

1 A Fully-Stochasticized, Age-Structured Population Model for Population Viability Analysis of  
2 Fish: Lower Missouri River Endangered Pallid Sturgeon Example

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11

12 **Abstract**

13

14 We develop a fully-stochasticized, age-structured population model suitable for  
15 population viability analysis (PVA) of fish and demonstrate its use using the endangered pallid  
16 sturgeon (*Scaphirhynchus albus*) of the Lower Missouri River as an example. The model  
17 incorporates three levels of variance: parameter variance (uncertainty about the value of a  
18 parameter itself) applied at the iteration level, temporal variance (uncertainty caused by random  
19 environmental fluctuations over time) applied at the time-step level, and implicit individual  
20 variance (uncertainty caused by differences between individuals) applied within the time-step  
21 level. We found that population dynamics were most sensitive to survival rates, particularly age-  
22 2+ survival, and to fecundity-at-length. The inclusion of variance (unpartitioned or partitioned),  
23 stocking, or both generally decreased the influence of individual parameters on population  
24 growth rate. The partitioning of variance into parameter and temporal components had a strong  
25 influence on the importance of individual parameters, uncertainty of model predictions, and  
26 quasiextinction risk (i.e., pallid sturgeon population size falling below 50 age-1+ individuals).  
27 Our findings show that appropriately applying variance in PVA is important when evaluating the  
28 relative importance of parameters, and reinforce the need for better and more precise estimates of  
29 crucial life-history parameters for pallid sturgeon.

30

31 **Key words:** hierarchical stochasticity, population viability analysis, parameter variance,  
32 temporal variance, pallid sturgeon, Lower Missouri River

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35 does not represent any official USGS finding or policy.

36

## 37 **Introduction**

38

39           Population viability analysis (PVA) has become a valuable tool to conservation managers  
40 because it allows predictions to be made about future population trends in the face of changing  
41 environmental conditions and uncertainty about key demographic parameters (Morris and Doak  
42 2002). McGowan et al. (2011a) note that parameter uncertainty is often ignored in population  
43 viability analyses, one of the tools most commonly used by resource managers, where without  
44 consideration of parameter uncertainty, extinction risk was underestimated. They describe the  
45 four sources of uncertainty present in population modeling: structural uncertainty, temporal  
46 variance, demographic stochasticity, and parameter uncertainty. Structural uncertainty is based  
47 on the representation of system dynamics and its application represented by competing models  
48 (e.g., presence of or lack of limitations such as a carrying capacity or some form of density  
49 dependence in demographic parameters). Temporal variance or environmental stochasticity is  
50 parameter variation over time resulting from environmental fluctuations. Demographic  
51 stochasticity is chance variation in the actual fates of different individuals as has been described  
52 by other researchers (e.g., Morris and Doak 2002, Akçakaya 2002). Parameter uncertainty or  
53 sampling uncertainty is uncertainty in the estimates of the model parameters themselves.

54           McGowan et al. (2011a) describes how temporal variance, demographic stochasticity,  
55 and parameter uncertainty can be incorporated hierarchically in a population model. First,  
56 parameter uncertainty is applied at the replicate level by sampling replicate-level means (from  
57 distributions defined by the overall mean and parameter uncertainty) and replicate-level  
58 variances (from distributions defined by the temporal uncertainty). Second, temporal variance is  
59 applied in what McGowan et al. (2011a) defines as the “time-step loop”, by sampling the values  
60 used in each year within a replicate from distributions defined by the replicate-level mean and  
61 variances for that replicate. Finally, demographic stochasticity is applied in what they define as  
62 the “individual loop” where the fate of each individual (e.g., survival, successful reproduction,  
63 etc.), based on the population size and life-history parameters of the previous time step, is  
64 determined by sampling from probability distributions that define these parameters for that time  
65 step.

66           The use of fully-stochasticized population models, as described by McGowan et al.  
67 (2011a), has been applied to bird PVAs (e.g., red knots, *Calidris canutus rufa*, McGowan et al.

