubation, and survival of young. Spawning activity begins after the peak of spring runoff during June–August at water temperatures typically 16°C or higher (Vanicek and Kramer 1969; Hamman 1981; Muth et al. 2000). In the lower Yampa River, reproduction was initiated within days of mean daily water temperature exceeding 18°C, with water temperature at initiation ranging 16.0–22.3°C on the Yampa River and 19.8–23.0°C on the lower Green River (Bestgen et al. 1997). As a rule of thumb, Colorado pikeminnow usually spawn at about the time of the summer solstice.

Colorado pikeminnow are broadcast spawners that scatter adhesive eggs over cobble substrate which incubate in interstitial spaces. In a laboratory setting, hatching success was greatest at 20–24°C with incubation time of 90–121 h (Hamman 1981; Marsh 1985). The eggs in the wild incubate in gravels for about 5 days. Newly hatched larvae are 6.0–7.5 mm long (Hamman 1981), which emerge from spawning cobbles 3–15 days after hatching and drift predominantly as protolarvae (Haynes et al. 1984; Nesler et al. 1988).

6.3 Sex Ratio

The information on sex ratio is highly variable because most observations have been made from field sampling during a short interval of the total spawning event. Generally, high turbidity precludes direct observation of spawners and fish are captured with trammel nets over spawning bars. Male to female ratios reported from catches over spawning bars are 9:1 (Holden and Stalnaker 1975), 13.85:1 (Tyus 1990), and 5.6:1 (Seethaler 1978). Ratios of active males to females visually observed spawning naturally under hatchery conditions are 2:1, and 2–3:1 (Hamman 1981). Colorado pikeminnow sampled from an Upper Colorado River spawning site in 1994, 1998, and 1999 (USFWS, unpublished data) yielded 42 different fish including 21 running ripe males and one running ripe female (21:1). Inclusion of suspected males (four) and females (12), however, resulted in a ratio of 1.9:1 (the gender of four fish was undetermined).

Because of the disparate empirical data from spawning bar surveys, Lentsch et al. (1998) used a consensus of biologists at a workshop to arrive at a species-wide male:female ratio of 4.5: 1 for calculating N_e, but Crowl and Bouwes (1998) used a sex ratio of 3:1 to develop a population model for the Colorado pikeminnow; this ratio was used in the 2002 Recovery Goals. New information shows a sex ratio of 1.11:1.0 from examination of 301 adults (> 250 mm) sampled in the Upper Colorado River subbasin in 1999 and 2000 (Osmundson 2006). The sex ratio of 1.11:1.0 is the currently acceptable ratio.

7.0 Age and Growth

7.1 Maximum Age and Size

The oldest Colorado pikeminnow documented from scale annuli were 11 years (610 mm TL) from the Green River (Vanicek and Kramer 1969; Seethaler 1978); 16 years from the White River; 12 years from the Upper Colorado River (Hawkins 1992); and 13 years (879 mm TL; Musker 1981) and 18 years (2 fish average of 804 mm TL; Hawkins 1992) from the Yampa River. Osmundson et al. (1997) cautioned that scale-based age estimates are probably unreliable for Colorado pikeminnow beyond about age 10, and concluded from growth-rate data that large fish (e.g., > 900 mm TL) average 47–55 years old with a minimum age of 34 years. The discrepancy in age determination has not been resolved, but scale-based age determination may not be reliable because of closely-spaced and indistinguishable annular rings caused by slowed growth of old fish, and possibly because scale resorption erodes, distorts, or eliminates one or more annular rings.

It appears that the first scale annulus does not form on the Colorado pikeminnow, and the first visible annulus reflects the second winter of life (Musker 1981; Hawkins 1992). Average length at the end of the second annulus formation ranged 90–123 mm TL (Hawkins 1992). The maximum length of fish collected in the wild is just over 800 mm TL. Asymptotic lengths, based on scale back-calculations and derived from Walford plots, indicate that maximum potential length of Colorado pikeminnow in the upper basin is 1,152 mm TL (Hawkins 1992). Historical accounts of fish in the lower basin indicate a maximum length of about 1.8 m TL. Kaeding and Osmundson (1989) hypothesized that growth and overall size of Colorado pikeminnow in the upper basin is limited by a more restrictive and cooler temperature regimes than in the lower basin.

7.2 Maturity

Vanicek and Kramer (1969) found that nearly all fish from the Green River age 7 and older (estimated at 454 mm TL from scale back-calculated lengths) were sexually mature. Seethaler (1978) determined that age-7 Colorado pikeminnow from the Green and Yampa rivers averaged 451 mm TL (scale back-calculations). He also necropsied 147 Colorado pikeminnow between 184 and 652 mm TL and found that all fish longer than 503 mm TL were sexually mature, and fish less than 428 mm TL were immature; 76% of 34 fish examined between 428 and 503 mm TL were sexually mature. Hamman (1986) found that hatchery-reared Colorado pikeminnow were sexually mature at age 5 (males) and age 6 (females) at total lengths of 317–376 mm and 425–441 mm, respectively. Osmundson et al. (1997) found that all fish examined were sexually mature at age 7 or 450 mm TL. Osmundson (2006) further examined wild fish and found that males were mature at 6 years and females were mature at 8 years; males spawned as early as 6 years with most at 8 years; most females did not spawn until age 9 and more likely 10 years of age.

7.3 Growth Rates

Age at length information for Colorado pikeminnow is available from several sources (Vanicek and Kramer 1969; Seethaler 1978; Musker 1981; Hawkins 1992; Osmundson 2002). Larvae at hatching are 6.0–7.5 mm long (Hamman 1981) and average about 40 mm TL (range, 29–47 mm) in October at about 3 months of age (Valdez 1990; Tyus and Haines 1991). Growth under laboratory conditions averaged about 13 mm/30 days (Hamman 1981). Growth of adults in the Green River was about 10.2 mm/year (Tyus 1988). Mean annual growth rate of fish from the Upper Colorado River aged 3–6 years ranged from 32.2 (age 6) to 82.0 (age 3) mm/year and declined to 19.8 mm/year for fish 500–549 mm TL (Osmundson et al. 1997); fish ≥ 550 mm TL grew an average of 9.5 mm/year. Preliminary evidence

indicates that females grow larger and perhaps live longer than males (Vanicek 1967; Tyus and Karp 1989).

Hawkins (1992) surmised that because Colorado pikeminnow hatch in late summer, they either fail to form scales in their first winter or fail to form a first annulus. He assumed that all previous studies had missed the first annulus, and determined that age-7 fish averaged 396 mm TL, and age-8 fish averaged 440 mm TL. Hawkins defined mature Colorado pikeminnow as fish over 428 mm TL, based primarily on findings of Seethaler (1978). Osmundson et al. (1997) used growth-rate data from mark-recapture information and scale back-calculations from fish of the Upper Colorado River subbasin and determined that age-7 Colorado pikeminnow averaged 456 mm TL (range, 430–479 mm TL). Mark-recapture, growth-rate data from Osmundson (2002) were also used to develop length to age relationships. Based on the best available information on age at sexual maturity and age to length relationships, adult Colorado pikeminnow are defined as fish that are 450 mm TL or larger. This is based on the conservative assumption that all age-7 fish are sexually mature, and average length at age 7 is 450 mm TL. Subadults (age 6) are defined as those fish that are 400–449 mm TL.

A list of von Bertalanffy parameters for Colorado pikeminnow from different rivers of the upper basin is presented in Table B-10, and the graphical representations of each are presented in Figure B-7. The $L\infty$ is the theoretical maximum length of the fish, the K is the growth coefficient or the annual rate of growth, and t_o is the point in time at which the fish has zero length.

Table B-10. Growth parameters of Colorado pikeminnow for von Bertalanffy function.

Citation	Years	River	n	$L\infty$	K	t_o
Vanicek and Kramer (1969)	1964-66	Green	182	1144	0.07475	0.64959
Seethaler (1978)	1974-76	Green	68	752	0.15767	1.29628
Musker (1981)	1979-81	All	139	1147	0.08611	1.01437
Hawkins (1992)	1978-90	Green	116	1246	0.05347	0.43075
Hawkins (1992)	1978-90	White	48	781	0.09543	0.25031
Hawkins (1992)	1978-90	Yampa	148	1221	0.06675	0.60655
Hawkins (1992)	1978-90	Combined	326	1152	0.06293	0.58136
Osmundson and White (2009)	1991-2005	Colorado	--	865	0.0666	-0.0137

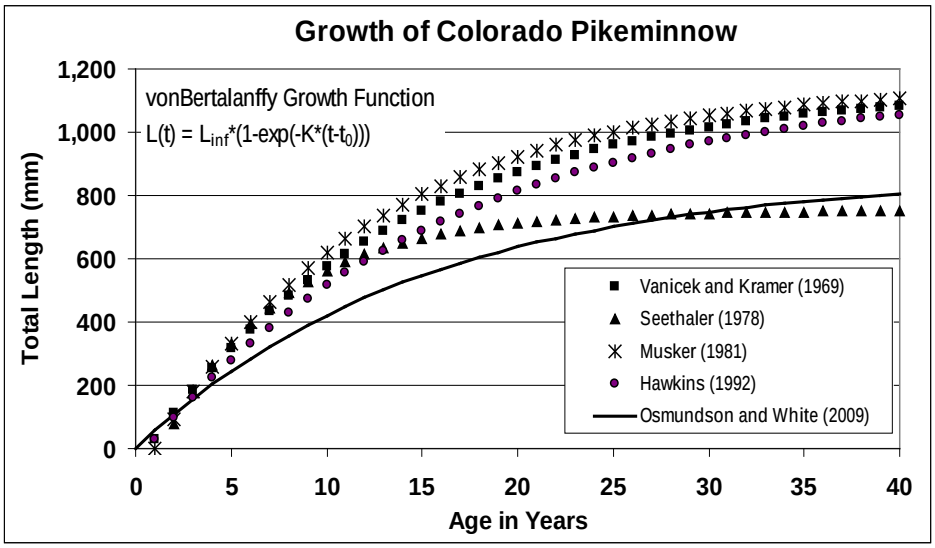


Figure B-7. Predicted length at age for Colorado pikeminnow computed from von Bertalanffy growth function. Based on parameters in Table B-10 from Vanicek and Kramer (1969), Seethaler (1978), Musker (1981), as presented in Hawkins (1992); and from Osmundson and White (2009).

The growth rates illustrated in Figure B-7 are for wild Colorado pikeminnow from various rivers of the Upper Colorado River Basin. Growth rates of wild Colorado pikeminnow from the San Juan River are not determined because of the small numbers of wild fish. A large number of age-0 Colorado pikeminnow (6–8 months of age) are stocked into the San Juan River annually and the growth rate of these known-age fish appears similar to wild upper basin fish (Figure B-8). However, stocked fish are larger than wild fish of the same age and age-at-length for Colorado pikeminnow from the San Juan River appears to be different than wild fish from the upper basin.

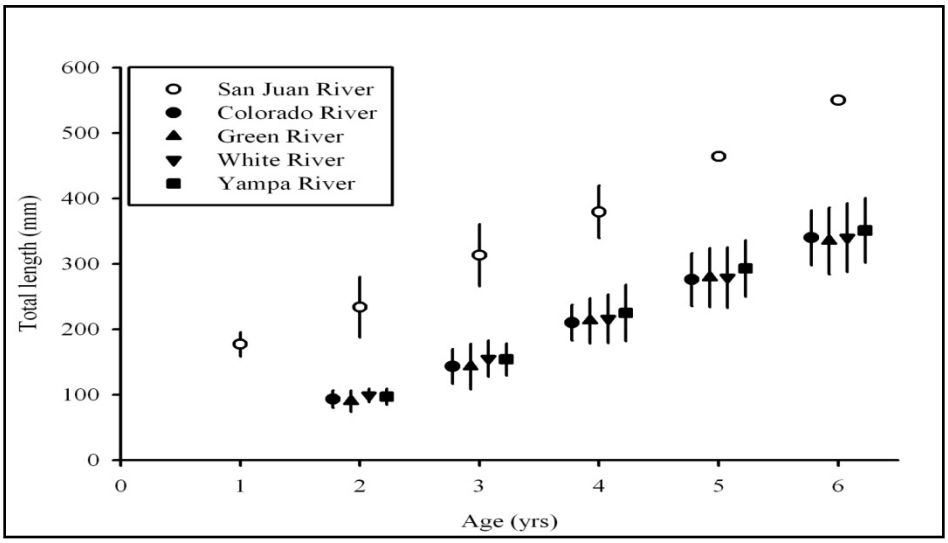


Figure B-8. Mean lengths of age 1–6 Colorado pikeminnow stocked in the San Juan River as age-0, compared to mean lengths of wild fish from rivers of the Upper Colorado River Basin. Figure provided by S. Durst (USFWS).

7.4 Generation Time

Generation time is the average age at which a female gives birth to her offspring, or the average time for a population to increase by a factor equal to the net reproductive rate. Generation time (GT) is computed as:

$$GT = age_{sSM} + (1/d),$$

where: age_{sSM} = average age at sexual maturity, and

d = death rate (Seber 1982; Gilpin 1993).

Osmundson (2006) estimated that males spawn as early as 6 years with most at 8 years; and that most females do not spawn until age 9 years and more likely 10 years. Hence, generation time for Colorado pikeminnow was computed from an average age of sexual maturity (8 years) and the annual adult survival rate (0.80; see section 5.0 Survival):

$$GT = 8 + [1/(1-0.80)] = 8 + 5 = 13 \text{ years.}$$

8.0 Length and Weight

The Colorado pikeminnow is a warm-water riverine fish species found only in the Colorado River System of North America. It is the largest minnow native to North America with an estimated length of 1.8 m and a weight of 36 kg (Miller 1961). The species is presently restricted to the cooler Upper Colorado River Basin where the largest fish found today are about 1 m in length and weigh about 12 kg (Figure B-9; USFWS 2002).

Figure B-9. Adult Colorado pikeminnow captured at the Redlands Diversion fish passage on the Gunnison River and released alive and unharmed; approximate size of fish = 1 m and 12 kg. Photo by Bob Burdick, U.S. Fish and Wildlife Service.

Length-weight relationships for Colorado pikeminnow from four rivers in the upper basin (Hawkins 1992) are presented for length (L) and weight (W) and shown in Figure B-10.

- Green River Log10W = -5.692 + 3.206 * Log10L,
- Colorado River Log10W = -6.384 + 3.463 * Log10L,
- Yampa River Log10W = -6.026 + 3.339 * Log10L, and
- White River Log10W = -5.555 + 3.156 * Log10L.

Slopes and parameters of length-weight relationships were not significantly different among rivers (Hawkins 1992), and similar relationships were provided by Vanicek and Kramer (1969) and Seethaler (1978). Exponents > 3.0 suggest allometric growth in Colorado pikeminnow; i.e., the relationship of weight as a cube of the length (exponent > 3.0) changes as the fish grows, whereas exponents of ≤ 3.0 indicate isometric growth or a constant relationship between length and weight (Lagler 1956).
Mean relative condition of adult Colorado pikeminnow (> 428 mm TL) ranged from about 0.92 to about 1.12 (Hawkins 1992). Highest condition usually occurred in June and was probably related to increase in fat reserves or gametes in preparation for spawning. Lowest condition occurred in July and August

following pre-spawning migration and spawning activity. Condition usually increased in fall after the migratory period when fish returned to their home ranges.

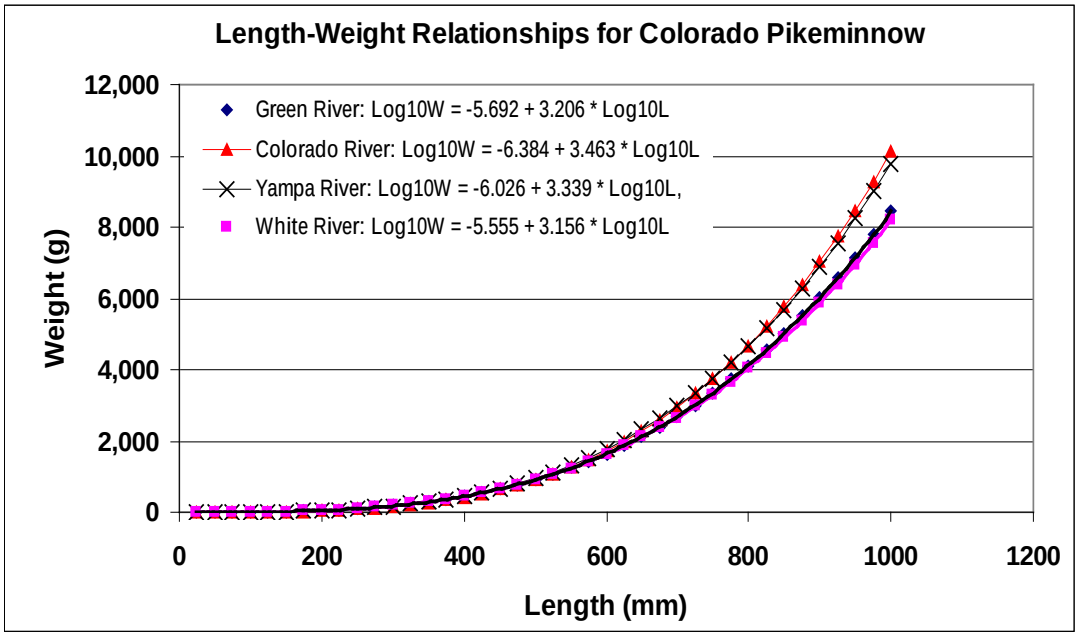


Figure B-10. Length-weight relationships for Colorado pikeminnow (Hawkins 1992).

9.0 Movement and Exchange among Populations

9.1 Drift and Movement

The Colorado pikeminnow is a long-distance migratory species, classified as "potadromous" or migratory within the river basin (Tyus 1990). Recently hatched larvae in the Green River subbasin drift passively downstream for up to about 120 km before they are entrained in a nursery backwater, usually a sand bed channel or embayment Bestgen et al. 2006). The young remain in or near these nursery areas for the first 2–4 years of life; then move upstream to recruit to adult populations and establish home ranges. In the Upper Colorado River, distance moved was inversely related to fish size; displacement of fish < 550 mm TL averaged 33.6 km and displacement for fish ≥ 550 mm TL was only 7.5 km (Osmundson and Burnham 1998). Similar average movement of 31.8 km was observed for 43 radio-tagged adults during fall and spring in the Green River (Archer et al. 1985). Adult Colorado pikeminnow remain in home ranges during fall, winter, and spring and may move considerable distances to and from spawning areas in summer. Individuals move to spawning areas shortly after runoff in early summer, and return to home ranges in August and September (Tyus 1990). Round-trip movements of up to 950 km have been reported (Irving and Modde 2000), with some fish "straying" between rivers within the Green River subbasin (Tyus 1985, 1990; Tyus and McAda 1984). Adults may return in consecutive years to overwinter in the same areas (Wick et al. 1985; Valdez and Masslich 1989).

9.2 Exchange among Populations

Populations of Colorado pikeminnow in the Green River and Upper Colorado River subbasins consist of separate spawning stocks whose progeny and adults mix; nevertheless, these populations are demographically independent. Radio-tagged adults show considerable fidelity to respective spawning areas, with some exchange of individuals between these areas in different years (Tyus 1985, 1990). Although adults show fidelity to three primary spawning sites (1 each in the Yampa, Green, and Upper Colorado rivers), fish in these subbasins are linked genetically (Ammerman and Morizot 1989) through movement and exchange of individuals. Recent findings of fish in tributaries also demonstrate the potential for range expansion during high population levels (Marsh et al. 1991; Masslich and Holden 1996; Cavalli 1999; Zimmerman 2005).

The Colorado pikeminnow in the Upper Colorado River Basin is distributed in three subbasins, where the migratory nature of the species and documented mixing of stocks indicate that the species functions as a metapopulation for two of these subbasins—the Green River and Upper Colorado River (Figure B-11). The largest self-sustaining population occurs in the Green River subbasin where there is direct and unimpeded connection to tributaries, including the Yampa and White rivers (Tyus and McAda 1984), and to a smaller self-sustaining population in the Upper Colorado River subbasin.

Larvae hatched in the lower Yampa River may drift 50–120 mi downstream to nursery backwaters. High densities of age-0 Colorado pikeminnow have been found downstream of the confluence of the Green and Upper Colorado rivers and in the Lake Powell inflow (Valdez 1990), suggesting that fish from both systems are transferred passively or move actively downstream into these regions. Osmundson et al. (1998) showed that subadult Colorado pikeminnow in the Colorado River move back upstream as they mature. Gilpin (1993) hypothesized that this upstream return by subadults provides connectivity and gene flow between the Green and Upper Colorado rivers, resulting in a panmictic population for the entire upper basin with evidence of source/sink dynamics.

