A periodic stage structured matrix model of Pallid Sturgeon

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# Abstract

# Introduction

# Objectives

* Conditions resulting in a growing population
* Sensitivities and elasticities
* Population augmentation

# Methods

## Study area

### Conceptual population model structure

The conceptual population model structure was developed to meet three primary objectives: 1) provide a quantitative framework to forecast pallid sturgeon population dynamics given inputs from the CEMs described by Jacobson et al. (2014), 2) provide a flexible model structure template that can be used to model several populations (i.e., upper basin, lower basin) and varying spatial resolutions as needed, and 3) account for whether a pallid sturgeon were produced in the Missouri River System or the hatchery system (Figure 3.1). A secondary consideration in the development of the model structure was the availability of biological data commonly collected during population assessments (e.g., size, weight, age, sex, origin), which will be necessary to parameterize and calibrate the model. It should be recognized that this population modeling effort is a work in progress and will be modified as needed to meet the needs of the EA as well as collaborative input from regional pallid sturgeon experts.

## A stage-structure organization of pallid sturgeon life history

Stages were used to organize pallid sturgeon life history and as a framework to model population dynamics. Seven stages were used in the model to capture biologically important pallid sturgeon stage transitions similar to those identified in Wildhaber et al. (2011) and correspond to life stage-specific CEMs (Jacobson et al., 2014) (Table 3.1). Pallid sturgeon life history in the Missouri River System was organized into the following stages:

* Embryo (; 5-8 days): period from fertilization to hatching
* Free embryo (; 8-12 days days post hatch (dph)): period from hatching until the larval fish initiates feeding
* Exogenously feeding larvae and age-0 (; 8-12 dph - June 1): period from full development of fin rays over the winter period until June 1 of the following year.
* Juvenile (; age-1 to age-9): period of pallid sturgeon sexual immaturity, a fish can remain in this stage until age-9
* Spawning adult (;age-7 to age-41): this stage includes juvenile fish that have become sexually mature and are read to spawn and adult fish that have already spawned and are ready to spawn again
* Post-spawn Adult (): a pallid sturgeon that has released its gametes, model assumes fish remain in this state until June the following year
* Recrudescent adult (): a post-spawn pallid sturgeon, replenishing gametes, may remain in this state for up to 4 years post-spawn

Each stage represents an important portion of pallid sturgeon life history in the Missouri River System that varies in duration from days to years. The effect of hatchery operations on the population was accounted for with the addition of stages specific to the hatchery system (figure 3.1). These stages included:

* Broodstock (): sexually mature fish ready to spawn that are removed from the Missouri River System and used as a source of gametes to fertilize and produce offspring in a controlled hatchery environment.
* Fingerlings (): pallid sturgeon hatched in a hatchery setting and reared for 3–4 months and released back into the Missouri River System.
* Yearlings (): pallid sturgeon hatched in a hatchery setting and reared for 10–12 months and released back into the Missouri River System.

In order to model population dynamics, fish transition from one stage to another in a directed fashion as illustrated as arrows among text boxes in Figure 3.1. For example, juvenile pallid sturgeon can remain a juvenile stage or move into a spawning adult stage. Spawning adults can transition into two states, a post-spawn adult stage or they can be removed from the population and enter hatchery broodstock. Stages are further organized by hatchery and natural origin fish to account for hatchery operations within the system. Sexually mature fish are removed from the spawning stage and become hatchery broodstock (Figure 3.1). These fish are then spawned and returned to the Missouri River System as post-spawn adults. The offspring of these fish are reared under hatchery conditions and stocked into the Missouri River System as fingerlings or yearlings. Hatchery origin fish are stocked into the Missouri River System where they interact and eventually spawn in the natural system, resulting in naturally produced offspring.

The stage structure of the population model captures additional biological realism in the population model, by accounting for age dependent demographic rates and values (e.g., fecundity) (Figure 3.4). Within the coarser stage-structure of the model, pallid sturgeon life history stages were organized within the following age -structure: 1) Age-0: embryo, Free embryo, and Exogenously feeding larvae and age-0, 2) Age-1 to Age-9: Juvenile, Spawn, Post spawn, Recrudescent, and 3) Age-10 to Age-41: Spawn, Post spawn, Recrudescent. Including age-structure within the existing stage structure provided several benefits including: 1) similarity with existing age-structured population viability models (e.g. K. D. Steffensen et al. (2013a), Bajer and Wildhaber (2007), 2) allowing for age-dependence in demographic rates, and 3) potential to incorporate typical fisheries data. The model provides a conceptual framework to simulate pallid sturgeon dynamics and identify informational gaps. Even given the model uncertainties, the model can be used to explore model sensitivities in order to prioritize research and evaluate scenarios with the understanding that numerous caveats and conditions are warranted.