68 2011b; whooping cranes, *Grus americana*, Moore et al. 2012; piping plovers, *Charadrius*  
69 *melodus*, McGowan et al. 2014). We could find only one fish PVA with hierarchical variance  
70 (Vélez-Espino and Koops 2012) where parameter variance and demographic stochasticity were  
71 applied as draws from binomial distributions and Poisson distributions, respectively. Previous  
72 sturgeon population models have included models that incorporate no variance (e.g., shovelnose  
73 *Scaphirhynchus platorynchus* and pallid sturgeon *S. albus*, Bajer and Wildhaber 2007; Atlantic  
74 sturgeon *Acipenser oxyrhynchus*, white sturgeon *A. transmontanus*, and shortnose sturgeon *A.*  
75 *brevirostrum*, Gross et al. 2002), random or model generated parameter uncertainty (lake  
76 sturgeon *A. fulvescens*, Schueller and Hayes 2010; pallid sturgeon, Steffensen et al. 2013; white  
77 sturgeon, Jager et al. 2001 and 2013; shovelnose sturgeon, Goto et al. 2015; Gulf sturgeon *A.*  
78 *oxyrhynchus desotoi*, Pine et al. 2001; green sturgeon *A. medirostris*, Heppell 2007), and models  
79 that include some combination thereof (lake sturgeon, Vélez-Espino and Koops 2009; old world  
80 species of sturgeon, Jarić et al. 2010 and 2011, Gessner and Jarić 2014, Doukakis 2010). Here,  
81 using pallid sturgeon as the motivating example, we demonstrate how using a fully-  
82 stochasticized model with partitioned variance can produce different results from models that are  
83 not fully stochasticized.

84

### 85 1.1 Motivating example

86

87 The endangered pallid sturgeon is endemic to the turbid waters of the Missouri and  
88 Lower Mississippi rivers (Dryer and Sandvol 1993; Mayden and Kuhajda 1997). Since early  
89 1990s, juvenile pallid sturgeon reared from wild broodstock have been stocked in the Lower  
90 Missouri River in an effort to recover their populations (Huenemann 2014). Even in the presence  
91 of stocking, recruitment to the juvenile stage of wild-produced pallid sturgeon has not been  
92 documented in the Lower Missouri River (Steffensen et al. 2013). Recovery efforts have  
93 included habitat restoration through periodic flow modifications and specific hydro-engineering  
94 to potentially improve spawning success of adults and survival of juveniles (U.S. Fish and  
95 Wildlife Service--USFWS 2003). Progeny of hatchery-origin fish stocked in 1995-1997 have  
96 reached sexual maturity (Albers et al. 2013, Wildhaber and Bryan 2006) and have begun to  
97 spawn in the Lower Missouri River (DeLonay et al. 2009). In 2003, in response to the 2000  
98 USFWS Biological Opinion associated with the pallid sturgeon (USFWS 2000), the U.S. Army

99 Corps of Engineers (USACE) initiated the Pallid Sturgeon Population Assessment Program  
100 (PSPAP) to monitor the fish community of the Missouri River. For the Lower Missouri River,  
101 anecdotal information from over a decade ago put the pallid sturgeon population at only several  
102 thousand wild individuals (Duffy et al. 1996; USFWS 2000). More recently, an 80.5 km reach  
103 (of 1305 km of river) was estimated to contain 2032 hatchery pallid sturgeon (Steffensen et al.  
104 2012) and another 43.3 km reach was estimated to contain between 238 and 441 hatchery pallid  
105 sturgeon (Winders and Steffensen, 2014).