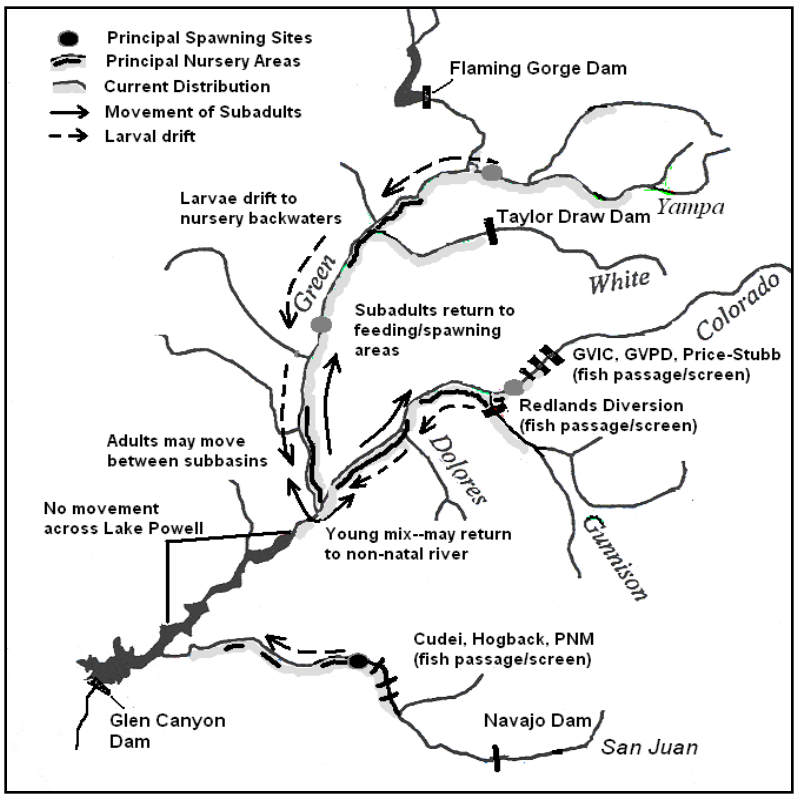


Figure B-11. Distribution of Colorado pikeminnow populations in the Upper Colorado River Basin (shaded areas) with arrows showing larval drift to nursery backwaters, mixing of young at the confluence, movement of adults between subbasins, and return of individuals as subadults to upstream feeding and spawning areas. Dams and diversions that are barriers to fish movement and have been retrofitted with fish passage and screens to minimize entrainment in canals are identified.

Osmundson and White (2009) documented during 1991–2005 a total of 33 inter-system movements of PIT-tagged Colorado pikeminnow (23 adults ≥ 450 mm TL, 10 subadults); including 18 fish from the Upper Colorado River subbasin to the Green River subbasin (mean = 482 mm TL, range = 347–752 mm TL), and 15 fish from the Green River to the Upper Colorado (mean = 523 mm TL, range = 301–721 mm TL). During 2006–2009, 6 fish moved from the Upper Colorado River to the Green River and 7 fish moved from the Green River to the Upper Colorado River (personal communication, Travis Francis, USFWS), for a total of 24 fish from the Colorado to the Green and 22 fish from the Green to the Upper Colorado; or 46 documented inter-system movements altogether in 19 years.

Using an approximate capture probability of 0.04 for the mean lengths of these fish (Osmundson and White 2009), the estimated numbers of fish that moved across these subbasins in 19 years were 600 and 550, respectively, or about 1,150 fish altogether. This equals to about 61 fish/year or 1.3% to 2.2% of the range of 4,857 to 2,803 adults estimated for the two subbasins combined for the years 2000 and 2003, respectively. This level of inter-subbasin exchange does not include the young fish, otherwise too small to PIT tag, that mix at the confluence of the Green and Upper Colorado rivers and may recruit into a non-natal population. This level of exchange does not appear to affect the demographic characteristics of these populations, as indicated by independent population dynamics for the subbasins.

Hastings (1993) showed through simple coupled logistics models that patches (i.e., populations) with an annual exchange rate of up to about 10% of individuals tend to behave independently; whereas, an exchange of > 10% is likely to affect recruitment, age structure, and survival and may provide an important stabilizing role to populations. Metapopulations have both demographic and genetics connectivity (Hastings and Harrison 1994; Lowe and Allendorf 2010) and the level of exchange seen for the Green River and Upper Colorado River subbasins far exceeds the genetic standard of one migrant per generation that ensures genetic panmixia (Mills and Allendorf 1996).

Although Colorado pikeminnow have not been recorded moving between the San Juan River and the Upper Colorado River, razorback sucker (*Xyrauchen texanus*) that were PIT tagged in the San Juan River have been recaptured in the Upper Colorado River (personal communication, Travis Francis, USFWS). The razorback sucker is a potadromous species like the Colorado pikeminnow and capable of long movements.

Three razorback sucker stocked in the San Juan River moved across Lake Powell to locations within the mainstem Upper Colorado River. Two fish were stocked at 167 and 253 mm TL in the San Juan River in 2006, and one was stocked at 360 mm TL in 2004. All three razorback sucker were stocked at river mile (RMI) 158.6 at the Hogback Diversion (~11 mi upstream from Shiprock, New Mexico), and all three fish were recaptured in 2008 at the following locations in the Upper Colorado River:

- Fish No. 1 (470 mm TL; growth of 110 mm) traveled 213 mi down the San Juan River and San Juan arm of Lake Powell and then 191 mi up the Colorado River arm of Lake Powell and the Upper Colorado River and was recaptured near Kane Springs Canyon (RMI 58.3), about 5 mi downstream from the Moab highway 191 bridge; i.e., 404 mi total including 138 mi of Lake Powell.

- Fish No. 2 (322 mm TL; growth of 69 mm) traveled the same distance and an additional 24 mi up the Colorado River to RMI 82.1 near Stearns Creek within Professor Valley; i.e., 428 mi total including 138 mi of Lake Powell.

- Fish No. 3 (382 mm TL; growth of 215 mm) moved 49 mi further than Fish No. 2 and was recaptured at RMI 130.6 in the May Flat area, about 1 mi downstream of the Colorado/Utah state line; i.e., 477 mi total including 138 mi of Lake Powell.

10.0 Habitat

10.1 River Gradients

Spawning sites of Colorado pikeminnow in the Green River, Upper Colorado River, and Yampa River are located in river reaches with gradients of 5.3 and 11.3, 7.7, and 8.2 ft/mi, respectively; whereas nursery areas in the Green River and Upper Colorado River occur in reaches with lower gradients of 1.6 and 3.0 and 2.3 ft/mi, respectively (Figure B-12). The gradients of the San Juan River for Navajo Dam to Animas River, Animas River to Bluff, and Bluff to Clay Hills are 13.2, 7.4, and 8.3 ft/mi, respectively, which are within the range of gradients used for spawning, but higher than gradients used as nursery areas in other rivers; this suggests that formation and availability of nursery habitat (e.g., backwaters) in the San Juan River is influenced by channel gradient.

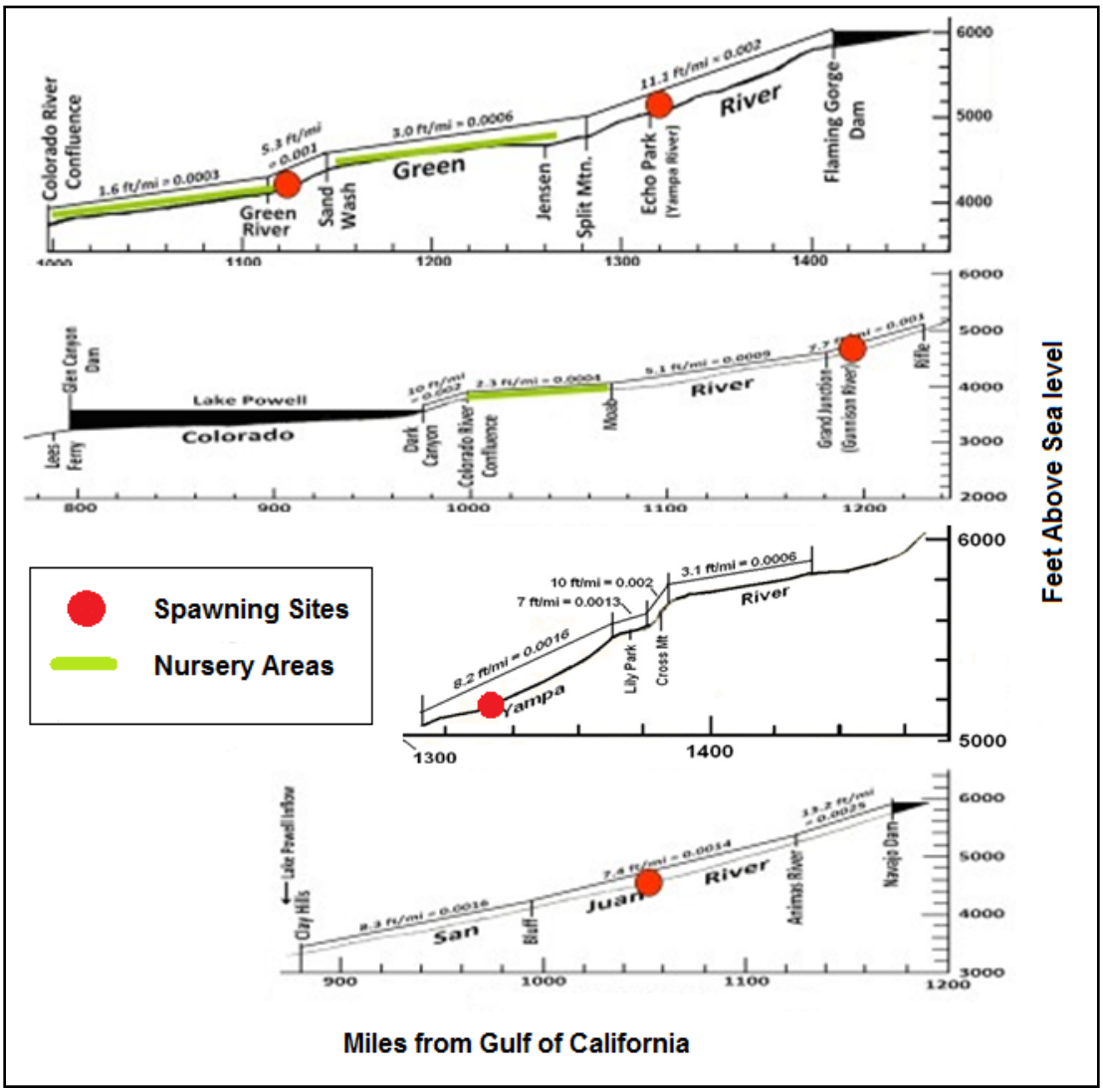


Figure B-12. Gradients for spawning sites and nursery areas used by Colorado pikeminnow in the Green River, Upper Colorado River, Yampa River, and San Juan River. Spawning sites and nursery areas from LaGory et al. (2003) and river gradients from U.S. Department of the Interior (1946).

10.2 Access to Habitats in the San Juan River

Colorado pikeminnow in the Green and Upper Colorado rivers use different reaches for different life stages (Bestgen et al. 2010); e.g., in the Green River, spawning occurs in the canyons of the Yampa River, whereas nursery and rearing occurs in the alluvial sandy reaches of the middle and lower Green River. Access to all reaches of the San Juan River up to Navajo Dam is impeded by 8 diversions or small dams (Figure B-13; personal communication, Sharon Whitmore, USFWS). Fish passage upstream to the Animas River has been provided for all diversions, except for Fruitland Diversion, which is currently in planning and design. Structures that allow access to fish from the Animas River upstream to Navajo Dam are currently low priority and include Citizens Ditch and Hammond Irrigation Canal. It is unclear if Colorado pikeminnow would move upstream of the Animas River given the cool water temperatures from Navajo Dam (see section 10.3). Diversions on the Animas River also impede upstream movement into that river, including the Farmington Lake Diversion (RM 12) and the Farmer's Ditch Diversion (RM 22).

Another impediment to movement is a waterfall that has formed in the San Juan arm of Lake Powell as a result of lowered reservoir elevation; sediment deposited at high reservoir elevation filled the historic river channel and the river has carved a new channel over hard rock formations and formed a steep drop in the river bed. This waterfall is believed to be an impediment to fish movement except when it is inundated by high lake levels.

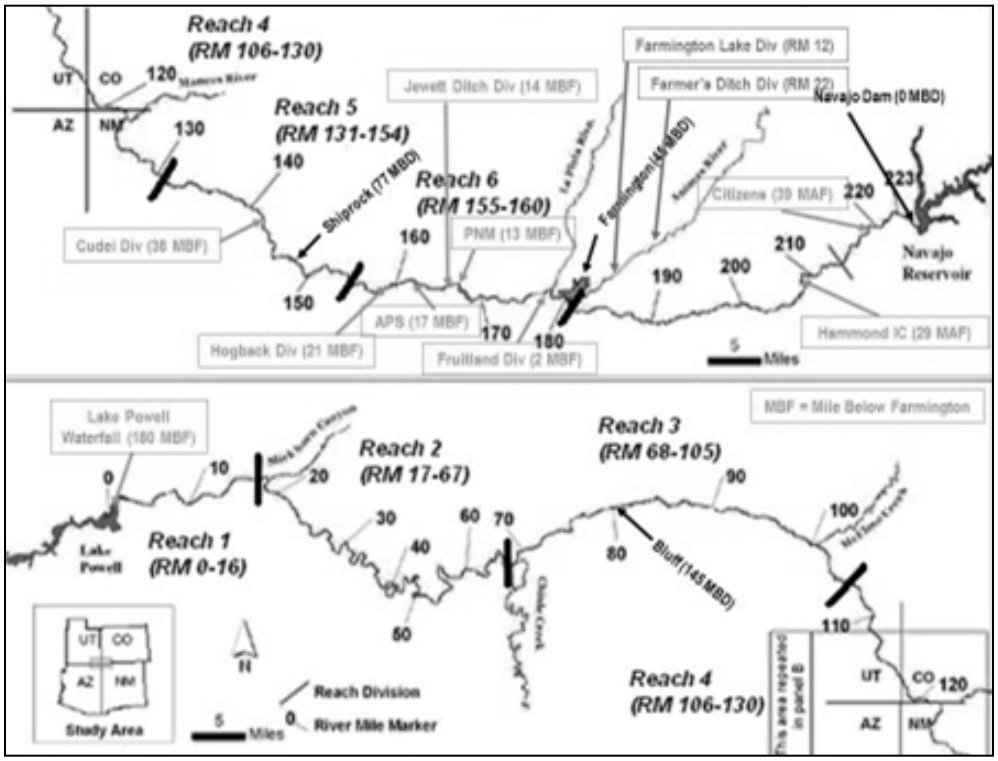


Figure B-13. Locations of diversions that impede fish passage on the San Juan River.

10.3 Longitudinal Temperature Suitability of the San Juan River

The temperature of the San Juan River cooled considerably after completion of Navajo Dam in 1962. Pre-dam temperature (1954) at Blanco (about 18 mi below Navajo Dam) was 20-25°C in summer and 0°C in winter; whereas post-dam temperature (1994) is 4-8°C in summer and 4°C in winter (Figure B-14).

The timing of warmest temperature in the San Juan River at Blanco has also shifted from pre-dam highs during Jun 1 – Sep 1 to post-dam highs during Aug 1 – Oct 1. A shift to warmest temperatures in late summer and fall reflects the warmest dam-release temperatures that result when fall overturn mixes warm surface water into the area of penstock withdrawals.

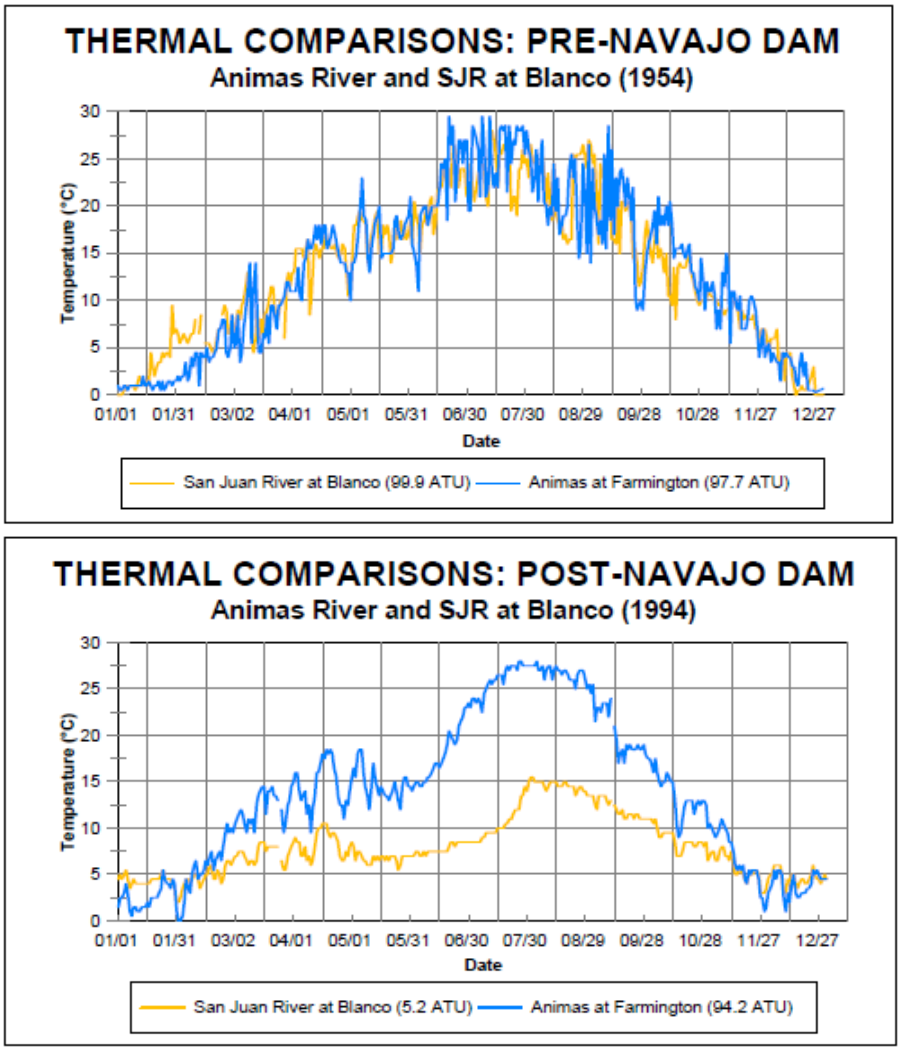


Figure B-14. Temperature of the San Juan River before and after construction of Navajo Dam in 1962. Figures from Cutler (2006).

Expanding the range of the Colorado pikeminnow upstream of Farmington will require warming releases from Navajo Dam. One option for warming temperature of the San Juan River is to modify releases from Navajo Dam with a temperature control device (Cutler 2006).

10.4 Mesohabitat Use

Colorado pikeminnow live in warm reaches of the Colorado River mainstem and larger tributaries, and require uninterrupted passage for spawning migrations and dispersal of young. The species is adapted to a hydrologic cycle characterized by large spring peaks of snowmelt runoff and low, relatively stable base flows in summer and winter. Throughout most of the year, juveniles, subadults, and adults utilize relatively deep, low-velocity eddies, pools, and runs that occur in nearshore areas of main river channels (Tyus and McAda 1984; Valdez and Masslich 1989; Tyus 1990, 1991; Osmundson et al. 1995; Table B-11). In spring, adults utilize floodplains, flooded tributary mouths, flooded side canyons, and eddies that are available only during high flows (Tyus 1990, 1991; Osmundson et al. 1995).

Table B-11. Seasonal frequency (%) of use of mesohabitats in the Grand Valley of the Upper Colorado River subbasin by radio-tagged adult Colorado pikeminnow, 1986–1989 (Osmundson et al. 1995). Habitats: FR = fast runs, SR = slow runs, RA = rapids, RI = riffles, ED = eddies, PO = pools, SH = shorelines, BA = backwaters, and GP = off-channel flooded gravel pits.

Months	Habitats (% of time used by radio-tagged fish)								
	FR	SR	RA	RI	ED	PO	SH	BA	GP
Apr–Jun (Spring)	3–19	13–32	0–1	0–2	2–9	8–12	3–8	22–42	3–25
Jul–Sep (Summer)	7–26	26–55	3–5	3–10	9–16	13–16	0–4	3–7	0–4
Oct (Fall)	0	61	0	0	4	26	0	9	0
Nov-Feb (winter)	0	27–41	0	0	0–8	42–62	0	5–15	0
March	4	43	0	0	7	32	0	14	0

10.5 Spawning Sites

Two potential spawning areas were located in “the mixer area” at RM 131 and 132 during a radiotelemetry study of Colorado pikeminnow on the San Juan River (Miller 1994). Three of four radio-tagged fish were simultaneously located at an island/chute/ eddy complex at RM 132 in mid-July 1993 and subsequently at a second site immediately downstream. Visual observations of a paired male and female were made that confirmed the radiotelemetry information. More recently, spawning-related activity has been seen in the San Juan River near the Four Corners area (~RM 120; personal communication, Scott Durst, USFWS).

Colorado pikeminnow spawning sites in the Green River subbasin have been well documented. The two principal locations are in Yampa Canyon on the lower Yampa River and in Gray Canyon on the lower Green River (Tyus 1990, 1991). These reaches are 42 and 72 km long, respectively, but most spawning is believed to occur at one or two short segments within each of the two reaches. Another spawning area may occur in Desolation Canyon on the lower Green River (Irving and Modde 2000), but the location and importance of this area has not been verified.

Although direct observation of Colorado pikeminnow spawning is not possible because of high turbidity, radiotelemetry indicates that spawning occurs over cobble-bottomed riffles (Tyus 1990). High spring flows and subsequent post-peak summer flows are important for construction and maintenance of spawning substrates (Harvey et al. 1993). In contrast with the Green River subbasin, where known

spawning sites are in canyon-bound reaches, currently suspected spawning sites in the Upper Colorado River subbasin are at six locations in meandering, alluvial reaches (McAda 2003).

After hatching and emerging from the spawning substrate, Colorado pikeminnow larvae drift downstream to backwaters in sandy, alluvial regions, where they remain through most of their first year of life (Holden 1977; Tyus and Haines 1991; Muth and Snyder 1995). These backwaters are formed after spring runoff within the active channel and are not floodplain features. Colorado pikeminnow larvae occupy these in-channel backwaters soon after hatching. They are most abundant in backwaters that are large, warm, deep (average, about 0.3 m in the Green River), and turbid (Tyus and Haines 1991). Such backwaters are created when a secondary channel is cut off at the upper end, but remains connected to the river at the downstream end. These chute channels are deep and may persist even when discharge levels change dramatically. An optimal river-reach environment for growth and survival of early life stages of Colorado pikeminnow has warm, relatively stable backwaters, warm river channels, and abundant food (Muth et al. 2000).