## Model specification

### Embryos

Embryos represent the successful fertilization of an oocyte by a spermatocyte. In its simplest form the number of embryos at time was modeled the contribution of natural and hatchery origin spawns as:

(1)

where equation indices, parameters and variables are defined in Table 3.1.

### Free embryos

Free embryos represent embryos that have escaped predation and other sources of mortality and hatched. These dynamics occur within a short period of time, week-month, and therefore the number of embryos at time was models as a function of the number of as:

(2)

where equation indices, parameters and variables are defined in Table 3.1.

### Exogenously feeding larvae and age-0

Exogenously feeding larvae and age-0 pallid sturgeon represent the longest duration life stage modeled during the first year of life, lasting for months. However this life stage still occurs within the first year of life and therefore the number of exogenously feeding larvae and age-0 at time is a function of the number of free embryos at time as:

(3)

where equation indices, parameters and variables are defined in Table 3.1.

### Juvenile (age-1)

Juvenile pallid sturgeon can remain in this stage for many years. Additionally, this stage is also the recipient of population supplementation in the form of hatchery stockings of fingerlings (age-0) and yearlings (~age-1). It is at this stage that differentiation between natural and hatchery origin fish are recognized. Specifically, the model assumes that naturally produced fish are fish that were spawned, fertilized, and hatched in the system, whereas hatchery origin fish were an external input from a hatchery system. The number of natural origin age-1 juveniles was modeled as a function of exogenously feeding larvae and age-0 as:

(4)

where equation indices, parameters and variables are defined in Table 3.1. The number of hatchery origin juveniles at time was a function of hatchery inputs and modeled as:

(5)

where equation indices, parameters and variables are defined in Table 3.1. The model assumes that fingerlings are subject to similar mortalities as natural origin fish at the same stage and are added just prior the next transition and therefore no mortality occurs over this short period of time

### Juvenile (age-2)

Juveniles exceeding 2 years of age have effectively escaped the demographic bottleneck of low survivals associated with preceding early life history stages. Annual survival is estimated to exceed 0.9. Similar to age-1 juveniles the model accounts for hatchery and natural origin fish with the additional accounting for yearlings stocked in the system as

(6)

where equation indices, parameters and variables are defined in Table 3.1.

### Juvenile (>age-2)

The remaining age classes contain within the juvenile stage are modeled in the same manner regardless of origin, with the future number of juveniles predicted as a function of the current number of juveniles less juveniles that became sexually mature and transitioned into the spawning stage. The annual transition from one age to another was modeled as:

(7)

where equation indices, parameters and variables are defined in Table 3.1.

### Spawning adults

The spawning adult stage represents fish that are sexually mature, either as juvenile fish that finally achieving sexual maturity or adult fish that have previously spawned and are returning to sexual maturity after a period of gamete regeneration. This process was modeled as:

(8)

where equation indices, parameters and variables are defined in Table 3.1.

### Post spawn adults

Once sexually mature pallid sturgeon spawn they transition into a post spawn stage in the same annual period. Additionally, sexually mature fish that were removed from the spawning population during broodstock collections that were returned in a post spawn stage. Formally, this within year dynamics is represented as:

(9)

where equation indices, parameters and variables are defined in Table 3.1. Equation assumes no mortality occurs during the spawning period and broodstock collection operations.

### Recrudescent adult

Pallid sturgeon in a post-spawning stage in year transition to a recrudescent adult stage in year . During this stage fish are actively replenishing gametes, typically remaining in a recrudescent stage for up to four years. One year post spawning, fish transition from a post spawn stage to a recrudescent stage as:

(10)

where equation indices, parameters and variables are defined in Table 3.1.

### Recrudescent adult (>1 year post spawn)

Recrudescent adults that are greater than 1 year post spawn were modeled as a linear function of the number of recrudescent adults in the previous year and age that survived and did not return to a spawning state. This relationship was expressed as:

(11)

where equation indices, parameters and variables are defined in Table 1.

## Model values

Many sources were used to determine values required by equations 3.1 to 3.11 and simulate pallid sturgeon population dynamics. Four types of data were required: 1) initial stage-specific population abundances, 2) demographic values (e.g., sex ratio), 3) demographic rates (e.g., survival), and 4) demographic functions (e.g., maturity, fecundity). Initial stage-specific abundances for upper and lower basin natural and hatchery origin populations used to initialize the population model can be found in Table 3.2. Survival estimates and associated range of uncertainties and sources used in the simulation model are found in Table 3.3. Additional demographic values (e.g., sex ratio), uncertainties and sources are found in Table 3.1. Functions relating age or time since an event were required to predict additional age or time dependent demographic rates. In the simulation model, fecundity (eggs per female) was predicted as a function of age (Figure 4) using the following:

(12)

where equation indices, parameters and variables are defined in Table 3.1.