106 Bajer and Wildhaber (2007) developed an initial, deterministic age-structured model for  
107 pallid sturgeon populations in the Lower Missouri River to conduct a PVA. The model was most  
108 sensitive to age-0 survival rates, along with being sensitive to survival rates of juveniles and  
109 young adults. Wildhaber et al. (2007, 2011) presented a conceptual life-history model for pallid  
110 sturgeon that demonstrated the importance of transition probabilities (i.e., survival rate estimates  
111 in Bajer and Wildhaber (2007)) of the various life stages in determining population structure and  
112 forecasting future population trends. Since Bajer and Wildhaber (2007) published their model,  
113 much more has been learned about pallid sturgeon population biology. At the time their model  
114 was published, survival estimates were based, primarily, on observations from other sturgeon  
115 species. More recent work provides some measures of survival and local population size for  
116 pallid sturgeon (Steffensen et al. 2010, 2012; Winders and Steffensen 2014); although these are  
117 the only published estimates, they must be used only to provide relative patterns and not absolute  
118 numbers because they are based on PSPAP data. A U.S. Geological Survey (USGS) internal  
119 review of Bayesian-based population estimates based on PSPAP data (Wildhaber et al. in  
120 review) raised concerns that PSPAP data potentially violates mark-recapture model assumptions  
121 such as instantaneous sampling, permanent emigration, and zero tag loss, and so all existing  
122 estimates should be treated with caution. Albers et al. (2013) provides more direct and more  
123 accurate relationships between fork length (FL) and fecundity for pallid sturgeon in the Lower  
124 Missouri River than those utilized by Bajer and Wildhaber (2007). In addition, George et al.  
125 (2012) found a younger age at first reproduction and Albers et al. (2013) found a higher  
126 frequency of spawning for pallid sturgeon than were assumed by Bajer and Wildhaber (2007).

127 Growth of sturgeon in PVAs is often described by von Bertalanffy growth curves (VBG;  
128 Heppell 2007; Jager 2001; Jager et al. 2013; Pine et al. 2001; Vélez-Espino and Koops 2009), as  
129 has the growth of pallid sturgeon (Bajer and Wildhaber 2007; Shuman et al. 2011). Shuman et al.

130 (2011) provides estimates of growth models for Missouri River Research Priority Management  
131 Areas (RPMA) of which the Lower Missouri River is RPMA 4. They do this using all available  
132 data in RPMA 4 from 1998 to 2007 on hatchery-origin pallid sturgeon with a maximum age of  
133 nine years. They evaluated the fit of five different length-at-age growth models for all four  
134 RPMAs, finding that the VBG model for RPMA 4 had the second best fit behind a power  
135 function model. Bajer and Wildhaber (2007) also report a VBG model for hatchery and wild  
136 pallid sturgeon using data from all RPMAs with a maximum age of 41 years. A recent pallid  
137 sturgeon PVA in the Lower Missouri River was done by Steffensen et al. (2013) that did not  
138 include a VBG model or a fecundity-to-weight relationship and used one absolute fecundity for  
139 all weights and age classes. Though details were not specified, stochasticity seems to have been  
140 applied by resampling model parameters from normal distributions at the start of each  
141 deterministic model run. Furthermore, the high level of uncertainty of the published survival  
142 estimates for pallid sturgeon in the Lower Missouri River used in their PVA (Steffensen et al.  
143 2010; Steffensen et al. 2013; Winders and Steffensen 2014) necessitates a study of extinction  
144 probabilities to understand the importance of those estimates to any forecast of Lower Missouri  
145 River pallid sturgeon populations.

146

## 147 *1.2 Application to Pallid Sturgeon*

148

149 No previous PVAs for sturgeon have included a full complement of species-specific  
150 population parameters along with their associated levels of uncertainty. Bajer and Wildhaber  
151 (2007) and Steffensen et al. (2013) demonstrated the importance of the model assumptions for  
152 forecasting pallid sturgeon population trends. If the utilized model parameter values and real-  
153 world values differ by orders of magnitude then standard sensitivity analyses may produce  
154 misleading results about the importance of those parameters. Furthermore, McGowan et al.  
155 (2011a) demonstrated that the importance of incorporating uncertainty in population modeling is  
156 not in the central tendencies of estimates that result from the models, since they were essentially  
157 the same with and without uncertainty, but in the increased probability of the populations  
158 becoming extinct in the presence of uncertainty.

159 In this paper we build on the deterministic age-based population dynamics model for the  
160 pallid sturgeon in the Lower Missouri River developed by Bajer and Wildhaber (2007) through

161 incorporation of a full suite of species-specific population parameters and full, hierarchical  
162 stochasticity as described by McGowan et al. (2011a). The population model is used in a PVA to  
163 not only better define the importance of current population parameter estimates on model  
164 predictions, but to gain a better understanding of potential extirpation and/or extinction  
165 probabilities for the endangered pallid sturgeon. We modeled the population with and without  
166 continued stocking to assess the impact of current management efforts. In demonstrating the  
167 effectiveness of this approach for an endangered fish species such as the pallid sturgeon we show  
168 how such a fully-stochasticized modeling approach could be a valuable tool for managing other  
169 fish species.