10.6 Habitat Suitability Indices

Habitat suitability index curves were developed from two workshops of species experts using a Delphi Decision Process (Valdez et al. 1987). The specific metrics of each curve are provided in a hard copy report, but these data are not available electronically. The report provides a compilation of curves developed in the rivers of the upper basin, including the Green River (Holden 1977), San Juan River (Twedt and Holden 1980), Yampa and White rivers (Prewitt and Carlson 1980), Upper Colorado River (Valdez et al. 1982), and Yampa River (Rose 1984). Suitability indices for habitats used by Colorado pikeminnow < 25 mm TL and 25−149 mm TL in the Upper Colorado River Basin (Figure B-15; Valdez et al. 1987) illustrate the high degree of backwater use by age-0 fish. Habitat suitability curves for Colorado pikeminnow in the San Juan River were developed by Miller (1995) using much of the information provided by Twedt and Holden (1980) and Valdez et al. (1987).

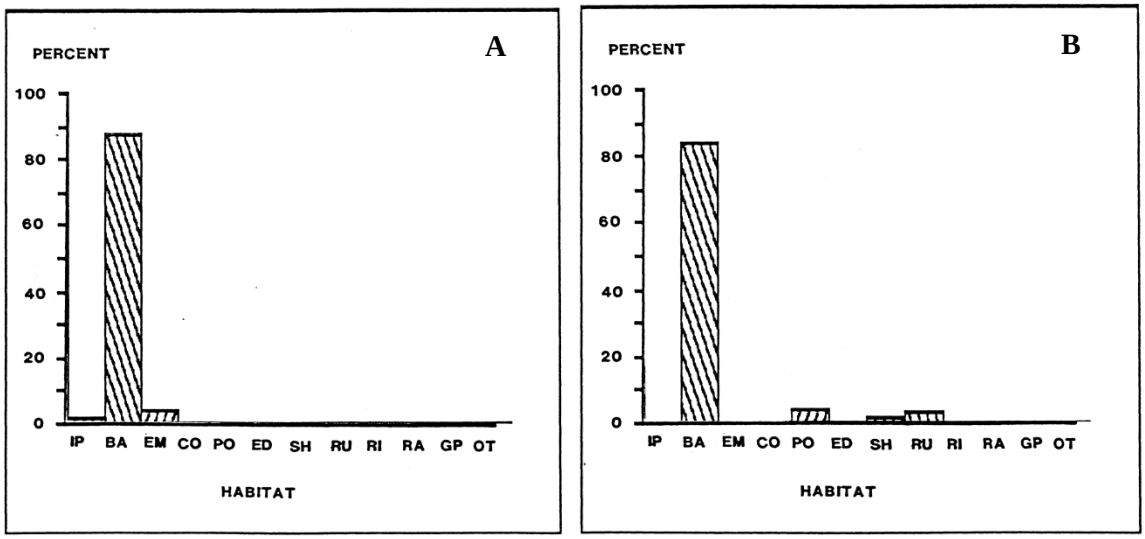


Figure B-15. Suitability indices for habitats used by Colorado pikeminnow (A) < 25 mm TL and (B) 25−149 mm TL in the Upper Colorado River Basin (Valdez et al. 1987).

10.7 Estimated Capacity of Backwater Habitat for Age-0 Fish

As shown in Figure B-15, backwaters are the most common habitat used by Colorado pikeminnow in their first year of life (i.e., age-0) in the Upper Colorado River Basin. Ecosystems Research Institute (ERI 2014) determined that the number and surface area of backwater habitats vary by year and geomorphic reach for the San Juan River during fall baseflow (Figure B-16). For the period of measurements, the largest amount of backwater habitats measured during baseflow occurred in the fall 1995 and winter 1996. From the fall of 1996 to the fall of 2003, backwater surface area decreased substantially from a river wide high of 145,969 m^2 to a low of 20,294 m^2 in 2003 (i.e., 86% decrease). Since 2003, backwater habitat area has increased annually, reaching a post-2003 high of 67,786 m^2 in 2011 (ERI 2014). The average surface area of each backwater in the lower reach was only 32 m^2, accounting for 5,880 m^2 of backwater surface area (only 11% of the river-wide total compared to 29% in 2011).

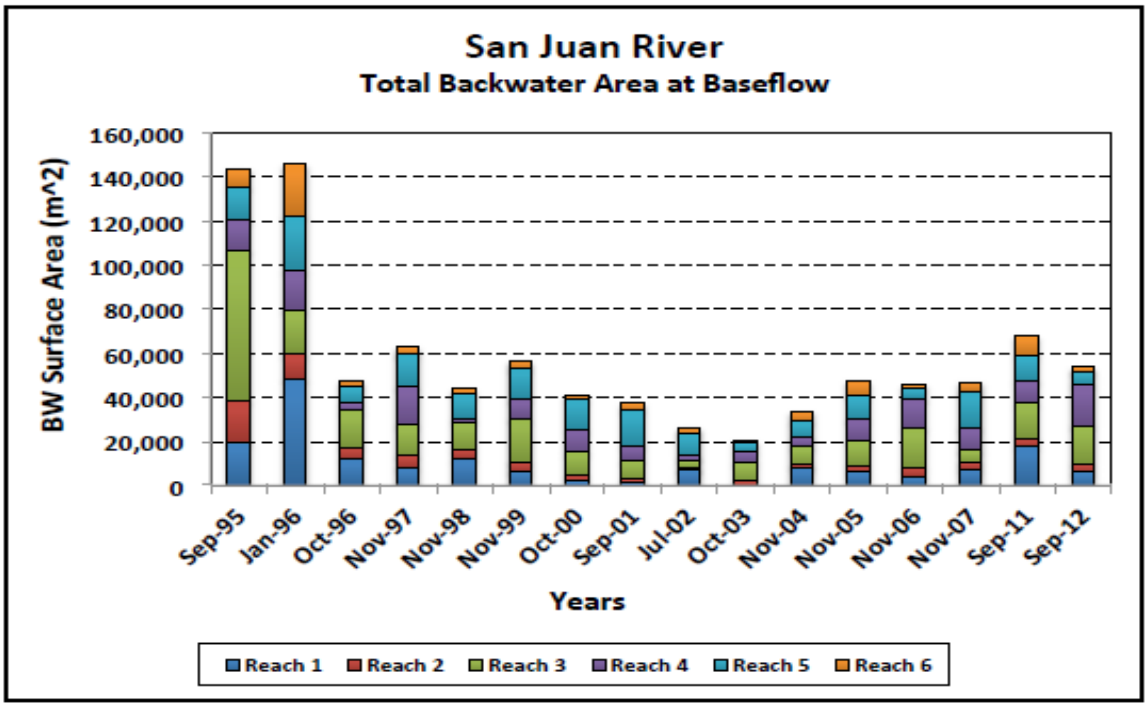


Figure B-16. Densities of backwater habitats by year and geomorphic reach for the San Juan River, as measured during fall baseflow. Figure from Lamarra (2014).

Understanding the availability of backwater habitat in the San Juan River is important for knowing if nursery habitat may be limiting the Colorado pikeminnow population. In order to estimate the numbers of age-0 Colorado pikeminnow that could be supported in the San Juan River, a relationship was derived for the total numbers of age-0 Colorado pikeminnow estimated from catch rates in backwaters < 400 m^2 of the Green and Upper Colorado rivers (Figure B-17).

Only backwaters with surface area < 400 m^2 were included in the relationship to apply it to backwaters of comparable size in the San Juan River. Ecosystems Research Institute (ERI 2014) determined that most backwaters of the San Juan River are < 400 m^2 in size. The relationship derived from these data was used to estimate the numbers of age-0 fish that could be supported by backwaters in the San Juan River.

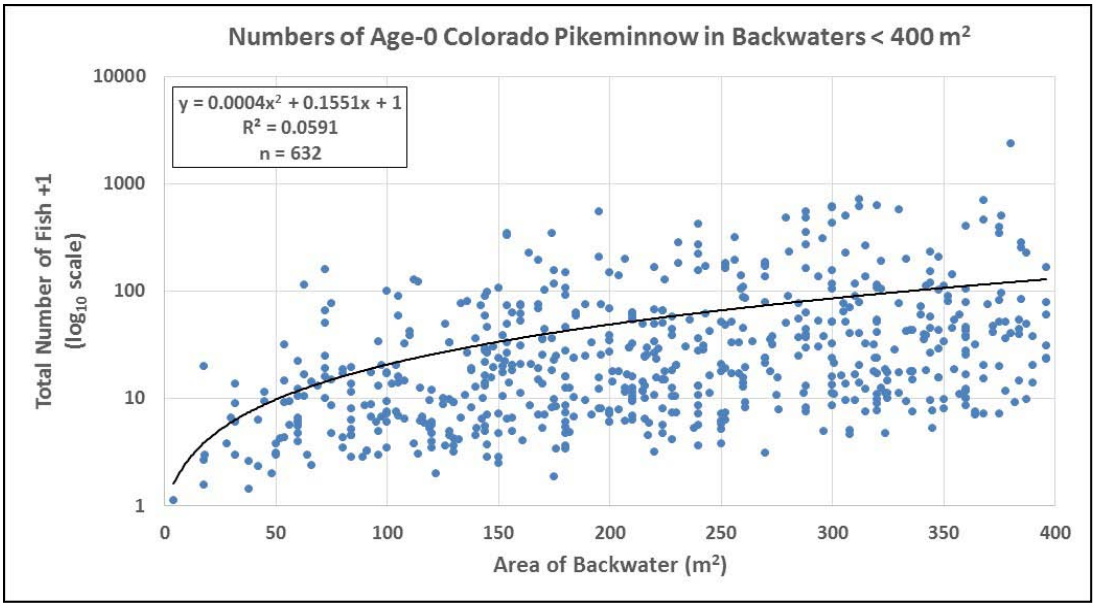


Figure B-17. Numbers of age-0 Colorado pikeminnow in 632 backwaters < 400 m² surface area of the Green and Upper Colorado rivers, 1986**–2010. Data provided courtesy of Upper Colorado River** Endangered Fish Recovery Program (Travis Francis, Database Manager, USFWS).

Data collected by ERI (2014) indicate that a high surface area and density (via counts) for backwaters were found in the lower 16 mi of the San Juan River although lower in 2012 than in 2011. The average surface area of each backwater in the lower reach was only 32 m^2, accounting for 5,880 m^2 of backwater surface area (only 11% of the river-wide total compared to 29% in 2011). In the non-canyon reaches of the San Juan River (3-6), large backwater complexes were found in Reaches 3 and 4. In Reach 3, densities average 10 per mile, with an average surface areas of just less than 100 m^2. The largest sized backwaters were found at RM 119 (7 backwaters with a total area of 7,532 m^2). This single river mile accounted for 15% of the total backwaters in the river. In addition, RM 122 and RM 133 had over 1,200 m^2 of backwater surface area with average sizes near 600 m^2.

The information provided by ERI (2014) was used to estimate the average size of backwaters for each of the six reaches of the San Juan River. The possible numbers of age-0 Colorado pikeminnow in backwaters was computed on the basis of this average size of backwaters by reach as shown in Table B-12. For the years 1995 and 1996 there was sufficient backwater habitat at baseflows in the San Juan River for about 28,000 age-0 Colorado pikeminnow. In subsequent years, total possible numbers of age-0 ranged from 4,359 to 13,469. The estimated numbers of age-0 Colorado pikeminnow in backwaters of the San Juan River were derived from highly variable data from Upper Basin backwaters and from estimated average sizes of backwaters. Caution is advised in relying on these as actual numbers of fish possible; however, the apparent low magnitude of age-0 numbers suggests that total area of backwater habitat may limit recruitment of Colorado pikeminnow in the San Juan River. Additional analyses of these and other data will be necessary to better understand availability of habitat for young Colorado pikeminnow in the San Juan River.

Table B-12. Total backwater area (a:), numbers of backwaters of average size (b:), and estimated numbers of age-0 Colorado pikeminnow (c:) for each of six reaches of the San Juan River. River Miles by Reach: 1 = 2**−16, 2 = 17−67, 3 = 68−105, 4 = 106−130, 5 = 131−154, 6 = 155−180. Total b**ackwater area from ERI (2014).

Reach[a]	Sep-95	Jan-96	Oct-96	Nov-97	Nov-98	Nov-99	Oct-00	Sep-01	Jul-02	Oct-03	Nov-04	Nov-05	Nov-06	Nov-07	Sep-11	Sep-12
1 (32 m²) a:	19,769	48,269	11,862	8,224	12,173	6,670	1,886	1,235	7,057	0	7,926	6,261	4,063	7,521	17,549	6,110
b:	617.78	1,508.41	370.69	257.00	380.41	208.44	58.94	38.59	220.53	0.00	247.69	195.66	126.97	235.03	548.41	190.94
c:	3,319	8,104	1,992	1,381	2,044	1,120	317	207	1,185	0	1,331	1,051	682	1,263	2,946	1,026
2 (30 m²) a:	18,249	11,152	5,547	5,399	4,151	3,703	2,784	1,631	815	2,060	1,631	2,791	3,943	3,025	3,617	3,728
b:	608.30	371.73	184.90	179.97	138.37	123.43	92.80	54.37	27.17	68.67	54.37	93.03	131.43	100.83	120.57	124.27
c:	3,049	1,863	927	902	694	619	465	273	136	344	273	466	659	505	604	623
3 (100 m²) a:	68,406	20,300	16,473	13,860	12,433	19,761	10,339	8,608	3,667	8,359	7,952	10,937	17,913	5,453	16,415	17,397
b:	684.06	203.00	164.73	138.60	124.33	197.61	103.39	86.08	36.67	83.59	79.52	109.37	179.13	54.53	164.15	173.97
c:	13,346	3,961	3,214	2,704	2,426	3,855	2,017	1,679	715	1,631	1,551	2,134	3,495	1,064	3,203	3,394
4 (300 m²) a:	14,029	17,797	3,540	17,452	1,784	8,797	10,543	6,694	1,809	5,296	4,293	9,822	13,306	9,847	9,805	18,728
b:	46.76	59.32	11.80	58.17	5.95	29.32	35.14	22.31	6.03	17.65	14.31	32.74	44.35	32.82	32.68	62.43
c:	3,859	4,896	974	4,801	491	2,420	2,900	1,842	498	1,457	1,181	2,702	3,660	2,709	2,697	5,152
5 (150 m²) a:	14,971	24,723	7,519	14,473	10,796	14,375	13,951	16,152	10,453	3,378	7,336	10,990	5,047	16,958	11,662	5,897
b:	99.81	164.82	50.13	96.49	71.97	95.83	93.01	107.68	69.69	22.52	48.91	73.27	33.65	113.05	77.75	39.31
c:	3,220	5,318	1,617	3,113	2,322	3,092	3,001	3,474	2,248	727	1,578	2,364	1,086	3,648	2,508	1,268
6 (30 m²) a:	8,299	23,727	2,838	3,400	2,439	3,075	1,333	3,153	2,191	1,201	4,362	6,494	1,540	4,148	8,738	1,774
b:	276.63	790.90	94.60	113.33	81.30	102.50	44.43	105.10	73.03	40.03	145.40	216.47	51.33	138.27	291.27	59.13
c:	1,387	3,965	474	568	408	514	223	527	366	201	729	1,085	257	693	1,460	296
Total Area:	143,723	145,968	47,779	62,808	43,776	56,381	40,836	37,473	25,992	20,294	33,500	47,295	45,812	46,952	67,786	53,634
Total Age-0:	28,181	28,107	9,198	13,469	8,384	11,620	8,923	8,002	5,149	4,359	6,643	9,803	9,839	9,882	13,419	11,760
Mean Q	1,193	783.4	1,273	1,175	1,494	910.1	1,273	646.3	410.7	633.4	796.3	908	979	1,086	896.5	767.4

[a] average backwater area (m²) for each reach was determined from information provided by ERI (2014)

The linkage between numbers of age-0 Colorado pikeminnow in backwaters and baseflows of the San Juan River is a positive relationship with close association for all years sampled, except for Sep-95 and Jan-96, years that were preceded by high flows that scoured the channel and increased backwater numbers and area (ERI 2014; Figure B-18). At baseflows seen from 1996 to 2012, the maximum number of age-0 Colorado pikeminnow that can be supported in backwaters of the San Juan River is < 15,000.

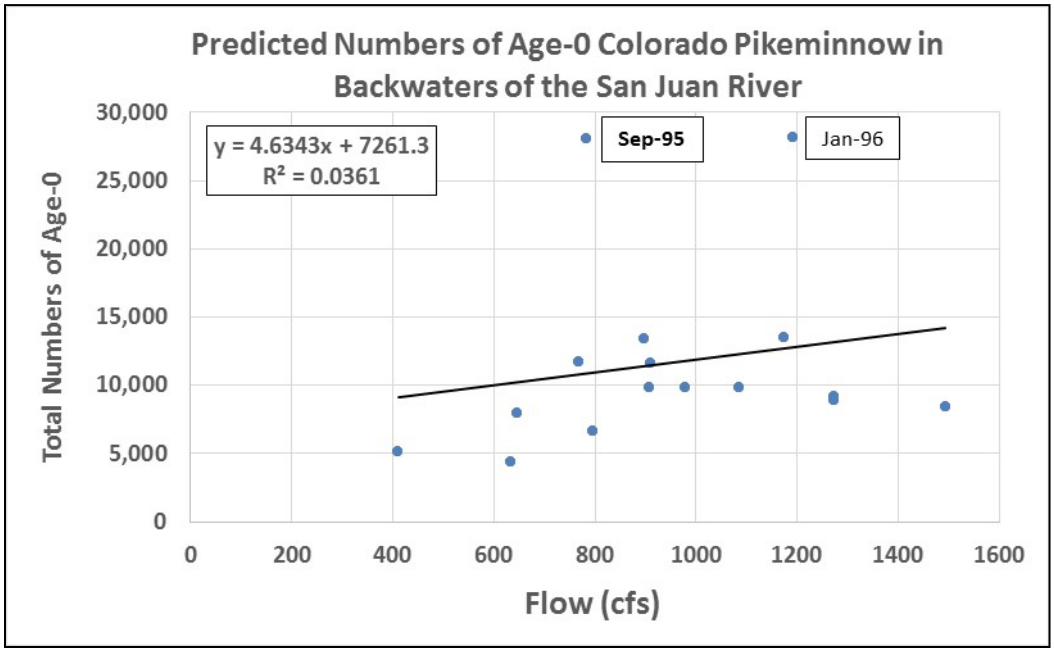


Figure B-18. Predicted numbers of age-0 Colorado pikeminnow in backwaters of the San Juan River at baseflows.

An assessment of the abundance of age-0 native fish species and nursery habitat quality and availability in the San Juan River was conducted by Archer et al. (2000). The information contained in that report provides a good background assessment of the availability of nursery habitat that is supplemented by ERI (2014) and is important to consider in future analysis of nursery habitat in the San Juan River. Table B-13 from Archer et al. (2000) is provided to illustrate the similar habitat areas compared to ERI (2014) as shown in Table B-12.

Table B-13. Total area (m2) of low-velocity habitats in nursery habitat study sections in the San Juan River, April 1994-1997. Table from Archer et al. (2000).

Reach	1994	1995	1996	1997
1	7,418	5,629	4,878	6,263
2	2,794	911	2,675	5,227
3	1,350	3,917	4,580	6,198
4	NA	NA	3,800	16,170

11.0 Genetics

11.1 Genetic Diversity

The only detailed genetics investigations of the Colorado pikeminnow examined the relationships between hatchery fish and wild populations shortly after the species was first taken into captivity (Ammerman and Morizot 1989); and among two captive groups and samples of wild individuals after some stocking of hatchery fish (Williamson et al. 1999; Morizot et al. 2002). Ammerman and Morizot (1989) used starch gel electrophoresis and found that samples of fish from the Green and Upper Colorado rivers were similar genetically to two hatchery stocks first established in 1973 and 1978 (unbiased genetic identity = 0.99; Nei 1978), indicating that the fish initially used to develop a hatchery broodstock were genetically representative of the wild population. At least 9 of the 44 presumptive loci were polymorphic, and average heterozygosities were high (2.6-5.3%) for an endangered species.

Morizot et al. (2002) evaluated the genetic relationships among two captive populations of Colorado pikeminnow from the Dexter National Fish Hatchery and Technology Center, New Mexico, and 15 samples of wild adult, juvenile, and age-0 fish from the Green, Yampa, Colorado, and San Juan rivers. The products of 89 or more loci were resolved by starch gel electrophoresis and histochemical staining; 8 loci were polymorphic in at least one sample. This comparison of genetic diversity through allozyme techniques showed little difference among the populations of the Upper Colorado River Basin (Williamson et al. 1999; Morizot et al. 2002), but the authors stressed the need to maintain local adaptability of several populations in any potential broodstock program.

Allele frequencies from 633 wild fish and 94 hatchery fish did not differ significantly among geographically separated breeding populations, suggesting essential panmixia of the Colorado pikeminnow across the four rivers sampled (i.e., Green, Yampa, Colorado, and San Juan; Morizot et al. 2002). FST values are a measure of genetic differentiation among populations with values ranging from 0 (no difference) to 1 (complete differentiation), and are directly related to variance in allele frequency. Mean FST values ranged from 0.003 among wild age-0 Green River and Colorado River fish (n = 426) to 0.108 among all wild adults (n = 207) and captive broodstock (n = 60).

Significant deviations from Hardy−Weinberg equilibrium were observed at four loci in the Colorado River and Green River samples of adults, juveniles, and age-0 fish, although no hatchery samples showed such deviations. The most striking geographic variability observed was the presence of the rare private alleles GR*b and TPI-2*c in Green River samples and GPI-2*c, PEPB*a, and PEPS*b in Colorado River samples. The lowest genetic variability was observed in the San Juan River samples, possibly the result of prior population bottlenecks.