A sexual maturity function which calculated the probability of a juvenile fish transitioning to an adult fish as a function of age (Figure 3.4). This function was parameterized to reflect the minimum and maximum age at sexual maturity reported by K.D. Keenlyne (1997). Similarly, the probability of a recrudescent adult returning to sexual maturity was predicted as a function of years post spawning (Figure 3.5). These probabilities were selected to approximate the a spawning interval of 2.5 years (K. D. Steffensen et al., 2013a).

## Initializing the model

Initializing the model required three steps including 1) stochastically selecting stage-specific demographic rates, 2) stochastically selecting stage-specific abundances, and 3) allocating stage-specific abundance among age classes. Demographic rates were stochastically generated from triangular distributions representing the minimum, most likely, and maximum values for each parameter. For early life history stages where no survival estimates exist, survivals were randomly selected whose product equaled age-0 survival (). Stage-specific initial abundances were randomly selected from triangular distributions generated from minimum, expected, and maximum values reported in Tables 3.2 and 3.3. Age-specific abundances within each age-class were then stochastically generated assuming a stable age distribution. Once fish were allocated to age-classes within the adult stage, they were uniformly allocated among spawning and recrudescent stages.

## Analysis: simulating population dynamics

## Sensitivity

A sensitivity analysis was used to evaluate the effect of parameter uncertainty on population dynamics simulated for the lower and upper Missouri River basins. The sensitivity analysis was performed by randomly drawing parameters within parameter extremes assuming triangular distributions. Randomly selected values were used to initialize the population model and the population simulated over a 100 year period. Population abundance at year 100 was retained for juvenile and adult stages of hatchery and natural origin. This process was replicated 10k times to capture parameter variability. Yearling stocking was set to the basin-specific average values, it was assumed for this analysis that fingerling stocking will not continue due to low survival. Model parameter values were then assigned to quantiles (0-25, 25-50, 50-75, and 75-100%). Stage- and origin-specific expected abundances (i.e., mean) were calculated for each quantile and used to construct tornado plots to visualize how parameter uncertainty contributes to variation in abundances at = 100. Tornado plots are a useful tool for visualizing the effect of parameters on model output, population abundance at = 100 in this case, and are commonly used evaluate model sensitivity (Conroy & Peterson, 2013).

## Scenarios

The parameterized model was also used to evaluate several scenarios and address three questions regarding the upper and lower basin pallid sturgeon populations.   
*1) What is the population growth rate () under: A) present stocking conditions, and B) No stocking*?

This scenario was evaluated using the same steps of the sensitivity analysis with the exception that an additional scenario was added where stocking values were set to zero and simulated for the upper and lower basin populations. A stochastic growth rate was calculated for each of the 10k replicates as the geometric mean of within replicate annual growth rates.

*2) How far to move early life history survival to achieve ≥ 1 without stocking?*

Early life history survival is an important determinant of population growth rate and dynamics in fish populations. The use of population supplementation can circumvent poor survival of early life history stages and maintain or increase population abundances. In this scenario the question of how high does early life history survival need to be in order to maintain or increase the population (i.e., ≥ 1) in the absence of stocking. This question was evaluated by performing a grid search of values for and (). Specifically was evaluated for values of 0.001 to 0.003 by increments of 0.002 and was evaluated for values of 0.01 to 0.1 by increments of 0.01 for the upper and lower basin populations. Stocking values were set at 0 and the population simulated for a 100 year period. We simulated 100 replicate model runs for each unique combination of and . The mean stochastic and proportion of the 100 replicates with a mean stochastic ≥ 1 calculated for each combination of and . Results were visually assess for each parameter combination as a binary response, whether 95% of the 100 replicates had a stochastic ≥ 1.

*3) Depensation effect can we assess population needed to get past critical depensation?*

Spawning population abundance is hypothesized to limit the embryo production. The mechanism underlying this hypothesis relates to the likelihood of spawning aggregations occurring, especially when spawning abundances are low and sexually mature fish may have difficulties finding one another. To evaluate this we substituted in equation 3.1 with a model that predicts as a sigmoidal function of spawning adult population numbers as

(13)

where equation indices, parameters and variables are defined in Table 3.1. The relationship reduces the probability of eggs becoming embryos, especially at low spawning population abundances (i.e., depensatory effect) (Figure 3.6). The probability increases with increasing spawning population abundance until a maximum probability is reached. There is no existing information to inform this relationship and therefore this scenario is intended to demonstrate the capability of the model to evaluate additional scenarios. A visual analysis of the previous stocking scenarios (average stocking and no stocking) accounting for the hypothesized depensation effect to illustrate the analysis. Results of this analysis are not meaningful as the underlying depensatory relationship and parameters needed to predict embryo production are entirely unknown. This analysis is purely for demonstrative purposes.