170

## 171 **1. Methods**

172

### 173 *2.1 Study Area*

174

175 The focus area of this study is the Missouri River from Gavins Point Dam, South Dakota  
176 at river kilometer (rk) 1305.2 downstream to the confluence of the Missouri and Mississippi  
177 rivers near St. Louis, Missouri (rk 0) (RPMA 4, Shuman et al. 2011).

178

### 179 *2.2 Model Development*

180

181 Using Bajer and Wildhaber's (2007) deterministic pallid sturgeon population Leslie  
182 matrix model as a starting framework, we developed a fully-stochasticized, age-structured  
183 population projection matrix model for the pallid sturgeon population in the Lower Missouri  
184 River that incorporated species-specific parameterization and inclusion of parameter and  
185 temporal uncertainty in population forecasting and extinction probability (Table 1). We restricted  
186 the modeling to females (Donovan and Welden 2002), under the assumption that male  
187 abundance was sufficient to fertilize eggs (Quinn and Deriso 1999). Male numbers only played a  
188 role in determining the number of eggs that were identified as females based on the sex ratio  
189 distribution. Patterns observed for the female portion of the population were assumed to reflect  
190 whole population trends; therefore, we implicitly assumed that parameter distributions were the

191 same for both sexes. As Bajer and Wildhaber (2007) and Steffensen et al. (2013) did, we started  
192 the model out with age classes from 0 (starting from eggs) to 41 based on Keenlyne et al. (1992).

193 Following McGowan et al. (2011a), we estimated the number of females in age class  $i$   
194 surviving to the current year,  $t$ , ( $N_{i,t}$ ) as

195

$$196 \quad (1) \quad N_{i,t} \sim \text{Binomial}(N_{i-1,t-1}, \phi_{i-1,t-1});$$

197

198 where  $N_{i-1,t-1}$  is number of females in age class  $i-1$  in the previous year ( $t-1$ ), and  $\phi_{i-1,t-1}$  is the  
199 probability of survival of a female from age  $i-1$  in the previous year ( $t-1$ ) to age  $i$  in the current  
200 year ( $t$ ). Where Bajer and Wildhaber (2007) assumed that survival rates in pallid sturgeon were  
201 similar to Gulf sturgeon (Pine et al. 2001), we were able to utilize recently published estimates of  
202 pallid sturgeon survival (Table 1). Age-specific survival rate estimates for larval (i.e., age-at-  
203 stocking to age-1, incorrectly labeled as age-0 survival), age-1, and age-2+ pallid sturgeon were  
204 obtained from Steffensen et al. (2010). We used the age-0 survival rate (hatching to age-1)  
205 empirically found by Steffensen et al. (2013) to produce a stable population after 38 years (the  
206 same length of the simulation used by Steffensen et al. 2013). We estimated the egg survival rate  
207 as the ratio of age-0 survival to larval survival. Because survival rate estimates for individual  
208 ages classes beyond age 1 have not been published, we drew survival rates for age classes 2 and  
209 older independently but from the same underlying mean and standard deviation drawn for  $\phi_{2+}$  for  
210 that time step. Recent estimates of pallid sturgeon population rates (Steffensen et al. 2010, 2013)  
211 were obtained from PSPAP data; PSPAP data are known to contain multiple violations of the  
212 assumptions of mark-recapture analysis (Wildhaber et al. in review). Therefore, these estimates  
213 should not be used directly for any management related purpose. Our use of these estimates for  
214 this study is valid because we are investigating the relative sensitivity to model parameters, not  
215 making absolute predictions of future Pallid Sturgeon population sizes or survival rates. Our use  
216 of these estimates for this study is valid because we are investigating the relative sensitivity to  
217 model parameters, not making absolute predictions of future Pallid Sturgeon population sizes or  
218 survival rates. Because there is little information about many Pallid Sturgeon life history  
219 parameters, and because the elasticity of the response of population dynamics to a parameter can  
220 depend on the magnitude of that parameter (Mills et al. 1999; Vélez-Espino et al. 2006), we

221 tested a wide range of potential values of each parameter (see “Sensitivity analysis”, section  
222 2.2.2).