11.2 Genetic Effective Population Size

An N_e of 500 is commonly used for fishes (Waples 1990; Bartley et al. 1992; Allendorf et al. 1997) and other vertebrate species (Mace and Lande 1991; Ralls et al. 1996), and has been used as the basis for deriving an estimate of N_e for other endangered fishes (e.g., Reiman and Allendorf 2001). Using an N_e of 500, a 1.11:1 sex ratio, and an N_e/N_g ratio of 0.20, an adjusted N_e of 2,510 adults (i.e., 502/0.20, rounded to 2,500) was derived as the estimated number of Colorado pikeminnow necessary to maintain a genetic effective population size.

To maintain an N_e of 500 with a 1.11:1 sex ratio, the total number of breeding adults (N_b) must be increased according to the following relationship:

$$N_e = 4M_bF_b/M_b+F_b$$

Where: M_b = number of breeding males,

F_b = number of breeding females, and

$N_b = M_b + F_b$.

Hence: $N_e = 4\ (264)(238)/502 = 500$ (i.e., 264 males and 238 females are needed to maintain an N_e of 500).

In a letter to the USFWS dated 21 May 1998, Dr. Robert C. Lacy, Department of Conservation Biology, Chicago Zoological Society, recommended an N_e/N_g of 0.20 for Colorado pikeminnow based on the average for salmonids reported by Allendorf et al. (1997).

An adjusted N_e was computed for the Colorado pikeminnow using the genetic parameters described above (USFWS 2014):

Adjusted $N_e = N_e/(N_e/N_g)$

Where: N_e = genetic effective population size, 502;

N_e/N_g = proportion of adults contributing genes to

next generation (~0.20 from R. Lacy, 1998);

12.0 Predation

Predation and competition by non-native fishes have been recognized as threats to the Colorado pikeminnow since the 1950s (Miller 1961), but the impact of predation on survival of Colorado pikeminnow has not been isolated from other causes of mortality. At least 67 species of non-native fishes have been introduced into the Colorado River System during the last 100 years, many of which prey upon and compete with the 35 species that are native to the System (Valdez and Muth 2005). The range in sizes of non-native fishes that prey on and compete with Colorado pikeminnow encompasses the entire life history of the species and there is no apparent refuge size where predation and competition is reduced.

12.1 Green River and Upper Colorado River

About 20 non-native fish species occupy the same habitat as the Colorado pikeminnow in the upper basin. Nursery backwaters and low-velocity shorelines are the areas of highest predation on young Colorado pikeminnow (Haines and Tyus 1990; Tyus 1991; Holden 1999; McAda 2003; Muth et al. 2000). Predation of young fish limits survival and recruitment (e.g., Muth and Nesler 1993; Bestgen et al. 1997; McAda and Ryel 1999; Valdez et al. 1999; Bestgen et al. 2007a, 2007b). Osmundson (1987) confirmed predation by black bullhead (*Ameiurus melas*), green sunfish (*Lepomis cyanellus*), largemouth bass (*Micropterus salmoides*), and black crappie (*Pomoxis nigromaculatus*) as a significant mortality factor of age-0 Colorado pikeminnow stocked in riverside ponds along the Upper Colorado River. Adult red shiners (*Cyprinella lutrensis*) were also reported as significant predators of larval native fish in backwaters (Ruppert et al. 1993).

Northern pike (*Esox lucius*), smallmouth bass, and channel catfish (*Ictalurus punctatus*) have also been identified as the principal predators of subadult and adult Colorado pikeminnow in the last two decades. Northern pike escaped from Elkhead Reservoir into the Yampa River in the early 1980s (Tyus and Beard 1990) and established a reproducing population by the 1990s that expanded in the Yampa River and into the middle Green River (Tyus and Beard 1990; Hawkins and Nesler 1991; Nesler 1995) where they pose a competitive and predatory threat to native fishes of all sizes (Wick et al. 1985; Tyus and Karp 1989; Tyus and Beard 1990; Bestgen et al. 2007a, 2007b).

Smallmouth bass also escaped from Elkhead Reservoir into the Yampa River in the early 1990s and became abundant during low stream flows in 2001-2003; the species is prolific, highly predaceous at all life stages, and threatens small and medium-size native fishes. Adult channel catfish and northern pike often use the same habitats as subadult and adult pikeminnow, where these species compete for food and prey on each other, especially during periods of limited resource availability (Wick et al. 1985; Tyus and Karp 1989; Tyus and Beard 1990; Nesler 1995; Bestgen et al. 2007a, 2007b).

Channel catfish were first introduced into the Upper Colorado River Basin in 1892 (Tyus and Nikirk 1990) and are now common to abundant (Tyus et al. 1982; Nelson et al. 1995). The species is one of the most prolific predators and competitors in the upper basin due largely to resource overlap and tolerance to poor water quality conditions during droughts and in marginal habitats (Hawkins and Nesler 1991; Lentsch et al. 1996; Tyus and Saunders 1996). Colorado pikeminnow also prey on non-native fishes, but the spines of channel catfish may lodge in the throats of pikeminnow possibly leading to their death (McAda 1980; Pimental et al. 1985).

Non-native fish control in the upper basin has focused on five fish taxa; northern pike, smallmouth bass, channel catfish, centrarchids (sunfishes including largemouth bass, green sunfish, crappie), and cyprinids (minnows including red shiner, fathead minnow [*Pimephales promelas*], sand shiner [*Notropis stramineus*]) (Martinez et al. 2011). Efforts to control northern pike in the Yampa River began in 1999

(Hawkins et al. 2005) when fish taken from the river were relocated to nearby isolated ponds or reservoirs accessible to anglers and in conformance with the Procedures for Stocking Nonnative Fish Species in the Upper Colorado River Basin (USFWS 1996). Annual removal of northern pike in three reaches of the Yampa River (Juniper, Maybell, and Lily Park) has resulted in a net decline in numbers of pike captured (Wright 2010) which effectively reduces the number of large predators on pikeminnow as well as other native fishes. While the numbers of northern pike in the middle and lower Yampa River have been reduced, northern pike in the upper Yampa River persist in large numbers in reservoirs and complex floodplains, but control and translocation efforts continue to suppress this population to reduce downstream dispersal (Webber 2010). In the Yampa River (RM 50.2 and 134.2), annual estimated densities of northern pike (> 300 mm TL), a functionally similar predator to Colorado pikeminnow, reach a maximum density of 18.9 fish/mi in 2012 (Battige 2012).

Northern pike have also been effectively removed from the middle Green River starting in 2001 (Monroe and Hedrick 2008), and most pike in the middle Green River are immigrants from the Yampa River; there appears to be little or no local reproduction by pike in the Green River. Northern pike are uncommon in the Upper Colorado River subbasin and no specific removal program is in place for this species.

Control of smallmouth bass began in the Yampa River in 2004 following a dramatic increase in the population. Smallmouth bass were rare in Yampa Canyon in 1997, but increased to 18% of the adult fish composition in 2004, concurrent with a decline in native species composition from 84% in 1997 to 45% in 2004 (Haines and Modde 2007). Efforts to control smallmouth bass have had variable success. Control measures are effective at suppressing numbers of bass, except for strong year classes such as 2007 in the middle Green River (Monroe and Hodge 2010) and 2008 in the middle and lower Yampa River (Hawkins et al. 2009, 2010). Similarly, suppression of smallmouth bass numbers has been effective in the Upper Colorado and Gunnison rivers, except during strong year classes such as 2005-2007 (Burdick 2010). Populations of smallmouth bass appear to increase in years of low stream flow and are suppressed in years of high flow, most likely because low flows favor habitat and temperature required for egg production and survival of young. Numbers of smallmouth bass have been reduced in Desolation/Gray Canyon largely because there is little or no local reproduction and the fish are largely immigrants from upstream populations (Badame et al. 2008).

Attempts to mechanically reduce numbers of channel catfish in Desolation/Gray Canyon (Badame et al. 2008; Chart and Lentsch 1999) and Yampa Canyon (Haines and Modde 2007; Fuller 2009) have had limited success and other strategies are being explored. Removal of centrarchids has also been implemented in Upper Colorado River floodplains and nursery backwaters (Burdick 2008), and sources of non-native fish have been identified through stable isotope analysis (Johnson et al. 2008; Whitledge et al. 2006, 2007) and isolated to prevent escapement of these fish to the Colorado River (Martinez et al. 2011).

12.2 San Juan River

Changes in the composition of the San Juan River's fish community occurred with construction of Navajo Dam and nonnative fish introductions. The historical fish community of the San Juan River was relatively depauperate with only eight species (Sublette et al. 1990), but recent investigations have documented 19 non-native fishes (Ryden 2000). Non-native fishes prey on and compete with the native species, but also provide may be potential a source of prey for Colorado pikeminnow (Franssen and Durst 2013). The nonnative fishes of greatest concern in the San Juan River are the channel catfish and common carp. An extensive non-native fish control program has been implemented on the San Juan River with the primary target of channel catfish (SJRIP 2009; Davis et al. 2010; Elverud 2010). Mechanical removal has resulted in reduced numbers of large channel catfish (> 525 mm TL) river-wide,

but there has been a shift towards smaller fish since 1996 and recolonization from upstream movement (Miller 2006; Franssen et al. 2014). Numbers of common carp have decreased substantially with removal of that species from the system.

Despite predictions that the catch numbers of age 1 and age 2+ Colorado pikeminnow are associated with the catch rate of predators (i.e., adult channel catfish > 300 mm TL), Franssen and Durst (2013) found no negative effects of adult channel catfish on numbers of Colorado pikeminnow captured. It is noted that other interactions may be negatively affecting Colorado pikeminnow in conjunction with the presence of nonnative fishes.

13.0 Parasites and Diseases

A survey of diseases and parasites of endangered fishes in the Upper Colorado River Basin in 1981 (Flagg 1982) revealed that Colorado pikeminnow are infected by a variety of parasites, but none appear to singly lead to death of individuals. The principal parasites are an intestinal tapeworm and an external parasitic copepod, and the protozoans *Myobolus* sp. and *Trichodina sp.*, as well as the trematode *Ornithodiplostomum* sp. Bass tapeworms (*Proteocephalus ambloplites*) were found in 65% of stomachs from fish larger than 200 mm TL in the Green River (Vanicek 1967). Vanicek (1967) also reported that P. Dotson (unpublished data, Utah Department of Fish and Game, Salt Lake City, 1962) found tapeworms in 80% of Colorado pikeminnow examined. A cestode identified as *Proteocephalus ptychocheilus* was found in Colorado pikeminnow from the upper basin (Flagg 1982). This may be the same species reported by Vanicek (1967), but further study has not been conducted to resolve the taxonomic discrepancy. Osmundson (1987) reported the first occurrence of Asian tapeworm (*Bothriocephalus achielognathii*) in hatchery-raised Colorado pikeminnow stocked in riverside ponds along the Upper Colorado River. Asian tapeworms were identified in wild Colorado pikeminnow from the Colorado River downstream of Moab, Utah, in 1991 (personal communication, D. Osmundson, USFWS). The parasitic copepod (*Lernaea cyprinacea*) is common in Colorado pikeminnow and has been reported by several investigators (Hagan and Banks 1963; Vanicek 1967; Flagg 1982). This parasite is believed to be alien to the Colorado River Basin, and transferred from other river basins via non-native fishes.

14.0 Diet

Adult Colorado pikeminnow are considered piscivores and the main historic predator of the Colorado River Basin (Vanicek and Kramer 1969; Minckley 1973; Holden and Wick 1982). Adults reach a large size with a large mouth capable of ingesting the largest fish native to the system; however, as a member of the minnow family, Colorado pikeminnow lack jaw, vomerine, and palatine teeth, and instead possess large pharyngeal teeth located on the first modified gill arch at the base of the throat. The teeth of this "pharyngeal mill" overlap with the swallowing action of the fish and serve to masticate and force food into the gullet.

Young Colorado pikeminnow consume mainly insects and crustaceans but quickly transition their diet to fish with size and age. The principal food items of young up to about 50 mm TL in nursery backwaters are cladocerans, copepods, and midge larvae (Vanicek 1967; Jacobi and Jacobi 1982; Muth and Snyder 1995). Insects became important for fish up to about 100 mm TL, after which fish are the main food item. Vanicek (1967) reported Colorado pikeminnow as small as 50 mm TL with fish remains in their guts, and Muth and Snyder (1995) reported fish remains in the gut of a Colorado pikeminnow 21 mm TL. Young in hatchery troughs may become cannibalistic at sizes of less than 50 mm TL (personal communication, F. Pfeifer, USFWS).

Adults consume primarily soft-rayed fishes, including bluehead sucker (*Catostomus discobolus*), flannelmouth sucker (*C.latipinnis*), red shiner, sand shiner, and fathead minnow (Osmundson 1999). Colorado pikeminnow have also been reported with channel catfish lodged in their throat that may be a cause of death for the pikeminnow (McAda 1980; Pimental et al. 1985). Colorado pikeminnow have been caught by anglers using various baits, including Mormon crickets (*Anabrus migratorius*; Tyus and Minckley 1988); carcasses of mice, birds, and rabbits (Beckman 1963); and artificial lures and spoons (Quartarone 1995).

15.0 Water Quality

15.1 Selenium

Selenium contamination is a water-quality factor that impacts localized portions of endangered fish populations in the Colorado River System (USFWS 1998, 2002b). Selenium is a naturally occurring element that is required at low concentrations by all life forms, but at high concentration in streams and lakes, it can lead to reduced reproduction and deformities in fish and in waterfowl. In the Upper Colorado River Basin, selenium comes from the Mancos shale where it is picked up by water seeping from canals and ponds, and percolating through soils beneath irrigated fields and lawns (B. Osmundson et al. 2000). It is shown to adversely affect reproduction and recruitment in freshwater fish species (e.g., Lemly 1996; Hamilton 2003; Holm et al. 2003, 2005; Palace et al. 2004a, 2004b; Hinck et al. 2007).

The effects of selenium on various life stages of the Colorado pikeminnow have been investigated (Hamilton 1995; Hamilton et al. 2003, 2004). Hamilton (1999) hypothesized that historic selenium contamination of the upper and lower Colorado River basins contributed to the decline of these endangered fish by affecting their overall reproductive success. Levels of selenium contamination in certain reaches of endangered fish critical and occupied habitat exceed those shown to impact fish and wildlife elsewhere (e.g., Stephens et al. 1992; Stephens and Waddell 1998; Thomas et al. 1998; Simpson and Lusk 1999; U.S. Bureau of Reclamation 2006; Thomas et al. 2008). Tissue samples from endangered fish inhabiting the San Juan River (Simpson and Lusk 1999) and from grow-out ponds of the Upper Colorado River (B. Osmundson et al. 2008) had selenium concentrations greater than toxicity guidelines for fish muscle tissue suggested by Lemly (1996) and NIWQP (1998) for protection of reproductive health in freshwater fish. The EPA and individual states have water quality standards for selenium toxicity; current EPA chronic selenium standards of 5 µg/L total and 4.6 µg/L dissolved are under review.

In 1994, muscle plugs were collected from a total of 39 Colorado pikeminnow captured at various Colorado River sites in the Grand Valley for selenium residue analysis (Osmundson et al. 2000). The muscle plugs collected from 16 Colorado pikeminnow captured at Walter Walker State Wildlife Area (WWSWA) contained a mean selenium concentration of 17 µ/g dry weight, which was over twice the recommended toxic threshold guideline concentration of 8 µ/g dry weight in muscle tissue for freshwater fish. Because of elevated selenium concentrations in muscle plugs in 1994, a total of 52 muscle plugs were taken during 1995 from Colorado pikeminnow staging at WWSWA. Eleven of these plugs were from fish previously sampled in 1994. Selenium concentrations in 9 of the 11 recaptured fish were significantly lower in 1995 than in 1994. Reduced selenium in fish may in part be attributed to higher instream flows in 1995 and lower water selenium concentrations in the Colorado River in the Grand Valley. In 1996, muscle plugs were taken from 35 Colorado pikeminnow from WWSWA, and no difference in mean selenium concentrations were detected from those sampled in 1995.

Some tributaries to the San Juan River carry higher concentrations of selenium than found in the mainstem (Thomas et al. 1998). Increased selenium concentrations may also result from the introduction of groundwater to the mainstem of the river along its course (Keller-Bliesner, Inc. 1999). Although these levels are diluted by the flow of the San Juan River, the net impact is a gradual accumulation of the element in the river as it travels downstream. For example, concentrations of selenium in water samples collected from the mainstem San Juan River exhibited a general increase in maximum recorded values with distance downstream from Archuleta, New Mexico, to Bluff, Utah, (<1 microgram per liter [µg/L] to 4 µg/L) (Wilson et al. 1995). The safe level of selenium concentrations for protection of fish and wildlife in water is considered to be <2 µg/L, and chronically toxic levels are considered to be >2.7 µg/L (Lemly 1993; Maier and Knight 1994; Wilson et al. 1995). Diet is the primary source for selenium in fish (Lemly

1993; Hamilton and Buhl 1995). Thus, sediment and biotic analyses are necessary to further elucidate the risk of selenium in water to fish and wildlife.

15.2 Mercury

The impact of mercury (or the functional relationship of mercury and reproductive impairment) on the Colorado pikeminnow was derived for purposes of the PVA and is described in the PVA report.

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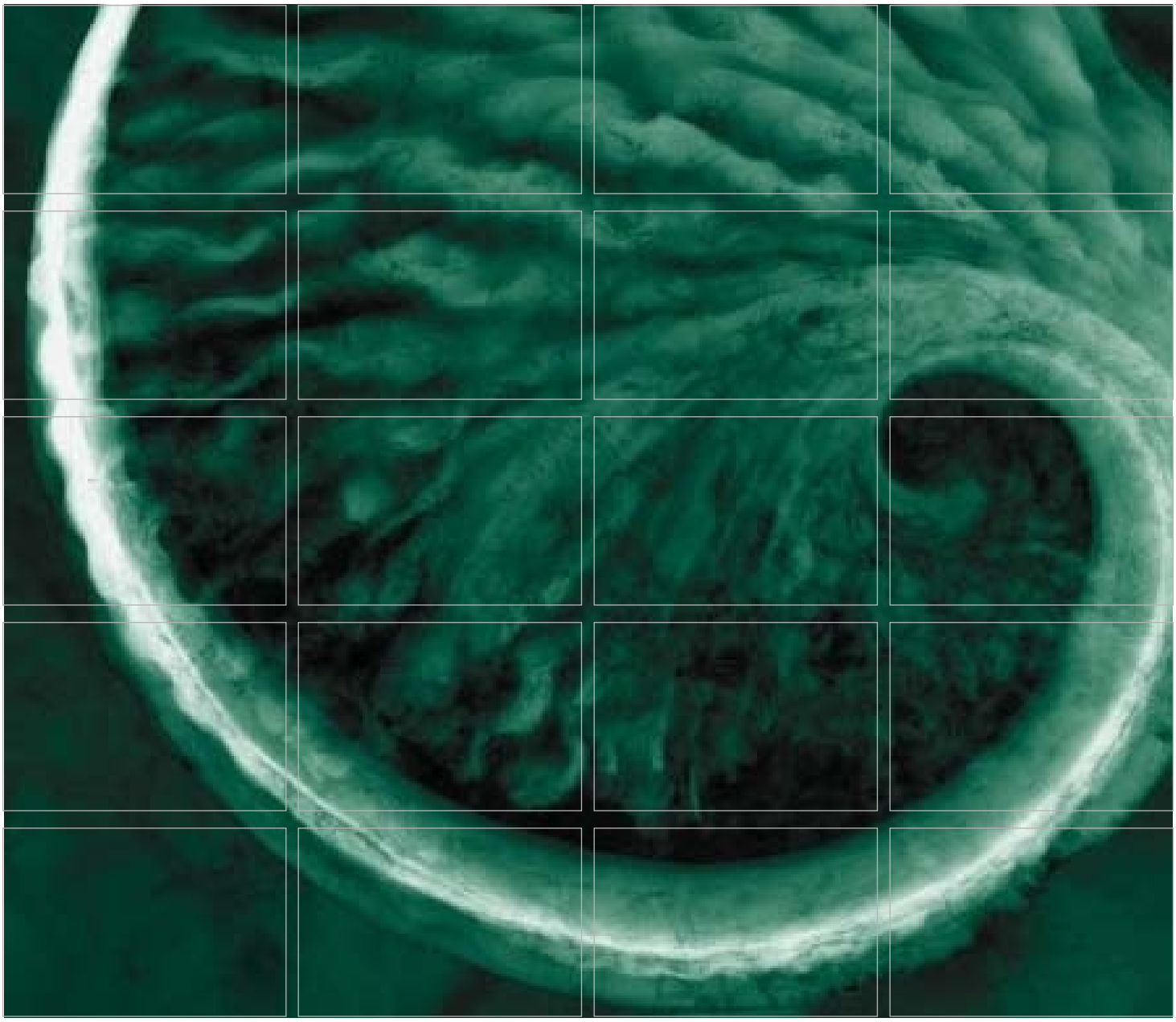
Appendix C

Mercury Functional Relationship
M. Shibata



Appendix C
Mercury Functional Relationship

Prepared for:

Colorado Pikeminnow
Population Viability
Analysis

BHP Billiton Mine Management Company (MMCo)
Farmington, NM

July 2014

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Appendix C
Mercury Functional Relationship

Colorado Pikeminnow Population Viability Analysis

BHP Billiton Mine Management Company
Farmington, NM

July 2014

Project No. 0224438

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Add-1. Metrics for Calculating Age from Body Length

1.0 Introduction

The purpose of this appendix is to describe the approach and present the results of the mercury (Hg) functional relationships that were developed for use in the population viability analysis (PVA) model for the San Juan River (SJR) Colorado pikeminnow (*Ptychocheilus lucius*) (Miller 2014). The Hg functional relationships characterize injuries to demographic inputs (e.g., fecundity, survivorship) as a function of Hg concentrations in fish tissues. The Hg functional relationships developed for the PVA model use the best available science to characterize the relationship[1] between tissue concentrations (also tissue residues or tissue burdens) of Hg in fish and demographic parameters. Methods and findings were shared with and approved by the PVA Team.