## Preliminary results

### Sensitivities

Stage-specific sensitivity analyses for expected population abundance in year 100 varied between upper and lower Missouri River pallid sturgeon populations simulated. The expected number of natural origin adults in year 100 was most sensitive to early life history survival for the upper basin, and a mix of hatchery origin adult abundance, early life history survivals and sex ratio for the lower basin (Figure 3.7). Similar patterns of parameter sensitivity resulted for natural origin juveniles (Figure 3.8). Hatchery origin adults and juvenile sensitivities also varied between basin with juvenile survival playing a role in upper basin population dynamics, and a mix of factors in the lower basin (Figure 3.9 and 3.10). Similarly sensitivity results varied between basin for total population abundance, with a stronger influence of hatchery supplementation in lower basin, followed by early life history survival, sex ratio, adult abundance (i.e., factors linked in embryo production) (Figure 3.10). While the upper basin dynamics were sensitive to early life history survival and sex ratio.

### Scenarios

*1) What is the population growth rate () under: A) present stocking conditions, and B) No stocking*?

Population dynamics given the degree of uncertainties in model parameters exhibited variable dynamics. Under average stocking scenarios, populations tended to increase for all stages and basins (Figures 3.12 to 3.15). The majority of replicates tended to decline over the 100 year simulations for natural origin juvenile and adult stage pallid sturgeons with the cessation of stocking, especially after existing hatchery origin fish senesced out of the systems (Figures 3.12 and 3.13). There were certain parameter combinations that resulted in increasing abundance of natural origin fish under no stocking scenarios. As expected, hatchery origin fish abundance decline to 0 over the 100 year simulations (Figures 3.13 and 3.14). Evaluating distributions of growth rates for each scenario, all stocking scenarios had a growth rate greater than 1 (Figure 3.16). With the cessation of stocking, upper basin simulations were more likely to have a growth rate less than 1 and approximately 50% of the simulations for the lower basin had growth rates less than 1.

*2) How far to move early life history survival to achieve ≥ 1 without stocking?*

There was uncertainty in how much critical survival parameters need to increase in order to achieve a population growth rate greater than 1. Varying combinations of and can achieve a population growth rate greater than 1 given the parameters used to model the population. In general, simulations indicated that combinations of exceeding 0.0012 and exceeding 0.02 for the upper basin and exceeding 0.001 and exceeding 0.02 for the lower basin resulted in positive population growth under stocking conditions simulated.

*3) Depensation effect can we assess population needed to get past critical depensation?*

The population model was flexible enough to accommodate evaluation of a depensation scenario relating spawning population abundance to embryo production. But to reiterate the underlying functional relationship relating a depensatory effect of spawning population abundance on embryo production is uncertain and results are therefore unreliable. Relative to previous stocking and no stocking scenarios, simulating the same scenarios including a depensatory effect of population size on embryo production resulted in lower total population abundances and reduced population growth rates (Figure 3.6).

## Stage structured population model

## Stages

* Cover stages that occurred within year…
* The annual period began with a pre-breeding population.
* Period A, duration 8-12 days
* Period B, duration 8-12 days
* Period C
* Period D
* Figure 2. Stage progression

## Demographic rates and relationships

*Fecundity.—*The per capita number of viable embryos produced was a function of the number of eggs produced and the probability those eggs were viable. fecundity, sex ratio, and probability of eggs being viable.

*Sexual maturity.—*

*Population dynamics, sensitivity, and elasticities*



Abbreviated methods:

1. The first step was to generate a 41 by 41 cell matrix with fecundities in the top row and survivals on the off diagonal.
2. Estimate length at age a von Bertalanffy growth function   
    *la = 1683•(1-exp(-0.036•((8:41) - -5.9)))* ([Reynolds and Tyre 2011](#_ENREF_1))
3. Estimate fecundity as   
    *(-43678+ 72.70•la)•0.33•0.33.*   
   This accounts for length effects on eggs produced, sex ratio (0.33), and spawning interval period (3 years). This assumes fish are sexually mature at age 8.
4. Fill off diagonal (Survival rates) with age 0 to 1 = 0.051 , Age 1 to 2 = 0.686, and age 2 to 40 = 0.0992 ([Steffensen et al. 2013](#_ENREF_2))
5. Decompose matrix to dominant eigen values (to get λ) and vectors (to calculate sensitivity and elasticity) (see R code at end of document). Sensitivity is the change in λ that results from a change in demographic rate. Elasticity values expresses the proportional change in λ that would occur as a result of a small proportional change in the numerical value for a given non-zero element of the matrix