223 We fit VBG equations to all available pallid sturgeon length-at-age data (Welker and  
224 Drobish 2010, Huenemann 2014, Steffensen et al. 2010) to estimate length-at-age of stocked  
225 pallid sturgeon and to enable comparison of our deterministic simulation results to results  
226 produced using Bajer and Wildhaber (2007) and Shuman et al. (2011) VBG equations for the  
227 Lower Missouri River (RPMA 4). The standard form of the VBG equation that was fit is:

228

$$229 \quad (2) \quad FL_i = L_\infty [1 - e^{-K(i-t_0)}]$$

230

231 where fork length ( $FL$ ) (in mm) at age  $i$  is  $FL_i$ , asymptotic  $FL$  is  $L_\infty$ , the theoretical age when  
232 length = 0 is  $t_0$ , and  $K$  is the growth coefficient that approximates how rapidly  $FL$  increases to  
233  $L_\infty$ . We fit the model to all available data ( $n = 2182$ , including individuals captured in years 1999  
234 and 2002 to 2010) to estimate overall mean  $L_\infty$ ,  $t_0$ , and  $K$  ( $L_\infty = 1194 \pm 86.9$ ;  $K = 7.419 \times 10^{-2} \pm$   
235  $9.399 \times 10^{-3}$ ;  $t_0 = -2.672 \pm 0.2175$ ; all parameters significant at  $P < 0.0001$ ).

236 We used a linear relationship between  $FL$  and number of eggs found in gravid female pallid  
237 sturgeon using weight-based spawn reports ( $n = 18$ , Huenemann 2012; Steffensen et al. 2012; J.  
238 Colehour, D. Hendrix, and C. Bockholt personal communications) and ultrasound estimates ( $n =$   
239 26, Albers et al. 2013) to estimate fecundity (data from years 2006-2013). We used  $FL_i$  in this  
240 equation to estimate age-specific egg production ( $E_i$ ) as

241

$$242 \quad (3) \quad E_i = \beta_0 + \beta_1 FL_i$$

243

244 This linear relationship between fecundity and FL differs from previously published log-linear  
245 relationships ( $\log_{10}(E_i) = \beta_0 + \beta_1 FL_i$ ; Albers et al. 2013) because we considered only fish found  
246 in the Lower Missouri river and included unpublished spawn results (J. Colehour, D. Hendrix,  
247 and C. Bockholt, personal communications). The log-transformation of fecundity by Albers et al.  
248 (2013) was necessary to mitigate heteroscedasticity in fecundity; when only Lower Missouri  
249 River fish were considered, no transformation was necessary to meet the assumptions of the  
250 linear model. We fit the model to all available data ( $n = 44$ , years 2006 to 2013) to estimate  
251 overall means for  $\beta_0$  and  $\beta_1$  ( $\beta_0 = -45224.64 \pm 24709.94$ ;  $\beta_1 = 83.69 \pm 25.85$ ;  $\beta_0$  significant at  $P$



252 Table 1. Model parameters from literature and recent data (see Methods) for demographic rates used in baseline scenario. Total parameter variance  
253 ( $\sigma_{total}^2$ ) for sex ratio, length-at-age, and fecundity-at-length was separated into parameter uncertainty ( $\sigma_{param}^2$ ) which was applied at the iteration  
254 level, and environmental or temporal variance ( $\sigma_{temp}^2$ ) which was applied at the time-step level (Gould and Nichols 1998). Parameters were limited to  
255 mathematically possible or biologically realistic values. A negative value for temporal variance indicates that parameter variance was responsible for  
256 all variance, so the total variance was applied to that level. Number in parentheses under the means indicate the overall number of samples (numbers  
257 of recaptures for survival rates; individuals examined for other parameters; EE for empirically estimated); data in parentheses below variance  
258 components indicate how many and which years were used to partition variance. Means and variances for length-at-age and fecundity-at-length  
259 include only the ages (0 to 27 years) or fork lengths (775 to 1058 mm) for which we found positive temporal variance.