2.0 Colorado Pikeminnow Population Viability Model: Demographic Metrics of Interest

The CPM PVA model employs an age-structured matrix model to predict population abundances given specified environmental conditions. Fundamental demographic inputs to the PVA model include estimates of age-specific fecundity (*f*) and survival rates (S_{age}). For the CPM PVA model, *fecundity* is defined as the average number of offspring that are produced per adult female and that survive to one year of age (Age 0). Fecundity is defined mathematically as:

Fecundity (*f*) = %spawning females • #eggs per female • %hatching success of eggs • %larval survivorship (S_0)

Survivorship (S_{age}) is the average annual age-specific survival from Age A to Age A + 1 year, as follows:

- Juvenile survival (S_1) is the survival of 1-yr-old juveniles to two years of age;
- Subadult-1 survival (S_2) is the survival of first-year subadults to three years of age;
- Subadult-2 through subdult-5 survival (S_3, S_4, S_5, S_6) is the annual survival rate of second-year subadults through six years of age; and
- Adult survival (S_7) is the annual survival rates of fish reaching sexual maturity and older.

Parameters used in the CPM PVA model to calculate fecundity and characterize age-specific survivorship were used to guide the selection of ecotoxicity studies/data used to develop Hg functional relationships. For example, reproductive ecotoxicity studies that examined and reported results for the following fecundity-related test endpoints were queried and reviewed: percent females spawning, number of eggs per female, percent of eggs that hatched, and percent survival of larvae [Age 0].

[1] Commonly referred to as dose-response curve

3.0 Review of Dillon *et al*. (2010)

The Dillon et al. (2010) study was recommended by the U.S. Fish and Wildlife Service (USFWS) for developing Hg functional relationships. Dillon et al. (2010) reports Hg dose–response curves for early life stage (ELS)[2] and juvenile-adult stage fish derived using data from peer-reviewed, published tissue-based ecotoxicity studies. For the most part, the Dillon et al. (2010) study uses the same dataset selected by Beckvar *et al.* (2006).

3.1 Fish Tissue-Based Ecotoxicity Study Features

Ecotoxicity studies reporting biological effects with respect to fish tissue residues are limited as compared to studies reporting the same with respect to environmental concentrations (e.g., concentrations in water and/or food). Data used by Dillon *et al.* (2010) were obtained from 11 fish tissue-based ecotoxicology studies for Hg— 3 of these 11 studies examined Hg in ELS fish tissues. Notable features of the Dillon *et a*l. (2010) study included:

- Focus on ecotoxicological endpoints[3] related most directly to lethality including, mortality, severe developmental abnormality, hatching success, and spawning success.
- Use of test results that were dose-responsive[4].
- Fish tissue-based Hg ecotoxicity data included observations that were significantly different or not significantly different from controls based on statistical tests.
- A percent control-normalized response (%CNR) was calculated for each experimental treatment and endpoint using:

  %CNR = (treatment response / control response) • 100

- Different test endpoints were standardized/consolidated using the common metric of *percent injury* (%injury), which is defined as:

  %injury = 100% - %CNR

- Injury was summed if multiple endpoints were reported within an experiment.
- Dose-response (%injury-Hg tissue residue) curves were created using GraphPad PRISM® using the general non-linear equation:

  %Injury = $100/\left[1+10^{(\log Injury_{50}-\log x)(\text{Hill Slope})}\right]$

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2 Reported effects (e.g., hatching success, %larval survivorship) at different concentrations in eggs or larval stage fish.

3 *Ecotoxicological endpoints* are the types of adverse effects (e.g., percent eggs hatching) examined in an ecotoxicity study.

4 Not specifically defined by authors

… where *x* is Hg tissue residue (mg/kg, ww)[5] and *Injury50* is the concentration causing a response halfway between 0% and 100% injury.

- Separate *%injury-Hg tissue residue* curves were created for juvenile-adult stage and ELS fish.

3.2 Strengths / Limitations of Using Dillon et al. (2010) To Support the Development of the PVA Model

The strengths / limitations of using Dillon *et al*. dose-response curves to establish Hg functional relationships to support the development of the PVA model are identified below and noted in Table C3-1:

Strength

- Dillon study and sources of data were obtained from studies in peer-reviewed journals; and
- Separate, single dose-response curves for ELS (eggs/larval tissues) and juvenile/adult stage are provided.
-

Limitations

- Authors did not define what was meant by "dose-responsive";
- Did not account for responses that were not significantly different from responses observed for controls — i.e., egg/larva/juvenile/ adult fish that were, by study design, not exposed to Hg;
- Over 50% of the data are derived from fathead minnow; and
- Pooled lethal (e.g., mortality) and sublethal (e.g., reproductive) data.

[5] *mg/kg, ww* = milligrams per kilogram, wet weight

Table C3-1. Strengths / Limitation of Using Dillon et al. (2010) to Support Development of CPM Hg Functional Relationships for the PVA Model

Subject	Description	Dose-Response Consequence
Strengths		
Peer-reviewed source	• Undergone validation / review	—
Separate dose-response for ELS and juvenile-adult	• Dose-response curves are for life stages of interest for use in the PVA model.	—
Limitations		
Pool lethal / sublethal data	• Likely to overestimate sublethal injury and underestimate lethal injury • Likely to result in expanded variance about best-fit curve	—
Majority of the data are derived from fathead minnow	• Fathead minnow are considered tolerant species • Fathead minnow are short-lived species (2-3 years) compared to CPM (40+ years)	underestimate
"Dose-responsive" data is not defined	• Presumably includes/examines data only if increasing injury is observed with increasing tissue residues	overestimate
Does not account for no difference from controls	• Any adverse difference from control is considered to be an injury although variance in data would suggest no difference	overestimate
Does not define %injury that is biologically significant	• Any injury is considered to be biologically significant	overestimate

4.0 Mercury Functional Relationships

As with much "found" data[6], some limitations identified for the Dillon *et al*. (2010) study can be ameliorated by stratifying the data and de-constructing the dose-response curves by age-class-, fecundity-, and survivorship-related metrics of interest (pers. comm. CPM PVA Team, 2014 March). Deconstruction of dose-response curves will provide Hg functional relationships that are appropriate for specific for age-class and demographic inputs used in the PVA modeling.

4.1 Mercury Tissue-Residue Ecotoxicity Data

With consensus of the PVA Team, methods used to select Hg tissue-residue ecotoxicity data were consistent with Dillon *et al*. (2010). Fish tissue-based Hg ecotoxicity data were obtained from studies that were found in peer-reviewed journals — i.e., no data from "grey literature" or similar sources were used. Starting with studies used in Dillon *et al*. (2010), Hg ecotoxicity studies for fishes were queried. Of the 86 studies identified, 48 abstracts were reviewed (Table C4-1).

[6] "Found data" are data collected for another purpose, but may be useful for the study at-hand.

Table C4-1. Query of Tissue-Based Ecotoxicity Studies — Summary

Query / Review	Count
Studies Identified	86
Abstracts Reviewed	48 of 86
Review Studies[1]	5
Tissue Residue Only Studies[2]	17
Tissue-Based Ecotoxicity Studies[3]	26

Notes:
1 review of existing literature
1 reported only tissue concentrations
2 some studies reported multiple endpoints

Of the 48 abstracts examined, data from 26 fish tissue-based ecotoxicity studies were selected and used to develop Hg functional relationships. These 26 ecotoxicity studies were selected because they met the following minimum reporting requirements:

- Test species
- Life stage exposed
- Exposure route
- Exposure duration
- Control treatment
- Tissue type analyzed
- PVA-relevant biological responses
- Bounded effect /no effect tissue concentrations

The other 22 studies either reported only tissue residues (i.e., no paired biological responses) or reviewed existing studies to characterize the state-of-the-science and/or develop assessment tools.

To develop Hg functional (injury) relationships to support of the PVA model, the following were performed:

- Tissue-based data for egg, larval, juvenile, and adult stage fish were selected;
- Hg ecotoxicity data were stratified by ELS and juvenile-adult fish tissues;
- Ecotoxicity data to support PVA modeling (life stage and demographic input) included:

Relevant Endpoints for PVA Model	Count
Reproduction / Fecundity (ELS)	• %hatching success of eggs • %larval survivorship
Reproduction / Fecundity (Adult)	• %spawning females • %maternity • %hatching success of eggs • %larval survivorship
Survivorship	• %juvenile survivorship • %adult survivorship

- "Dose-responsive" data were used—i.e., data where a trend of increasing injury with increasing fish tissue residue was observed in the study; and
- The same equations were used to calculate %CNR and %Injury.

Notable deviations from methods used by Dillon et al. (2010) were used to arrive at the Hg functional relationship dataset as follows:

- Where both female and male data were available, female data were used.[7]
- Where continuous and discontinuous exposure to Hg data were available, used continuous exposure data

Of the 26 fish tissue-based ecotoxicity studies reviewed, data from 14 studies were used to develop the Hg functional relationships to support PVA modeling[8], with approximately 70% overlap with the Dillon et al. (2010) dataset (Table C4-2).

Table C4-2. Tissue-Based Ecotoxicity Studies Used To Support Colorado Pikeminnow PVA Modeling — Summary

Query / Review	Count
Tissue-Based Ecotoxicity Studies[1]	26
Ecotoxicity Studies Considered for PVA	14 of 26
Number of Data	128
Data Overlap with Dillon	70%

Notes:
1 some studies reported multiple endpoints

A summary of the tissue-based ecotoxicity data is shown in Table C4-3. Fish tissue-based ecotoxicity data considered and selected for use in developing Hg functional relationships are provided in Attachment A.

[7] Initially, the PVA model for CPM only modeled female demography. As explained in Miller (2014), use of female data only is a common approach in the matrix-based analysis of wildlife populations in which there are few if any measurable differences in demographic behavior between males and females.

[8] Recall data from 11 studies were used in Dillon et al. (2010).

Table C4-3. Tissue-Based Ecotoxicity Data Used To Support Colorado Pikeminnow PVA Modeling — Summary

Attribute	Early Life Stage	Post-Larvae Life Stage (juvenile- adult life stages)	
	% Reproductive Injury	Adult* % Reproductive Injury	% Juvenile-Adult Survivorship Injury
No. Data (n)	27	64	32
No. Studies	3	6	6
No. Fish Species	3	3	5
Fish Species	mud minnow brook trout trout (unspecified)	fathead minnow mud minnow brook trout	fathead minnow Japanese medaka mud minnow brook trout walleye

* Studies reporting reproductive impairment based on Hg residues in juvenile fish tissues were not used in the PVA model

4.2 Mercury Functional Relationships for Percent Injury

Data were stratified and Dillon's dose-response curves were de-constructed for life stages and inputs of interest for the CPM PVA model:

- ELS reproductive (fecundity) injury;
- Adult reproductive (fecundity) injury;
- Juvenile survivorship; and
- Adult survivorship.

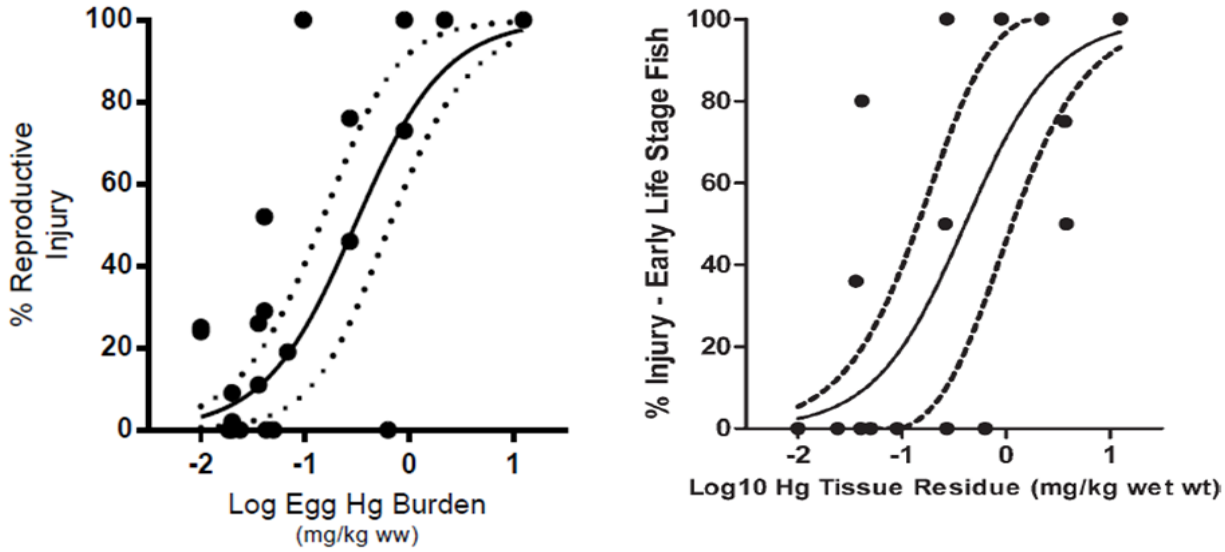
Note that the percent egg hatching injury as a function of Hg residues in the subsequently surviving juvenile fish tissues was not developed further because it was not included in the PVA model (Miller 2014).

4.3 Early Life Stage Reproductive Injury

The ELS reproductive injury as a function of Hg tissue residue relationship (dose-response curve) is shown in Figure C4-1. The Dillon et al. (2010) curve is shown alongside for perspective. Although initially considered, the Hg functional relationship for ELS reproductive injury was not used in the development of the PVA model. The PVA Team agreed that the percent reproductive injury as a function of Hg residues in egg/larval tissues would not be included in the PVA model (PVA Team 2014b) because Hg concentrations in ELS (i.e., eggs, larva) for SJR CPM have not been measured.

Figure C4-1. Early Life Stage: Percent Reproductive Injury vs. Log Tissue Hg Residue (mg/kg, ww)

(a) PVA Model *(b) Dillon et al. (2010) Early Life Stage Injury*



4.4 Adult Stage Reproductive Injury

The adult female reproductive injury as a function of Hg tissue residue relationship (dose-response curve) is shown in Figure C4-2. The Dillon et al. (2010) curve is shown alongside for perspective.

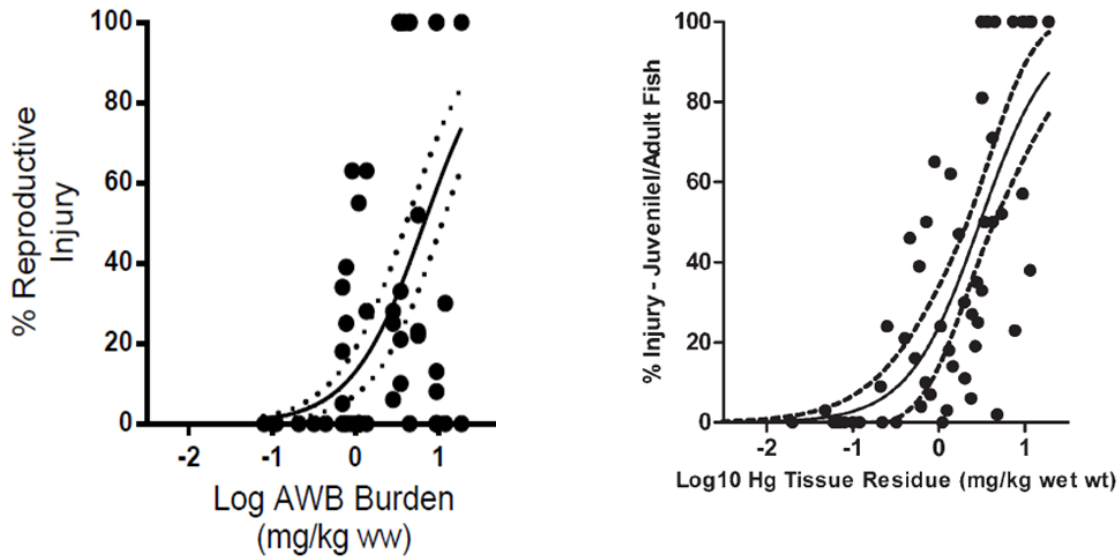
Ecotoxicity endpoints used to develop the Hg relationship included:

- Percent female spawning;
- Number of eggs per female;
- Percent hatching success of eggs; and
- Percent survivorship of newly hatched larvae.

In the PVA model, this relationship will be used to modify the fecundity (*f*) parameter as a function Hg concentration in the sexually mature (7-year-old) SJR CPM adult.

Figure C4-2. Adult Stage: Percent Reproductive Injury vs. Log Whole Body Hg Residue (mg/kg, ww)

(a) PVA Model *(b) Dillon et al. (2010) Juvenile-Adult Injury*



Note that the Dillon et al. curve includes mortality data for both juvenile and adult stage fish. The PVA model considers separately fecundity and survivorship for post-larval life-stages. Hence, deconstruction to separately characterize fecundity- and survivorship-related effects was considered to provide more appropriate relationships to support the PVA modeling effort.

The generalized model used to characterize %reproductive injury as a function of log Hg tissue residue is:

$$\%\text{reproductive injury } (y) = 100 \,/\, \left\{1 + 10^{(\log Injury_{50} - \log x)(Hill\ Slope)}\right\}$$

… where the $\log EC_{50} = 0.8247$ and the Hill Slope is 1.013.

4.5 Juvenile-Adult Stage: Survivorship Injury

The juvenile-adult survivorship injury *vs*. Hg tissue residue relationship (dose-response curve) is shown in Figure C4-3. Dillon et al. (2010) had no corresponding curve. Ecotoxicity study data used to develop the Hg relationship included:

- Percent juvenile survivorship; and
- Percent adult survivorship.

As seen in Figure C4-4, percent survivorship injury data for juvenile and adult life-stages showed a considerable amount of overlap. Hence, survivorship data for these two life-

stages were pooled to obtain an increased sample size to characterize post-larval survivorship (i.e., S_1 through S_7).

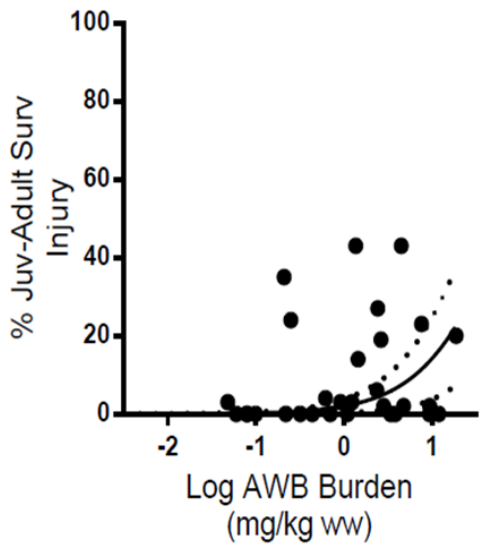
The generalized model used to characterize %juvenile-adult survivorship injury as a function of log Hg tissue residue is:

$$\%\text{survivorship injury } (y) = 100 \,/\, \left\{1 + 10^{(\log Injury_{50} - \log x)(Hill\ Slope)}\right\}$$

… where the $\log EC_{50}$ = 1.869 and the Hill Slope is 0.90.

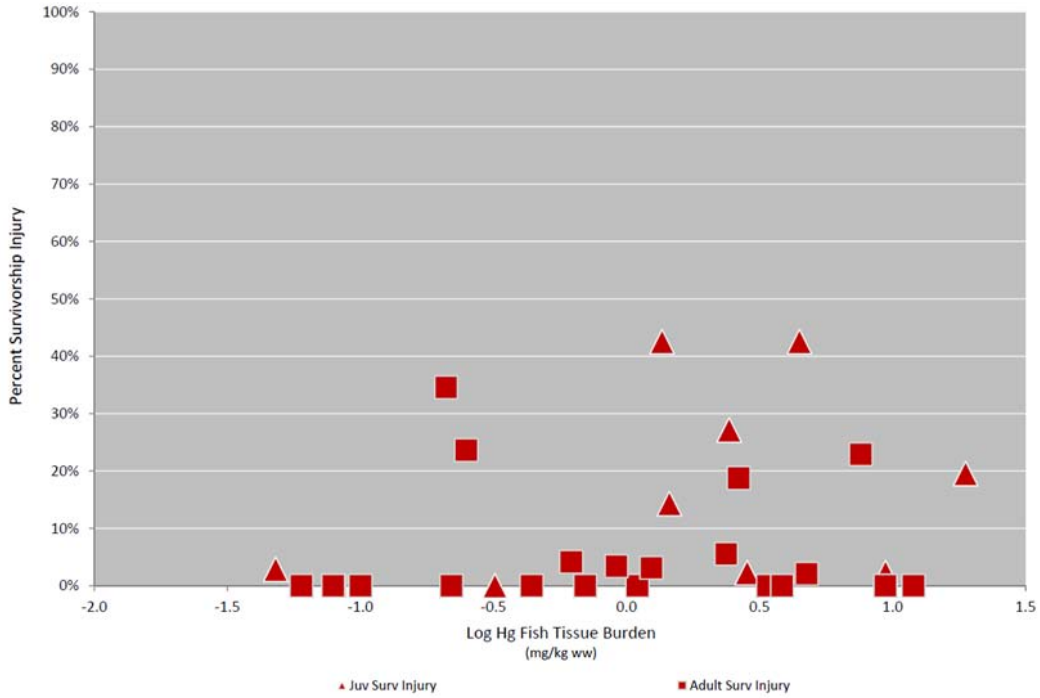
Figure C4-3. Juvenile-Adult Stage: Percent Survivorship Injury vs. Log Whole Body Hg Residue (mg/kg, ww)

(a) PVA Model



(b) Dillon et al. (2010) – not available in study

Figure C4-4. Juvenile-Adult Stage: Percent Survivorship Injury Plot



4.6 Uncertainty Analysis

Principal uncertainties in applying the Hg functional relationship directly in the PVA model for CPM are summarized in Table C4-4 and include:

- Test species-to-CPM extrapolation;
- %Injury does not consider whether response is significantly different from control;
- Only 'dose responsive' data were used to develop functional relationship—data showing no relationship (i.e., no increasing %injury) with Hg tissue residues were not used;
- Consolidated injury metric given considerable variability in study designs — (e.g., test endpoints, test duration); and
- Definition of percent injury that is biologically significant.