Parameter	Mean	$\sigma_{total}^2$	$\sigma_{param}^2$	$\sigma_{temp}^2$	Limits	Source
$\phi_{age-0}$	0.00011 (EE)	$6.0733 \times 10^{-10}$	$5.9082 \times 10^{-9}$ (6 years: 2003 to 2008)	$-5.3009 \times 10^{-9}$	[0,0.0004]	Steffensen et al. (2013); variances estimated from PSPAP data
$\phi_{larval}$	0.0510 (48)	$1.3055 \times 10^{-4}$	$1.2700 \times 10^{-3}$ (6 years: 2003 to 2008)	$-1.1395 \times 10^{-3}$	[0,1]	Steffensen et al. (2010); variances estimated from PSPAP data
$\phi_{age-1}$	0.3674 (EE)	$1.7567 \times 10^{-3}$	$1.8562 \times 10^{-2}$ (6 years: 2003 to 2008)	$-1.6805 \times 10^{-2}$	[0,1]	Mean empirically estimated; variances estimated from PSPAP data
$\phi_{age-2+}$	0.9220 (38)	$2.3573 \times 10^{-3}$	$2.3777 \times 10^{-3}$ (6 years: 2003 to 2008)	$-2.0409 \times 10^{-5}$	[0,1]	Steffensen et al. (2010); variances estimated from PSPAP data
Sex ratio (p(female))	0.4708 (699)	$4.6719 \times 10^{-3}$	$3.8173 \times 10^{-3}$ (9 years: 2006 to 2014)	$8.5469 \times 10^{-4}$	[0,1]	Albers et al. 2013; Albers unpublished data
Age of first spawn	10 (13)	1.0833	1.5333 (3 years: 1991, 2009, and 2013)	-0.4500	Min. = 1	Keenlyne and Jenkins 1993; George et al. 2012; Albers et al. (2013) and unpublished data
Proportion spawning females	0.2810 (331)	$5.7906 \times 10^{-3}$	$7.0981 \times 10^{-3}$ (9 years: 2006 to 2014)	$-1.3075 \times 10^{-3}$	[0,1]	Albers et al. 2013; Albers unpublished data
Length-at-age (mm)	214 to 1061 (2182)	87.3 to 16146	21.3 to 16076.5 (7 years: 2004 to 2010)	58.3 to 874.3	Min. = 1	PSPAP data
Fecundity-at- length (eggs)	0 to 205849.3 (44)	$6.8053 \times 10^7$ to $1.7138 \times 10^8$	$3.0816 \times 10^7$ to $1.7111 \times 10^8$ (4 years: 2008 to 2011)	$1.9518 \times 10^4$ to $5.9987 \times 10^7$	Min. = 0	Albers et al. 2013; Albers unpublished data

260 = 0.0743;  $\beta_1$  significant at  $P = 0.0023$ ).

261 Preliminary runs of the model showed that when variance was applied independently to  
262 individual parameters in the growth and fecundity relationships, extreme draws of one or more  
263 parameters in those equations would lead to biologically unrealistic FL, growth rates, or egg  
264 production rates. Because we were interested in the effect of variation of length-at-age or egg  
265 production and not in the effect of variation in individual parameters, we instead drew age-  
266 specific lengths and length-specific fecundities from 95% prediction intervals for the fitted  
267 models. For the non-linear VBG model of fork length, we used a first-order Taylor series  
268 approximation (a.k.a., the “Delta method”) to estimate the 95% prediction interval for fork  
269 length for each age from 0 to 66 (Spiess 2014). For the linear relationship between fecundity and  
270 length, we estimated the 95% prediction interval using the standard method for a linear model.  
271 Stochastic draws for fork length were further restricted to be  $\geq 1$  mm; similarly, stochastic draws  
272 for egg production were restricted to be non-negative.