Table C4-4. Summary of Uncertainty

Source of Uncertainty	Direction	Magnitude
Species Extrapolation	?	?
Use dose-responsive data only	overestimate	?
Consolidated injury metric	?	?
Difference from control	overestimate	?
Biologically significant percent injury	overestimate	?

see also Table C3-1
Legend:
overestimate – likely to overestimate %injury
? -- unknown

Test Species-to-CPM Extrapolation. The toxicity of Hg in fish tissues of CPM were based on a direct extrapolation from species used in tissue-based ecotoxicity studies. A common feature of test species is their robust nature to be raised and maintained under laboratory conditions. As seen in Table C4-3, ecotoxicity data for five fish species were used to characterize Hg functional relationships. Fathead minnow comprised much of the ecotoxicity data and are considered to be a robust / tolerant test species. However, little is known regarding the relative sensitivity of CPM with respect to the fish species listed in Table C4-3.

Use 'Dose-Responsive' Data Only. Dillon et al. (2010) focused and used data for 'dose-responsive' study endpoints. Although not specifically defined, it was apparent that only data that showed an increasing adverse effect with increasing Hg tissue residues were used. To provide a health-protective characterization of potential injury, the PVA Team determined the best scientific approach was to be consistent with Dillon et al. (2010). Hence, ecotoxicity data that showed no trend with increased Hg tissue concentration were not used to generate Hg functional relationships. The use of this dataset is considered to overestimate characterizations of injury as the evaluations excluded data that showed no ill effects with increasing Hg concentrations in fish tissues.

Consolidated Injury Metric. Consistent with Dillon et al. (2010), different test endpoints were normalized and consolidated into a single common metric, percent injury. This normalization assumes a degree of equivalency in sensitivity among endpoints. However, it is known that some test endpoints are more sensitive than others. In addition to being more compatible with the PVA model, this understanding that lethal and sublethal effects generally occur at different concentrations of Hg in tissues were reasons for de-constructing the Dillon et al. (2010) juvenile-adult dose-response curve into separate Hg functional relationship curves for reproductive injury and survivorship injury.[9]

Difference From Controls. Consistent with Dillon et al. (2010), tissue-based ecotoxicity data were used irrespective of whether observed effects were significantly different from the control treatment—i.e., the magnitude of an effect was treated as significantly different from the control treatment. This assumption is considered to overestimate

[9] Reproductive injury typically occurs at lower concentrations of Hg in tissues (i.e., is considered a "more sensitive" injury) than survivorship injury (see also Figure C5-1).

characterizations of injury as some effects were within the bounds observed in the control group.

Biologically Significant Percent Injury. As with Dillon et al. (2010), percent injury that is biologically significant for fecundity or survivorship was not defined. Hence, any injury was considered to be biologically significant. This assumption is considered to overestimate characterizations of injury as biological systems are capable of coping with some degree of injury.

5.0 Conclusions

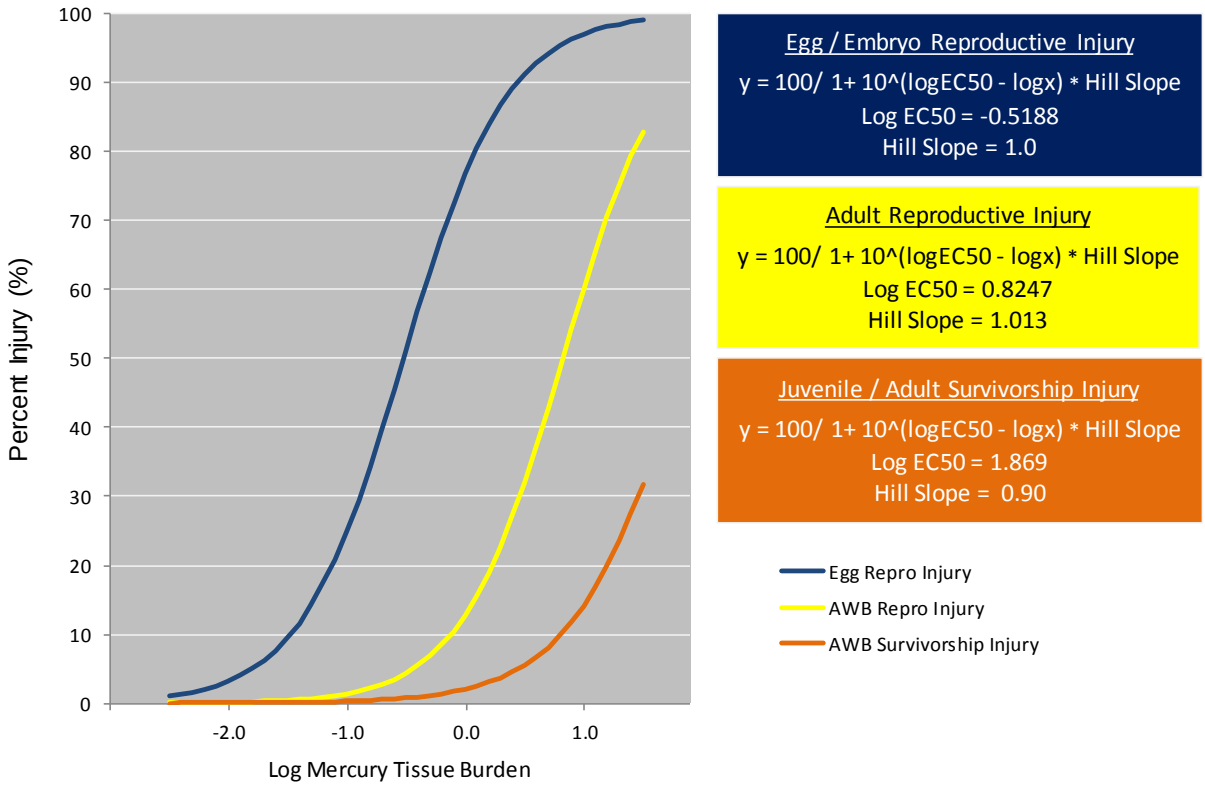
Models used to describe the relationship between percent injury and Hg tissue residues used in the PVA model are summarized in Table C5-1 and are shown in Figure C5-1. Note that the functional relationship for ELS that is shown in Figure C5-1 is for perspective only and was not used in the PVA model.

Table C5-1. Hg Functional Relationship Models Used in PVA Model

PVA Parameter	%Injury Model
fecundity (*f*)	$y = 100 / \{1 + 10^{(0.8247 - \log x)(1.013)}\}$
survivorship (S_1 to S_7)	$y = 100 / \{1 + 10^{(1.869 - \log x)(0.90)}\}$

… where *x* is the concentration of Hg in tissue (mg/kg ww) and *y* is the percent injury (%injury)

Figure C5-1. % Injury vs. Hg Functional Relationships Used in PVA Model



Where the direction of uncertainty is known/likely, assumptions used in the developing Hg functional relationships tended to overestimate percent injury as a function of Hg tissue residues (Table C4-4). Hence, incorporation of Hg functional relationships in the PVA model is considered to result in a health-protective evaluation of SJR CPM population trajectories.

6.0 Literature Cited

Beckvar N., T.M. Dillon, and L.B. Read. 2005. Approaches for linking whole-body fish tissue residues of mercury or DDT to biological effects thresholds. *Environ. Toxicol. Chem.* 24: 2094–2105.

CPM PVA Team. 2013. Colorado Pikeminnow Population Viability Analysis Workshop. December 17-18, 2013. Albuquerque, NM.

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Dillon, T., N. Beckvar, and K. Kern. 2010. Residue-Based Mercury Dose-Response in Fish: An Analysis Using Lethality-Equivalent Test Endpoints. *Environ. Toxicol. Chem.* 29: 2559–2565.

Miller, P.S. 2014. Population Viability Analysis for the Colorado Pikeminnow (*Ptychocheilus lucius*) in the San Juan River. Colorado Pikeminnow Population Viability Analysis.

Valdez, R.A. 2014. Life History and Demographic Parameters of the Colorado Pikeminnow. Colorado Pikeminnow Population Viability Analysis.

Attachment A

TISSUE-BASED ECOTOXICITY DATA CONSIDERED AND USED TO GENERATE MERCURY FUNCTIONAL RELATIONSHIPS TO SUPPORT THE COLORADO PIKEMINNOW POPULATION VIABILITY ANALYSIS MODEL

(please see supplemental electronic file)

Addendum

CHARACTERIZING MERCURY TISSUE RESIDUES IN COLORADO PIKEMINNOW WITH RESPECT TO LENGTH AND AGE

Mercury Tissue Residue vs. Body Length

Mercury (Hg) tissue residues measured in Colorado pikeminnow (CPM) as a function of body length were provided by Dr. J. Lusk (USFWS) (Figure Add-1). The PVA Team requested that a sigmoidal relationship be used to predict Hg tissue residues for fish less than 200 mm in length. GraphPad Prism® was used to best fit a sigmoidal curve through the data presented in Figure Add-1 — the best-fit sigmoidal model is shown in Figure Add-2.

Figure Add-1. Mercury Tissue Residue vs. Body Length of Colorado Pikeminnow (from Lusk 2013)

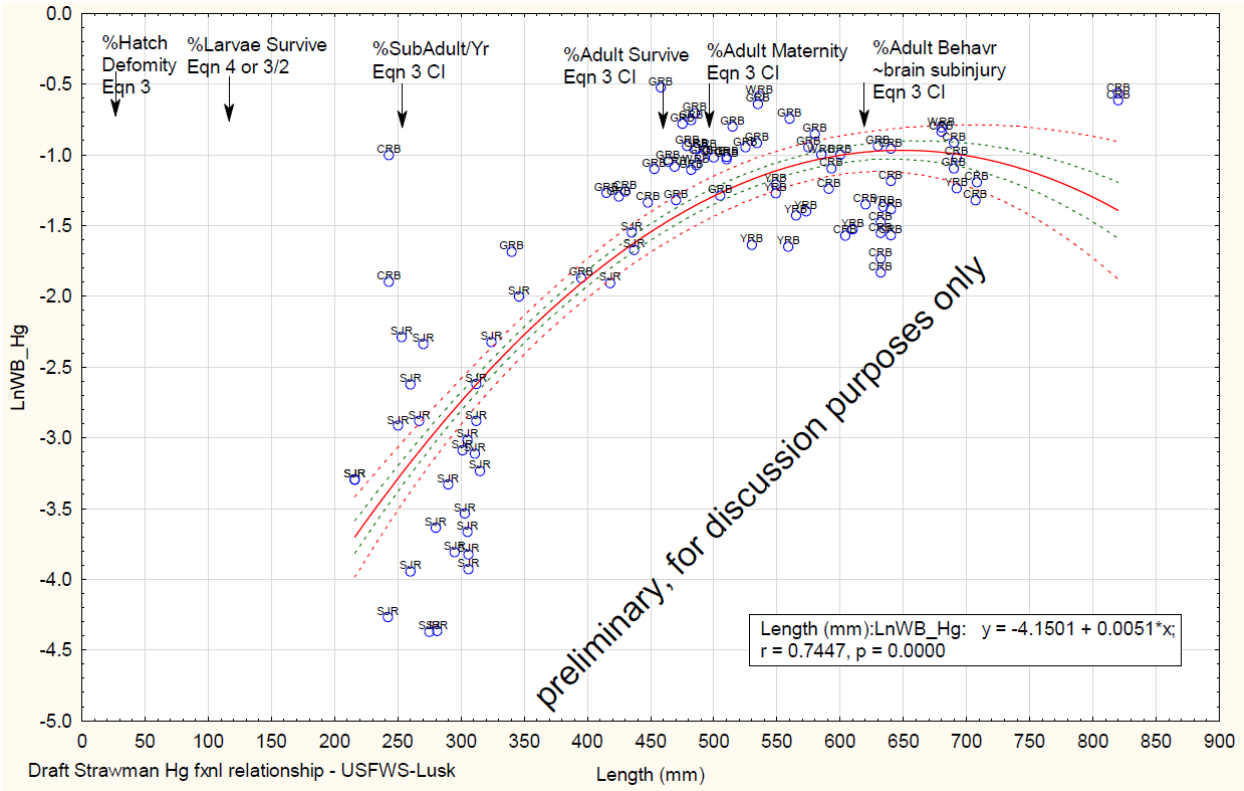


Figure Add-2. Mercury Tissue Residue *vs.* Body Length of Colorado Pikeminnow — Sigmoidal Model Fit to Data (from Lusk 2013)

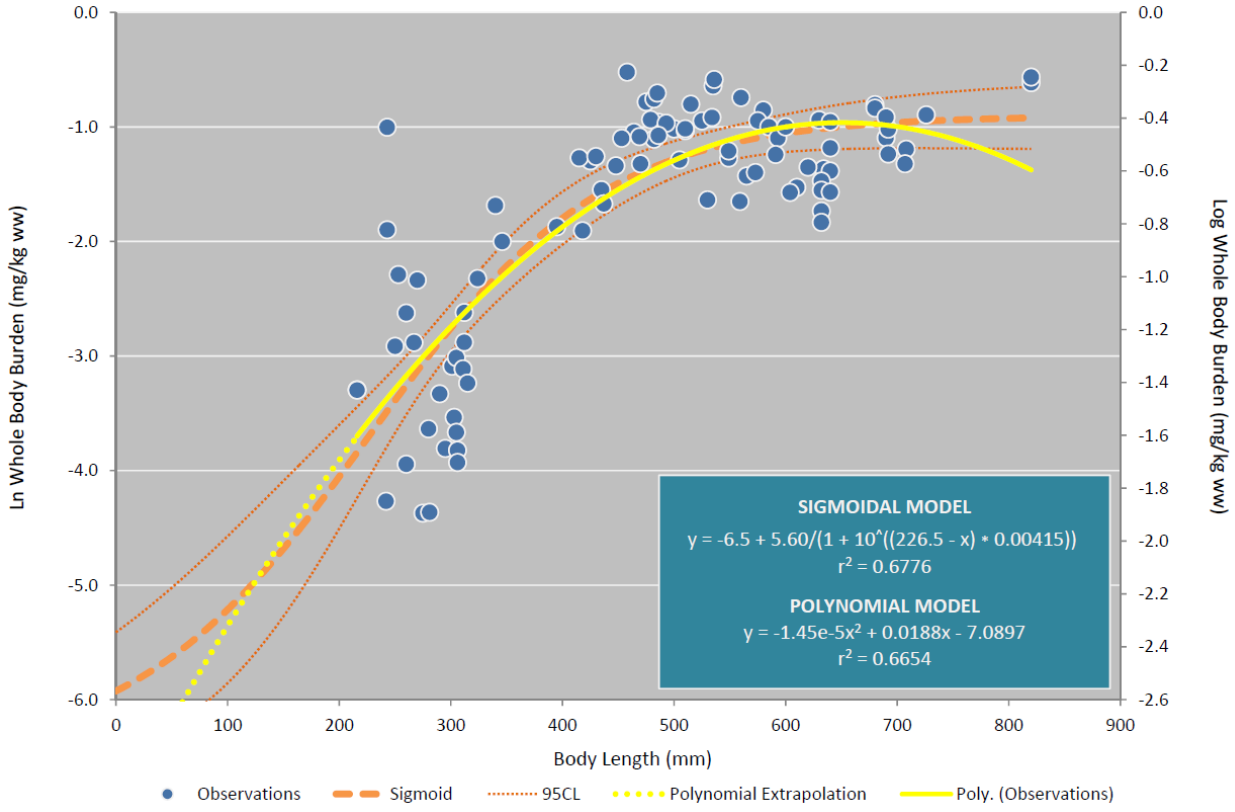


Table Add-1. Metrics for Calculating Age from Body Length

Von Bertalanffy Growth Function

$$L_{(t)} = L_{inf} \bullet \{1 - \exp[-K \bullet (t - t_0)]\}$$
$$t = \{\ln[1 - (L_{(t)} / L_{inf})] / -K\} + t_0$$

… where *t* is age (yrs), *L* is length at age *t*, *inf* is , and *K* is length at age *t*

Metrics from R.Valdez (2014)

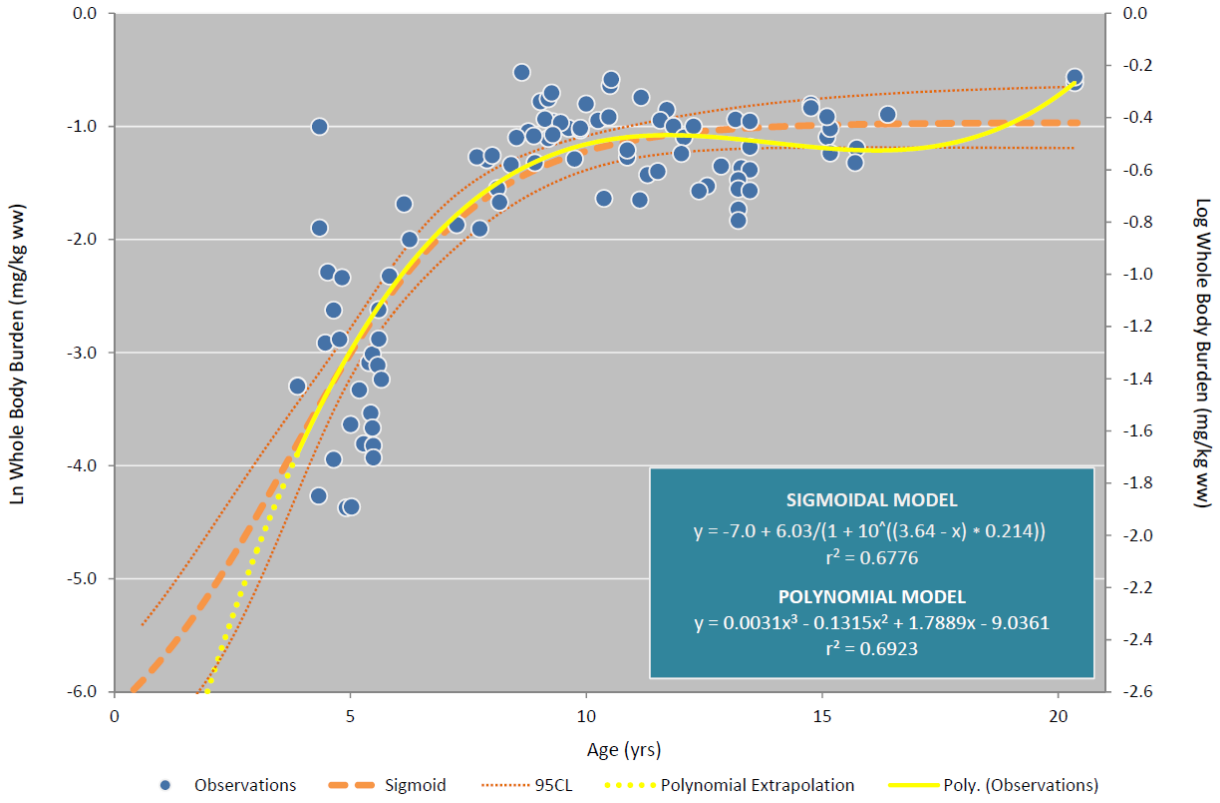
System	Colorado R.	Green R.	Green R.	Combined	Combined
Author	Osmundson & White 2009	Vanicek & Kramer 1969	Seethaler 1978	Musker 1981	Hawkins 1992
$\mathbf{L_{inf}}$	864.6	1144	752	1147	1152
K	0.0666	0.0748	0.1577	0.08611	0.0629
$\mathbf{t_0}$	-0.0137	0.6496	1.2963	1.0144	0.5814

Information shown in Figure Add-2 was converted to a Hg tissue residue as a function of Age as shown in Figure Add-3.

The model used to characterize Hg tissue residue as a function of body age is:

$$\text{Hg Residue [mg/kg ww]}\ (y) = -7.0 + \left\{6.03 \,/\, \left[1 + 10^{(3.64 - x)(0.214)}\right]\right\}$$

Figure Add-3. Mercury Tissue Residue *vs*. Age of Colorado Pikeminnow — Sigmoidal Model Fit to Data
(from Lusk 2013 and applying Von Bertalanffy Growth Function and metrics from Table Add-1.



Appendix D

Preliminary *VORTEX* Input Data Summary
S. Durst

VORTEX Population Viability Analysis Software
Input Data Required for Analysis

Data provided by: Scott Durst, U.S. Fish and Wildlife Service

Note: *Vortex* has the capability to model complex demographic rates, if a user thinks that greater specificity is needed. For example, breeding or survival rates could be specified as functions of adult age, population density, environmental conditions, etc. In addition, infectious disease can be modeled in more detail with the *Outbreak* software package that can be linked to *Vortex*, thereby creating a more realistic simulation of the impacts of disease on population dynamics. Contact CBSG if you would like to learn more about this additional flexibility.

Throughout the process of completing this form, it is critical to cite the appropriate data sources as justification for a given parameter value. Cite published articles wherever possible, and state the source of the data if such articles do not exist.

1. Species and geographic range for which data are provided below

Colorado pikeminnow in the San Juan, Upper Colorado, and Green River sub-basins. Also some data is derived from hatchery reared individuals, Southwestern Native Aquatic Resources and Recovery Center (SNARRC; formerly Dexter National Fish Hatchery and Technology Center).

2. Population structure: Single population or metapopulation?

If a metapopulation structure is present, demographic rates may be different for each subpopulation. You will need to document this when filling in the data below. Additionally, information on habitat connectivity, dispersal characteristics, etc. must be used when constructing a metapopulation model. Refer to the last page of the form to specify metapopulation structure data.

Single population. While there is no evidence to indicate the San Juan, Green, and Colorado River pikeminnow populations are part of the same metapopulation, it is certainly possible given the connection through Lake Powell

3. Breeding system

For "long-term" cases, paired individuals are assumed to stay with their partner until one dies or emigrates. For "short-term" cases, pairs are reshuffled each year.

Monogamous or Polygynous? _____ Long-term?_____ Short-term?_____

It appears that this species is an aggregate spawner that does not fit into these classifications.

4. At what age do females begin breeding?

5 in hatchery

5. At what age do males begin breeding?

For each sex, we need to specify the age at which the typical animal produces its first litter. The age at which they "begin breeding" refers to their age when the offspring are actually born or hatched, and not the age of sexual maturity when the parents mate.

4 in hatchery

Both sexes are thought to breed by age-7 in the wild. **Vanicek, C.D. and R.H. Kramer. 1969**. Life history of the Colorado squawfish *Ptychocheilus lucius* and the Colorado chub *Gila robusta* in the Green River in Dinosaur National Monument, 1964-1966. Transactions of the American Fisheries Society 98(2):193-208. **Seethaler, K. 1978**. Life History and Ecology of the Colorado Squawfish (*Ptychocheilus lucius*) in the upper Colorado River Basin. Thesis, Utah State University, Logan, UT. **Hamman, R.L. 1981**. Spawning and culture of Colorado squawfish in raceways. Progressive Fish Culturist 43(4):173-177. **Hamman, R.L. 1986**. Induced spawning of hatchery-reared Colorado squawfish. Progressive Fish-Culturist 48: 72–74.

6. What is the maximum breeding age?

Vortex will allow individuals to breed (if they happen to live this long) up to this maximum age. Indicate if reproductive senescence occurs in the wild before this maximum age.

45-55 years?

Osmundson, D.B., M.E. Tucker, B.D. Burdick, W.R. Elmblad and T.E. Chart. 1997. Non-spawning movements of subadult and adult Colorado squawfish in the Upper Colorado River. Final Report. U.S. Fish and Wildlife Service, Grand Junction, CO.

7. In the average year, and at optimal densities (see 12. below), what proportion of adult females produces a brood (litter or clutch)?

Unclear, sex ratios on spawning bars and hatchery scenarios range from 2:1 to 13:1.

Holden, P.B., and C.B. Stalnaker. 1975. Distribution of fishes in the Dolores and Yampa river systems of the upper Colorado basin. Southwestern Naturalist 19: 403–412. **Seethaler, K. 1978**. Life history and ecology of the Colorado squawfish (*Ptychocheilus lucius*) in the upper Colorado River basin. Master's Thesis. Utah State University, Logan, Utah. **Hamman, R.L. 1980**. Spawning and culture of Colorado squawfish, humpback chub, and bonytail chub during 1980 at Willow Beach National Fish Hatchery. Colorado River Fisheries Project workshop. U.S. Fish and Wildlife Service. **Hamman, R.L. 1981**. Spawning and culture of Colorado squawfish in raceways. Progressive Fish-Culturist 43: 173–177. **Hamman, R.L. 1986**. Induced spawning of hatchery-reared Colorado squawfish. Progressive Fish-Culturist 48: 72–74. **Tyus, H.M. 1990**. Potamodromy and reproduction of Colorado squawfish in the Green River basin, Colorado and Utah. Transactions of the American Fisheries Society 119: 1035–1047.

8. What is the magnitude of variation in the proportion of females that breed across years that is due to annual variability in the surrounding environment?
This quantity is typically defined as the extent of environmental variation (EV) for a given demographic rate. Ideally, we need this value specified as a standard deviation (SD) of the proportion breeding. If long-term quantitative data are lacking, we can estimate this variation in several ways. At the simplest intuitive level, in about 67% of the years the proportion of adult females breeding would fall within 1 SD of the mean, so (mean value) + SD might represent the breeding rate in a typically "good" year, and (mean value) – SD might be the breeding rate in a typically "bad" year.

Unknown

9. What is the sex ratio of offspring at birth?
What proportion of the year's offspring are males?

Unknown but presumably 1:1.

10. How many litters or clutches can be produced in a year?

Presumably one.

11. What is the maximum litter/clutch size?

For age-9 females 77,400 (range:57,766-113,341) for age-10 females 66,185 (range: 1,977-91,040).
Hamman, R.L. 1986. Induced spawning of hatchery-reared Colorado squawfish. Progressive Fish-Culturist 48: 72–74.

12. Is reproduction density – dependent? Yes or No
In many species, reproduction (defined here as the proportion of adult females that successfully breed in a given year) may be a function of density. Resource competition may lead to lower success at high densities, and difficulty in finding mates (Allee effect) may reduce success at low densities. Describe the form of density dependence for this species below, either graphically or numerically. What is the % breeding at optimal density? What is the % breeding when the population is at carrying capacity (see 25. below)? How does reproductive success change at high and/or low densities? What is the rate of change in reproductive success as density increases or decreases?

Unknown

13. Of females that are breeding, what percentage each year produce, on average,
1 brood? _____
2 broods? _____
… _____

Presumably pikeminnow only produce a single brood.

14. Of litters that are born in a given year, what percentage have litters/clutches of …
1 offspring? _____
2 offspring? _____
3 offspring? _____
4 offspring? _____
(and so on to the maximum litter size).

See #11.

14A. Alternatively, in cases of large average brood size (e.g., >10), it is easier to specify the summary statistics:
Mean _____ SD _____

See #11.

15. What is the percent mortality of females …
from birth to 1 year of age (i.e., juveniles)?

Age-0 over winter survival (YOY to age-1) means range from 34-51%.
Haines, G.B., D.W. Beyers, and T. Modde. 1998. Estimation of winter survival, movement, and dispersal of young Colorado squawfish in the Green River, Utah. Final report to the Upper Colorado River Endangered Fish Recovery Program, Denver, Colorado. **McAda, C.W., and R.J. Ryel. 1999**. Distribution, relative abundance, and environmental correlates for age-0 Colorado pikeminnow and sympatric fishes in the Colorado River. Final Report to Upper Colorado River Endangered Fish Recovery Program, Denver, Colorado. **Valdez, R.A., B.R. Cowdell, and L.D. Lentsch. 1999**. Overwinter survival of age-0 Colorado pikeminnow in the Green River, Utah, 1987–1995. Final Report to Upper Colorado River Endangered Fish Recovery Program, Denver, Colorado.

from age 1 to age 2? _____
from age 2 to age 3? _____ (no need to answer this if they begin breeding at age 2)
from age *x* to age *x*+1, for adults?

Adult survival average between 40-89%.
Gilpin, M. 1993. A population viability analysis of the Colorado squawfish in the upper Colorado River basin. Department of Biology, University of California at San Diego, La Jolla, California. **Osmundson, D.B., M.E. Tucker, B.D. Burdick, W.R. Elmblad and T.E. Chart. 1997**. Non-spawning movements of subadult and adult Colorado squawfish in the Upper Colorado River. Final Report. U.S. Fish and Wildlife Service, Grand Junction, CO. **Kevin R. Bestgen, John A. Hawkins, Gary C. White, Kevin D. Christopherson, J. Michael Hudson, Mark H. Fuller, D. Chris Kitcheyan, Ronald Brunson, Paul Badame, G. Bruce Haines, Julie A. Jackson, Cameron D. Walford & Tasha A. Sorensen 2007**. Population Status of Colorado Pikeminnow in the Green River Basin, Utah and Colorado, Transactions of the American Fisheries Society, 136:5: 1356-1380. **Osmundson, D.B. and G.C. White. 2009**. Population status and trends of the Colorado pikeminnow of the Upper Colorado River, 1991-2005. Final report. U.S. Fish and Wildlife Service, Grand Junction, Colorado.

16. What is the percent mortality of males ….
from birth to 1 year of age (i.e., juveniles)? _____
from age 1 to age 2? _____
from age 2 to age 3? _____ (no need to answer this if they begin breeding at age 2)
from age *x* to age *x*+1, for adults? _____

See #15

17. For each of the mortality rates listed above, enter the variation across years (environmental variation) as a standard deviation:

For females, what is the standard deviation in the mortality rate
from birth to 1 year of age (i.e., juveniles)? _____
from age 1 to age 2? _____
from age 2 to age 3? _____ (no need to answer this if they begin breeding at age 2)
from age *x* to age *x*+1, for adults? _____

For males, what is the standard deviation in the mortality rate
from birth to 1 year of age (i.e., juveniles)? _____
from age 1 to age 2? _____
from age 2 to age 3? _____ (no need to answer this if they begin breeding at age 2)
from age *x* to age *x*+1, for adults? _____

Unknown

18. Do you want to incorporate inbreeding depression? Yes or No **_____**.

Yes, if you think inbreeding might cause a reduction in fertility or survival
No, if you think inbreeding would not cause any negative impact
If you answered "Yes" to Question 15, then we need to specify the severity of the impacts of inbreeding by answering the following two questions:

Unknown

18A. How many lethal equivalents exist in your population?

"Lethal equivalents" describes the severity of inbreeding on demographic rates. In the default implementation of *Vortex*, this impact applies only to juvenile (first year) survival. The median number of lethal equivalents reported by Ralls et al. (1988) for 40 captive mammal populations was 3.14 with a range from 0.0 (no effect of inbreeding on survival) to about 15 (most inbred progeny die). More recently, O'Grady et al (2006) used data from 10 wild mammal and bird populations and found an average of 12 lethal equivalents, suggesting that stresses found in the wild may enhance the overall impact of inbreeding on fitness.

Unknown

18B. What proportion of the total lethal equivalents is due to recessive lethal alleles? _____

This question relates to how easily natural selection would remove deleterious genes if inbreeding persisted for many generations (and the population did not become extinct). In other words, how well does the population adapt to inbreeding? The question is really asking this: what fraction of the genes responsible for inbreeding depression would be removed by selection over many generations? Unfortunately, little data exist for mammals regarding this question; data on fruit flies and rodents, however, suggest that about 50% of the total suite of inbreeding effects is, on average, due to lethal alleles.

Unknown

19. Do you want environmental variation in reproduction to be correlated with environmental variation in survival? Yes or No _____
Answering "Yes" would indicate that good years for breeding are also good years for survival, and bad years for breeding are also bad years for survival. "No" would indicate that annual fluctuations in breeding and survival are independent. If no data are available, the most conservative approach is to correlate them to avoid underestimating risk (such a correlation is typical for most non-migratory species).

Unknown but could it be modeled both ways?

20. How many types of catastrophes should be included in the models?
You can model disease epidemics, or any other type of disaster, which might kill many individuals or cause major breeding failure in sporadic years. Remember that beneficial 'catastrophes' can also be modeled (i.e., cause increased survival or reproduction).

Unknown

21. For each type of catastrophe considered in Question 20,
What is the probability of occurrence? _____
(i.e., how often does the catastrophe occur in a given time period, say, 100 years?)
What is the breeding rate in a catastrophe year relative to breeding in normal years? _____
(i.e., 1.00 = no reduction in %females breeding; 0.75 = 25% reduction; 0.00 = no females breeding)
What is the survival rate in a catastrophe year relative to survival in normal years? _____
(i.e., 1.00 = no reduction in survival; 0.75 = 25% reduction; 0.00 = no survival: population extinction)

Unknown

22. Are all adult males in the "pool" of potential breeders each year? Yes or No **_____**
Are there some males that are excluded from the group of available breeders because they are socially prevented from holding territories, are sterile, or otherwise prevented from having access to mates? Caution is advised in restricting the male breeding pool under monogamy, as this may lower the percent of females breeding due to limitation of mates

Unknown

23. If you answered "No" to Question 22, then answer at least one of the following:
What percentage of adult males is available for breeding each year? _____
or
What percentage of adult males typically sires a litter each year? _____
or
How many litters are sired by the average breeding male (of those siring at least one litter)? ____

Unknown

24. What is the current population size?

In most cases, we assume that the population starts at a "stable age distribution", rather than specifying ages of individual animals in the current population. If information exists that allows us to specify the age or sex distribution of the starting population, we can enter these data directly.

3,311 individuals ≥ 250 mm in the Colorado River. 2,142 adults in the Green River, 4,500 age-2+ individuals in the San Juan River.

Kevin R. Bestgen, John A. Hawkins, Gary C. White, Kevin D. Christopherson, J. Michael Hudson, Mark H. Fuller, D. Chris Kitcheyan, Ronald Brunson, Paul Badame, G. Bruce Haines, Julie A. Jackson, Cameron D. Walford & Tasha A. Sorensen 2007. Population Status of Colorado Pikeminnow in the Green River Basin, Utah and Colorado, Transactions of the American Fisheries Society, 136:5: 1356-1380. **Osmundson, D.B. and G.C. White. 2009**. Population status and trends of the Colorado pikeminnow of the Upper Colorado River, 1991-2005. Final report. U.S. Fish and Wildlife Service, Grand Junction, Colorado. **Duran, B.R., Davis, J.E, and E. Teller Sr. 2011**. Nonnative species monitoring and control in the upper/middle San Juan River 2010. Report to San Juan River Basin Recovery Implementation Program. New Mexico Fish and Wildlife Service Conservation Office, U.S. Fish and Wildlife Service, Albuquerque, NM.

25. What is the habitat carrying capacity?

How many animals could be supported in the existing habitat?
We will assume that the habitat is not fluctuating randomly in quality over time, or that annual variation in habitat quality are accounted for in the model by yearly variation in mortality and reproductive rates.

Green River 2.5 pikeminnow/hour, Colorado river 435 pikeminnow, San Juan River 800 pikeminnow.

McAda, C.W., W.R. Elmblad, K.S. Day, M.A. Trammel, and T.E. Chart. 1998. Interagency Standardized Monitoring Program: summary of results, 1997. Annual Report to Upper Colorado River Endangered Fish Recovery Program, Denver, Colorado. **Osmundson, D.B., and K.P. Burnham. 1998**. Status and trends of the endangered Colorado squawfish in the upper Colorado River. Transactions of the American Fisheries Society 127: 957–970. **Osmundson, D.B. 1999**. Longitudinal variation in fish community structure and water temperature in the upper Colorado River. Final Report of U.S. Fish and Wildlife Service, Grand Junction, Colorado, to Upper Colorado River Endangered Fish Recovery Program, Denver, Colorado. **U.S. Fish and Wildlife Service. 2002**. Colorado pikeminnow (*Ptychocheilus lucius*) Recovery Goals: amendment and supplement to the Colorado Squawfish Recovery Plan. U.S. Fish and Wildlife Service, Mountain-Prairie Region (6), Denver, Colorado.

26. Will habitat (carrying capacity) be lost or gained over time? Yes or No _____

Unknown

26A. If you answered "Yes" to Question 26, then over how many years will habitat be lost or gained? _____

Unknown

26B. What percentage of habitat will be lost or gained each year? _____

Unknown

27. Will animals be removed from the population (to captive stocks, for translocation, through hunting, etc.)? Yes or No **_____**

No
Be sure to only include removals that are NOT already included in the mortality rates above.
If "Yes", then,
In what year do the removals start? _____
At what annual interval? _____
For how many years? _____
How many female juveniles? _____ 1-2 year old females? _____ 2-3 year old females? _____ adult females? _____ will be removed each time.
How many male juveniles? _____ 1-2 year old males? _____ 2-3 year old males? _____ adult males? _____ will be removed each time.

28. Will animals be added to the population (from captive stocks, through translocation, etc.)? Yes or No **_____**

Yes
For details and background see **Furr, D.W. 2012**. Augmentation of Colorado pikeminnow (*Ptychocheilus lucius*) in the San Juan River 2011. Report to the San Juan River Basin Recovery Implementation Program. New Mexico Fish and Wildlife Service Conservation Office, U.S. Fish and Wildlife Service, Albuquerque, NM.

If "Yes", then,
In what year do the supplementations start? _____
At what annual interval? _____
For how many years? _____
How many female juveniles? _____ Subadult females? _____ Adult females? _____ will be added each time.
How many male juveniles? _____ Subadult males? _____ Adult males? _____ will be added each time.

29. Will breeding be managed (breeding pairs controlled)? Yes or No **_____**

In the hatchery, yes, in the wild no.
If "Yes", then,
Is there is maximum allowable inbreeding level F? _____
Will breeders and pairs be selected based on mean kinship (vs. random)? _____
Is there a maximum number of mates per male per breeding season? _____
Will the number of breeding pairs be limited to the number needed to maintain K? _____
What is the annual success rate (e.g., litter or clutch produced) of recommended breedings? _____

30. Species / Population characteristics for model validation

Please provide any of the following information if available for the population under the demographic rates and conditions described above.

Age class ratios (e.g. juvenile:subadult:adult): _____

Unknown

Sex ratios (e.g. adult male: adult female): _____

Unknown

Population growth rate or trend: _____

Unknown

Generation time (T): _____

Unknown

31. Metapopulation structure

(Feel free to include a map of the area under consideration to assist in your description of the metapopulation structure below.)

If the biological system under consideration has a metapopulation structure, then:

Is dispersal age-specific? _____

Is dispersal gender-specific? _____

What is the dispersal rate from subpopulation X to subpopulation Y? _____

Is this dispersal rate symmetric? _____

Is there a morality cost to dispersal? _____

Unknown

Appendix E

Population Viability Analysis and Simulation Modeling: A Review
P. Miller, R. Lacy

Population Viability Analysis and Simulation Modeling

Phil Miller, Bob Lacy
Conservation Breeding Specialist Group (IUCN / SSC)

Introduction

Thousands of species and populations of animals and plants around the world are threatened with extinction within the coming decades. For the vast majority of these groups of organisms, this threat is the direct result of human activity. The particular types of activity, and the ways in which they impact wildlife populations, are often complex in both cause and consequence; as a result, the techniques we must use to analyze their effects often seem to be complex as well. But scientists in the field of conservation biology have developed extremely useful tools for this purpose that have dramatically improved our ability to conserve the planet's biodiversity.

Conservation biologists involved in recovery planning for a given threatened species usually try to develop a detailed understanding of the processes that put the species at risk, and will then identify the most effective methods to reduce that risk through active management of the species itself and/or the habitat in which it lives. In order to design such a program, we must engage in some sort of predictive process: we must gather information on the detailed characteristics of proposed alternative management strategies and somehow predict how the threatened species will respond in the future. A strategy that is predicted to reduce the risk by the greatest amount – and typically does so with the least amount of financial and/or sociological burden – is chosen as a central feature of the recovery plan.

But how does one predict the future? Is it realistically possible to perform such a feat in our fast-paced world of incredibly rapid and often unpredictable technological, cultural, and biological growth? How are such predictions best used in wildlife conservation? The answers to these questions emerge from an understanding of what has been called "the flagship industry" of conservation biology: Population Viability Analysis, or PVA. And most methods for conducting PVA are merely extensions of tools we all use in our everyday lives.

The Basics of PVA

To appreciate the science and application of PVA to wildlife conservation, we first must learn a little bit about population biology. Biologists will usually describe the performance of a population by describing its demography, or simply the numerical depiction of the rates of birth and death in a group of animals or plants from one year to the next. Simply speaking, if the birth rate exceeds the death rate, a population is expected to increase in size over time. If the reverse is true, our population will decline. The overall rate of population growth is therefore a rather good descriptor of its relative security: positive population growth suggests some level of demographic health, while negative growth indicates that some external process is interfering with the normal population function and pushing it into an unstable state.

This relatively simple picture is, however, made a lot more complicated by an inescapable fact: wildlife population demographic rates fluctuate unpredictably over time. So if we observe that 50% of our total population of adult females produces offspring in a given year, it is almost certain that more or less than 50% of our adult females will reproduce in the following year. And the same can be said for most all other demographic rates: survival of offspring and adults, the numbers of offspring born, and the offspring sex ratio will almost always change from one year to the next in a way that usually defies precise prediction. These variable rates then conspire to make a population's growth rate also change

unpredictably from year to year. When wildlife populations are very large – if we consider seemingly endless herds of wildebeest on the savannahs of Africa, for example – this random annual fluctuation in population growth is of little to no consequence for the future health and stability of the population. However, theoretical and practical study of population biology has taught us that populations that are already small in size, often defined in terms of tens to a few hundred individuals, are affected by these fluctuations to a much greater extent – and the long-term impact of these fluctuations is always negative. Therefore, a wildlife population that has been reduced in numbers will become even smaller through this fundamental principle of wildlife biology. Furthermore, our understanding of this process provides an important backdrop to considerations of the impact of human activities that may, on the surface, appear relatively benign to larger and more stable wildlife populations. This self-reinforcing feedback loop, first coined the "extinction vortex" in the mid-1980's, is the cornerstone principle underlying our understanding of the dynamics of wildlife population extinction.