273 Following the combination of Bajer and Wildhaber (2007) and McGowan et al. (2011a),  
274 age-specific fertility at each year  $t$  and age class  $i$  ( $F_{i,t}$ ) was estimated as number of eggs  
275 produced by spawning females resulting in female offspring

276

$$277 \quad (4) \quad F_{i,t} \sim E_{i,t} \times k \times \text{Binomial}(N_{i,t}, z_{i,t})$$

278

279 where  $k$  is proportion of females in the population or sex ratio ( $n = 699$  pallid sturgeon from 9  
280 years from Albers et al. 2013 and unpublished data; Table 1), and  $z$  is the proportion of spawning  
281 females ( $n = 331$  female pallid sturgeon from 9 years from Albers et al. 2013 and unpublished  
282 data; Table 1), or probability a female of reproductive age will spawn in a given year. The entire  
283 population model can then be expressed as

284

$$285 \quad (5) \quad N_t = \sum_{i=1}^m N_{i,t} + \sum_{i=g}^n F_{i,t-1} + \sum_{i=0}^w N_{i,t-1}^{stock}$$

286

287 where  $m$  is the maximum age of an individual,  $g$  is age of first reproduction ( $n = 13$  stocked fish  
288 from Keenlyne and Jenkins 1993, George et al. 2012, and Albers unpublished data; Table 1),  $n$  is  
289 age of last reproduction (i.e., age of senescence, unknown for pallid sturgeon so we assumed  $n =$   
290  $m$  and tested the effects of senescence here),  $w$  is the maximum age class stocked, and  $N_{i,t-1}^{stock}$  is

291 the number of females in age class  $i$  stocked at time  $t-1$ . Stocked animals were added to the  
292 population at the beginning of each time step, before reproduction and survival rates were  
293 applied, and were subject to the same demographic processes as wild fish. Stocked fish were not  
294 distinguished from or tracked independently of wild fish in the model and were eligible to  
295 reproduce and/or perish starting in the time step in which they were stocked. To assess the  
296 effects of stocking we ran each simulation with and without stocking, with the population with  
297 and without stocking subject to the same stochastic parameter draws. We simulated stocking of  
298 fish from age 0 to age 3. The number of fish stocked in each age class per year was set to mean  
299 historical stocking levels from 17 years of stocking in RPMA 4: 3539 age-0 individuals, 4087  
300 age-1 individuals, 65 age-2 individuals, and 31 age-3 individuals (Huenemann 2014). The  
301 current time step's sex ratio was applied to these numbers of stocked fish before they were added  
302 to the population.

303

#### 304 2.2.1 Determining run characteristics

305

306 We used the results of preliminary tests of the model to determine the run characteristics  
307 (number of iterations, number of years in population growth rate  $\lambda$  calculation, spin-up period,  
308 and initial population size) necessary for consistent results so that differences in  $\lambda$  could be  
309 attributable to our manipulations and not to instability in the model. We defined  $\lambda$  as the change  
310 in the age-1+ population from one year to the next (i.e.,  $N_{t+1}/N_t$ ). This value is both the antilog of  
311 the intrinsic rate of increase ( $r$ ) and the dominant eigenvalue of a population projection matrix  
312 (Birch 1948, Caswell 2001, Stevens 2009). Run characteristics were chosen to surpass minimum  
313 criteria set *a priori*. To determine the earliest year  $\lambda$  calculation could start and the number of  
314 years included in the mean  $\lambda$ , we ran the model for 150 years and calculated  $\lambda$  for as many years  
315 as possible with different numbers of years included in the overall mean  $\lambda$ . We considered the  
316 earliest year for which the empirical rate of change in  $\lambda$  from each year to the subsequent year  
317 ( $\Delta\lambda/\Delta t$ ) was  $\leq 0.0001$  to be the earliest starting year that would produce stable  $\lambda$  values. Because  
318  $\lambda$  stabilized after that year,  $\lambda$  calculation could begin any time after that without affecting the  
319 results. When the model was run for 38 years, as was done by Steffensen et al. (2013), the  
320 earliest year  $\lambda$  calculation could start was year 6 no matter what variance structure was included  
321 in the model. Therefore the selected spin-up period of 20 years surpassed the minimum number