Once wildlife biologists have gone out into the field and collected data on a population's demography and used these data to calculate its current rate of growth (and how this rate may change over time), we now have at our disposal an extremely valuable source of information that can be used to predict the *future* rates of population growth or decline under conditions that may not be so favorable to the wildlife population of interest. For example, consider a population of primates living in a section of largely undisturbed Amazon rain forest that is now opened up to development by logging interests. If this development is to go ahead as planned, what will be the impact of this activity on the animals themselves, and the trees on which they depend for food and shelter? And what kinds of alternative development strategies might reduce the risk of primate population decline and extinction? To try to answer this question, we need two additional sets of information: 1) a comprehensive description of the proposed forest development plan (how will it occur, where will it be most intense, for what period of time, etc.) and 2) a detailed understanding of how the proposed activity will impact the primate population's demography (which animals will be most affected, how strongly will they be affected, will animals die outright more frequently or simply fail to reproduce as often, etc.). With this information in hand, we have a vital component in place to begin our PVA.

Next, we need a predictive tool – a sort of crystal ball, if you will, that helps us look into the future. After intensive study over nearly three decades, conservation biologists have settled on the use of computer simulation models as their preferred PVA tool. In general, models are simply any simplified representation of a real system. We use models in all aspects of our lives; for example, road maps are in fact relatively simple (and hopefully very accurate!) 2-dimensional representations of complex 3-dimensional landscapes we use almost every day to get us where we need to go. In addition to making predictions about the future, models are very helpful for us to: (1) extract important trends from complex processes, (2) allow comparisons among different types of systems, and (3) facilitate analysis of processes acting on a system.

Recent advances in computer technology have allowed us to create very complex models of the demographic processes that define wildlife population growth. But at their core, these models attempt to replicate simple biological functions shared by most all wildlife species: individuals are born, some grow to adulthood, most of those that survive mate with individuals of the opposite sex and then give birth to one or more offspring, and they die from any of a wide variety of causes. Each species may have its own special set of circumstances – sea turtles may live to be 150 years old and lay 600 eggs in a single event, while a chimpanzee may give birth to just a single offspring every 4-5 years until the age of 45 – but the fundamental biology is the same. These essential elements of a species' biology can be incorporated into a computer program, and when combined with the basic rules for living and the general characteristics of the population's surrounding habitat, a model is created that can project the demographic behavior of our real observed population for a specified period of time into the future. What's more, these models can explicitly incorporate random fluctuations in rates of birth and death discussed earlier. As a result, the

models can be much more realistic in their treatment of the forces that influence population dynamics, and in particular how human activities can interact with these intrinsic forces to put otherwise relatively stable wildlife populations at risk.

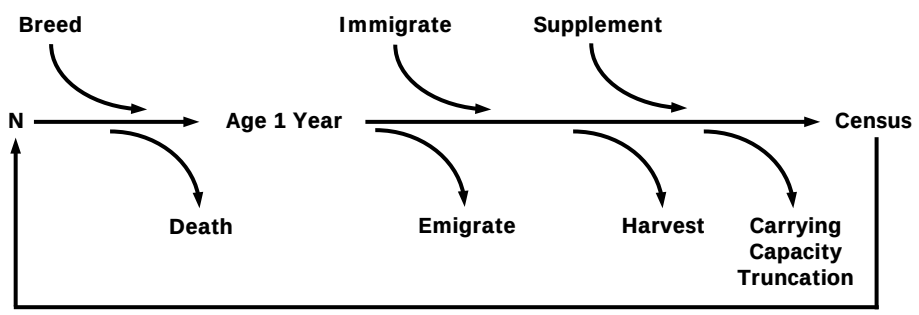
Many different software packages exist for the purposes of conducting a PVA. Perhaps the most widely-used of these packages is *VORTEX*, developed by the IUCN Conservation Breeding Specialist Group (CBSG) for use in both applied and educational environments. *VORTEX* has been used by CBSG and other conservation biologists for more than 15 years and has proved to be a very useful tool for helping make more informed decisions in the field of wildlife population management.

The *VORTEX* Population Viability Analysis Model

For the analyses presented here, the *VORTEX* computer software (Lacy 1993a) for population viability analysis was used. *VORTEX* models demographic stochasticity (the randomness of reproduction and deaths among individuals in a population), environmental variation in the annual birth and death rates, the impacts of sporadic catastrophes, and the effects of inbreeding in small populations. *VORTEX* also allows analysis of the effects of losses or gains in habitat, harvest or supplementation of populations, and movement of individuals among local populations.

Density dependence in mortality is modeled by specifying a carrying capacity of the habitat. When the population size exceeds the carrying capacity, additional morality is imposed across all age classes to bring the population back down to the carrying capacity. The carrying capacity can be specified to change linearly over time, to model losses or gains in the amount or quality of habitat. Density dependence in reproduction is modeled by specifying the proportion of adult females breeding each year as a function of the population size.

VORTEX Simulation Model Timeline



Events listed above the timeline increase N, while events listed below the timeline decrease N.

VORTEX models loss of genetic variation in populations, by simulating the transmission of alleles from parents to offspring at a hypothetical genetic locus. Each animal at the start of the simulation is assigned two unique alleles at the locus. During the simulation, *VORTEX* monitors how many of the original alleles remain within the population, and the average heterozygosity and gene diversity (or "expected heterozygosity") relative to the starting levels. *VORTEX* also monitors the inbreeding coefficients of each animal, and can reduce the juvenile survival of inbred animals to model the effects of inbreeding depression.

VORTEX is an *individual-based* model. That is, *VORTEX* creates a representation of each animal in its memory and follows the fate of the animal through each year of its lifetime. *VORTEX* keeps track of the sex, age, and parentage of each animal. Demographic events (birth, sex determination, mating, dispersal, and death) are modeled by determining for each animal in each year of the simulation whether any of the events occur. Events occur according to the specified age and sex-specific probabilities. Demographic stochasticity is therefore a consequence of the uncertainty regarding whether each demographic event occurs for any given animal.

VORTEX requires a lot of population-specific data. For example, the user must specify the amount of annual variation in each demographic rate caused by fluctuations in the environment. In addition, the frequency of each type of catastrophe (drought, flood, epidemic disease) and the effects of the catastrophes on survival and reproduction must be specified. Rates of migration (dispersal) between each pair of local populations must be specified. Because *VORTEX* requires specification of many biological parameters, it is not necessarily a good model for the examination of population dynamics that would result from some generalized life history. It is most usefully applied to the analysis of a specific population in a specific environment.

Further information on *VORTEX* is available in Lacy (2000) and Miller and Lacy (2003).

Results reported for each scenario include:

Deterministic r -- The deterministic population growth rate, a projection of the mean rate of growth of the population expected from the average birth and death rates. Impacts of harvest, inbreeding, and density dependence are not considered in the calculation. When $r = 0$, a population with no growth is expected; $r < 0$ indicates population decline; $r > 0$ indicates long-term population growth. The value of r is approximately the rate of growth or decline per year.

The deterministic growth rate is the average population growth expected if the population is so large as to be unaffected by stochastic, random processes. The deterministic growth rate will correctly predict future population growth if: the population is presently at a stable age distribution; birth and death rates remain constant over time and space (i.e., not only do the probabilities remain constant, but the actual number of births and deaths each year match the expected values); there is no inbreeding depression; there is never a limitation of mates preventing some females from breeding; and there is no density dependence in birth or death rates, such as a Allee effects or a habitat "carrying capacity" limiting population growth. Because some or all of these assumptions are usually violated, the average population growth of real populations (and stochastically simulated ones) will usually be less than the deterministic growth rate.

Stochastic r -- The mean rate of stochastic population growth or decline demonstrated by the simulated populations, averaged across years and iterations, for all those simulated populations that are not extinct. This population growth rate is calculated each year of the simulation, prior to any truncation of the population size due to the population exceeding the carrying capacity. Usually, this stochastic r will be less than the deterministic r predicted from birth and death rates. The stochastic r from the simulations will be close to the deterministic r if the population growth is steady and robust. The stochastic r will be notably less than the deterministic r if the population is subjected to large fluctuations due to environmental variation, catastrophes, or the genetic and demographic instabilities inherent in small populations.

P(E) -- the probability of population extinction, determined by the proportion of, for example, 500 iterations within that given scenario that have gone extinct in the simulations. "Extinction" is defined in the *VORTEX* model as the lack of either sex.

N -- mean population size, averaged across those simulated populations which are not extinct.

SD(N) -- variation across simulated populations (expressed as the standard deviation) in the size of the population at each time interval. SDs greater than about half the size of mean N often indicate highly unstable population sizes, with some simulated populations very near extinction. When SD(N) is large relative to N, and especially when SD(N) increases over the years of the simulation, then the population is vulnerable to large random fluctuations and may go extinct even if the mean population growth rate is positive. SD(N) will be small and often declining relative to N when the population is either growing steadily toward the carrying capacity or declining rapidly (and deterministically) toward extinction. SD(N) will also decline considerably when the population size approaches and is limited by the carrying capacity.

H -- the gene diversity or expected heterozygosity of the extant populations, expressed as a percent of the initial gene diversity of the population. Fitness of individuals usually declines proportionately with gene diversity (Lacy 1993), with a 10% decline in gene diversity typically causing about 15% decline in survival of captive mammals (Ralls et al. 1988). Impacts of inbreeding on wild populations are less well known, but may be more severe than those observed in captive populations (Jiménez et al. 1994). Adaptive response to natural selection is also expected to be proportional to gene diversity. Long-term conservation programs often set a goal of retaining 90% of initial gene diversity (Soulé et al. 1986). Reduction to 75% of gene diversity would be equivalent to one generation of full-sibling or parent-offspring inbreeding.

Strengths and Limitations of the PVA Approach

When considering the applicability of PVA to a specific issue, it is vitally important to understand those tasks to which PVA is well-suited as well as to understand what the technique is not well-designed to deliver. With this enhanced understanding will also come a more informed public that is better prepared to critically evaluate the results of a PVA and how they are applied to the practical conservation measures proposed for a given species or population.

The dynamics of population extinction are often quite complicated, with numerous processes impact the dynamics in complex and interacting ways. Moreover, we have already come to appreciate the ways in which demographic rates fluctuate unpredictably in wildlife populations, and the data needed to provide estimates of these rates and their annual variability are themselves often uncertain, i.e., subject to observational bias or simple lack of detailed study over relatively longer periods of time. As a result, the elegant mental models or the detailed mathematical equations of even the most gifted conservation biologist are inadequate for capturing the detailed nuances of interacting factors that determine the fate of a wildlife population threatened by human activity. In contrast, simulation models can include as many factors that influence population dynamics as the modeler and the end-user of the model wish to assess. Detailed interactions between processes can also be modeled, if the nature of those interactions can be specified. Probabilistic events can be easily simulated by computer programs, providing output that gives both the mean expected result and the range or distribution of possible outcomes.

PVA models have also been shown to stimulate meaningful discussion among field biologists in the subjects of species biology, methods of data collection and analysis, and the assumptions that underlie the analysis of these data in preparation for their use in model construction. By making the models and their underlying data, algorithms and assumptions explicit to all who learn from them, these discussions become a critical component in the social process of achieving a shared understanding of a threatened species' current status and the biological justification for identifying a particular management strategy as the most effective for species conservation. This additional benefit is most easily recognized when PVA is

used in an interactive workshop-type setting, such as the Population and Habitat Viability Assessment (PHVA) workshop designed and implemented by CBSG.

Perhaps the greatest strength of the PVA approach to conservation decision-making is related to what many of its detractors see as its greatest weakness. Because of the inherent uncertainty now known to exist in the long-term demography of wildlife populations (particularly those that are small in size), and because of the difficulties in obtaining precise estimates of demographic rates through extended periods of time collecting data in the field, accurate predictions of the future performance of a threatened wildlife population are effectively impossible to make. Even the most respected PVA practitioner must honestly admit that an accurate prediction of the number of mountain gorillas that will roam the forests on the slopes of the eastern Africa's Virunga Volcanoes in the year 2075, or the number of polar bears that will swim the warming waters above the Arctic Circle when our great-grandchildren grow old, is beyond their reach. But this type of difficulty, recognized across diverse fields of study from climatology to gambling, is nothing new: in fact, the Nobel Prize-winning physicist Niels Bohr once said "Prediction is very difficult, especially when it's about the future." Instead of lamenting this inevitable quirk of the physical world as a fatal flaw in the practice of PVA, we must embrace it and instead use our very cloudy crystal ball for another purpose: to make **relative**, rather than **absolute**, predictions of wildlife population viability in the face of human pressure.

The process of generating relative predictions using the PVA approach is often referred to as sensitivity analysis. In this manner, we can make much more robust predictions about the relative response of a simulated wildlife population to alternate perturbations to its demography. For example, a PVA practitioner may not be able to make accurate predictions about how many individuals of a given species may persist in 50 years in the presence of intense human hunting pressure, but that practitioner can speak with considerably greater confidence about the relative merits of a male-biased hunting strategy compared to the much more severe demographic impact typically imposed by a hunting strategy that prefers females. This type of comparative approach was used very effectively in a PVA for highly threatened populations of tree kangaroos (*Dendrolagus* sp.) living in Papua New Guinea, where adult females are hunted preferentially over their male counterparts. Comparative models showing the strong impacts of such a hunting strategy were part of an important process of conservation planning that led, within a few short weeks after a participatory workshop including a number of local hunters (Bonaccorso et al., 1998), to the signing of a long-term hunting moratorium for the most critically endangered species in the country, the tenkile or Scott's tree kangaroo (*Dendrolagus scottae*).

PVA models are necessarily incomplete. We can model only those factors which we understand and for which we can specify the parameters. Therefore, it is important to realize that the models often underestimate the threats facing the population, or the total risk these threats collectively impose on the population of interest. To address this limitation, conservation biologists must try to engage a diverse body of experts with knowledge spanning many different fields in an attempt to broaden our understanding of the consequences of interaction between humans and wildlife.

Additionally, models are used to predict the long-term effects of the processes presently acting on the population. Many aspects of the situation could change radically within the time span that is modeled. Therefore, it is important to reassess the data and model results periodically, with changes made to the conservation programs as needed (see Lacy and Miller (2002), Nyhus et al. (2002) and Westley and Miller (2003) for more details).

Finally, it is also important to understand that a PVA model by itself does not define the goals of conservation planning of a given species. Goals, in terms of population growth, probability of persistence, number of extant populations, genetic diversity, or other measures of population performance must be defined by the management authorities before the results of population modeling can be used.

Further Reading

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Sequence of program flow

(1) The seed for the random number generator is initialized with the number of seconds elapsed since the beginning of the 20th century.

(2) The user is prompted for an output file name, duration of the simulation, number of iterations, the size below which a population is considered extinct, and a large number of population parameters.

(3) The maximum allowable population size (necessary for preventing memory overflow) is calculated as:

$$K_{max} = (K + 3s)(1 + L)$$

in which K is the maximum carrying capacity (carrying capacity can be specified to change during a simulation, so the maximum carrying capacity can be greater than the initial carrying capacity), s is the annual environmental variation in the carrying capacity expressed as a standard deviation, and L is the specified maximum litter size.

(4) Memory is allocated for data arrays. If insufficient memory is available for data arrays then N_{max} is adjusted downward to the size that can be accommodated within the available memory and a warning message is given. In this case it is possible that the analysis may have to be terminated because the simulated population exceeds N_{max}. Because N_{max} is often several-fold greater than the likely maximum population size in a simulation, a warning that it has been adjusted downward because of limiting memory often will not hamper the analyses.

(5) The deterministic growth rate of the population is calculated from mean birth and death rates that have been entered. Algorithms follow cohort life-table analyses (Ricklefs 1979). Generation time and the expected stable age distribution are also calculated. Life-table calculations assume constant birth and death rates, no limitation by carrying capacity, no limitation of mates, no loss of fitness due to inbreeding depression, and that the population is at the stable age distribution. The effects of catastrophes are incorporated into the life table analysis by using birth and death rates that are weighted averages of the values in years with and without catastrophes, weighted by the probability of a catastrophe occurring or not occurring.

(6) Iterative simulation of the population proceeds via steps 7 through 26 below.

(7) The starting population is assigned an age and sex structure. The user can specify the exact age-sex structure of the starting population, or can specify an initial population size and request that the population be distributed according to the stable age distribution calculated from the life table. Individuals in the starting population are assumed to be unrelated. Thus, inbreeding can occur only in second and later generations.

(8) Two unique alleles at a hypothetical neutral genetic locus are assigned to each individual in the starting population and to each individual supplemented to the population during the simulation. *VORTEX* therefore uses an infinite alleles model of genetic variation. The subsequent fate of genetic variation is tracked by reporting the number of extant neutral alleles each year, the expected heterozygosity or gene diversity, and the observed heterozygosity. The expected heterozygosity, derived from the Hardy-Weinberg equilibrium, is given by

$$H_e = 1 - \sum \left(p_i^2\right)$$

in which p_i is the frequency of allele *i* in the population. The observed heterozygosity is simply the proportion of the individuals in the simulated population that are heterozygous. Because of the starting assumption of two unique alleles per founder, the initial population has an observed heterozygosity of 1.0 at the hypothetical locus and only inbred animals can become homozygous. Proportional loss of heterozygosity through random genetic drift is independent of the initial heterozygosity and allele frequencies of a population (Crow and Kimura 1970), so the expected heterozygosity remaining in a simulated population is a useful metric of genetic decay for comparison across scenarios and populations. The mean observed heterozygosity reported by *VORTEX* is the mean inbreeding coefficient of the population.

(9) For each of the10 alleles at five non-neutral loci that are used to model inbreeding depression, each founder is assigned a unique lethal allele with probability equal to 0.1 x the mean number of lethal alleles per individual.

(10) Years are iterated via steps 11 through 25 below.

(11) The probabilities of females producing each possible size litter are adjusted to account for density dependence of reproduction (if any).

(12) Birth rate, survival rates, and carrying capacity for the year are adjusted to model environmental variation. Environmental variation is assumed to follow binomial distributions for birth and death rates and a normal distribution for carrying capacity, with mean rates and standard deviations specified by the user. At the outset of each year a random number is drawn from the specified binomial distribution to determine the percent of females producing litters. The distribution of litter sizes among those females that do breed is maintained constant. Another random number is drawn from a specified binomial distribution to model the environmental variation in mortality rates. If environmental variations in reproduction and mortality are chosen to be correlated, the random number used to specify mortality rates for the year is chosen to be the same percentile of its binomial distribution as was the number used to specify reproductive rate. Otherwise, a new random number is drawn to specify the deviation of age- and sex-specific mortality rates from their means. Environmental variation across years in mortality rates is always forced to be correlated among age and sex classes.

The carrying capacity (*K*) for the year is determined by first increasing or decreasing the carrying capacity at year 1 by an amount specified by the user to account for changes over time. Environmental variation in *K* is then imposed by drawing a random number from a normal distribution with the specified values for mean and standard deviation.

(13) Birth rates and survival rates for the year are adjusted to model any catastrophes determined to have occurred in that year.

(14) Breeding males are selected for the year. A male of breeding age is placed into the pool of potential breeders for that year if a random number drawn for that male is less than the proportion of adult males specified to be breeding. Breeding males are selected independently each year; there is no long-term tenure of breeding males and no long-term pair bonds.

(15) For each female of breeding age, a mate is drawn at random from the pool of breeding males for that year. If the user specifies that the breeding system is monogamous, then each male can only be paired with a single female each year. Males are paired only with those females which have already been selected for breeding that year. Thus, males will not be the limiting sex unless there are insufficient males to pair with the successfully breeding females.

If the breeding system is polygynous, then a male may be selected as the mate for several females. The degree of polygyny is determined by the proportion of males in the pool of potential breeders each year.

The size of the litter produced by that pair is determined by comparing the probabilities of each potential litter size (including litter size of 0, no breeding) to a randomly drawn number. The offspring are produced and assigned a sex by comparison of a random number to the specified birth sex ratio. Offspring are assigned, at random, one allele at the hypothetical genetic locus from each parent.

(16) The genetic kinship of each new offspring to each other living animal in the population is determined. The kinship between new animal *A*, and another existing animal, *B*, is

$$f_{AB} = 0.5(f_{MB} + f_{PB})$$

in which f_{ij} is the kinship between animals *i* and *j*, *M* is the mother of *A*, and *P* is the father of *A*. The inbreeding coefficient of each animal is equal to the kinship between its parents, $F = f_{MP}$, and the kinship of an animal to itself is $f_A = 0.5(1 + F)$. (See Ballou 1983 for a detailed description of this method for calculating inbreeding coefficients.)

(17) The survival of each animal is determined by comparing a random number to the survival probability for that animal. In the absence of inbreeding depression, the survival probability is given by the age and sex-specific survival rate for that year. If a newborn individual is homozygous for a lethal allele, it is killed. Otherwise, the survival probability for individuals in their first year is

$$e^{-b(1-\Pr[Lethals])F}$$

multiplied by
in which *b* is the number of lethal equivalents per haploid genome, and Pr[*Lethals*] is the proportion of this inbreeding effect due to lethal alleles.

(18) The age of each animal is incremented by 1.

(19) If more than one population is being modeled, migration among populations occurs stochastically with specified probabilities.

(20) If population harvest is to occur that year, the number of harvested individuals of each age and sex class are chosen at random from those available and removed. If the number to be removed do not exist for an age-sex class, *VORTEX* continues but reports that harvest was incomplete.

(21) Dead animals are removed from the computer memory to make space for future generations.

(22) If population supplementation is to occur in a particular year, new individuals of the specified age class are created. Each immigrant is assumed to be genetically unrelated to all other individuals in the population, and it carries the number of lethal alleles that was specified for the starting population.

(23) The population growth rate is calculated as the ratio of the population size in the current year to the previous year.

(24) If the population size (N) exceeds the carrying capacity (K) for that year, additional mortality is imposed across all age and sex classes. The probability of each animal dying during this carrying capacity truncation is set to $(N - K)/N$, so that the expected population size after the additional mortality is K.

(25) Summary statistics on population size and genetic variation are tallied and reported.

(26) Final population size and genetic variation are determined for the simulation.

(27) Summary statistics on population size, genetic variation, probability of extinction, and mean population growth rate are calculated across iterations and output.