322 of years required for model dynamics to stabilize (see Appendix A for more details). To find the  
323 number of iterations needed for consistency between runs, we required that the number of  
324 iterations be >1000 and that the width of the 95% percentile interval of  $\lambda$  changed by less than  
325 0.001 for each additional 1000 iterations added; 2000 was the minimum number of iterations that  
326 met these criteria (see Appendix A for more details). Finally, to determine the minimum initial  
327 population size needed for consistent results, we tested the model with a range of initial  
328 population sizes  $N$  from 2 to 200 individuals per recruited (age-1+) age class and required that  
329 the empirical rate of change in median  $\lambda$  per additional fish per age class,  $\Delta\lambda/\Delta N$ , was  $\leq 0.001$ .  
330 The minimum total population size (without stocking) that met this criterion was 26 individuals  
331 per age class. Therefore our initial population size of 7122 individuals, recently reported by  
332 Winders and Steffensen (2014), was large enough to ensure that the effect of initial population  
333 size on  $\lambda$  in simulation scenarios was negligible. The initial 7122 individuals were spread over  
334 ages 1 to 41, with 174 females in age classes 1 to 29 and 173 females in age classes 30 to 41 (i.e.,  
335 after 173 fish were put into each age class, the remaining 29 fish were seeded starting with the  
336 youngest age class). We used a uniform age distribution for the initial population because the  
337 true age distribution for Lower Missouri River Pallid Sturgeon is unknown. Rather than make  
338 additional assumptions about the age distribution, we initialized the model with a uniform  
339 distribution because the uniform distribution is a more natural null model of population age  
340 structure than any distribution based on previous model results or survival rate estimates. The 20  
341 year spin up period ensured that model dynamics were driven by processes within the model  
342 rather than by transient dynamics.

343

### 344 2.2.2 Sensitivity analysis

345

346 Initial means of the distributions of probabilities of survival of each age class, the  
347 estimates of egg production per female by size resulting from the observed relationship,  
348 proportion of the population that is female, and the estimates of length-at-age resulting from the  
349 VBG equation were increased or decreased 5% from reported values one at a time with their  
350 variance estimates held constant (Table 1). We also assessed the importance of survival of each  
351 age class 2-40 by running the model with each age-specific survival rate set to 1. The change in  
352 the distribution of  $\lambda$  that occurred with the change in a parameter or function relative to the

353 baseline scenario was the measure of the relative sensitivity of model to each parameter or  
354 function.

355           Because there is limited or no information about intervals between consecutive spawn,  
356 age of first spawn, age of reproductive senescence, and maximum age for pallid sturgeon, we  
357 tested the effect of varying these parameters on population dynamics. We used the proportion of  
358 females in reproductive condition for a year (i.e., proportion spawning) as a proxy for the  
359 reciprocal of spawn interval. We evaluated the relationship between the proportion spawning and  
360  $\lambda$  by running simulations for each value from every year to once every 12 years, corresponding to  
361 a range of proportions spawning from 1 to 0.0833, respectively. This experimental range  
362 encompasses the suspected range of 3 to 10 years reported by Mayden and Kuhajda (1997) and  
363 Albers et al. (2013). We evaluated the relationship between age of first female reproduction,  $g$ ,  
364 and  $\lambda$  by running simulations with ages of first female reproduction from 5 to 20 years which  
365 encompasses the range of suggested ages of 8 to 12 years of first reproduction (Keenlyne and  
366 Jenkins 1993, George et al. 2012 and Albers unpublished data). Because no information about  
367 the age when reproduction ceases, or reproductive senescence, exists for pallid sturgeon, we  
368 measured the effect on  $\lambda$  of ages of reproductive senescence from 11 to 41. We measured the  
369 effect on  $\lambda$  of a range of maximum ages from 16 to 66 years (the observed maximum age of 41,  $\pm$   
370 25 years). To clarify how age-specific survival rates affected population growth rates, we also  
371 varied age-0 survival, age-1 survival, and age-2+ survival rates across a range of potential  
372 values. Age-0 survival rate was varied from 0 to 0.001 in increments of 0.00005; age-1 and age-  
373 2+ survival rate were varied from 0 to 1 in increments of 0.05. Finally, we used the Donovan and  
374 Welden (2002) inoculation method to test age-specific reproductive potentials by seeding 3,000  
375 pallid sturgeon in each of the individual age classes separately, with all other age classes initially  
376 set to zero. The measured responses, reproductive value, for each age class other than age-0 were  
377 the median population sizes of recruited (age-1+) individuals after 38 years. This test also served  
378 to evaluate the potential effects of stocking different age classes on pallid recovery.

379           We ran the model for 38 years for most tests, but ran the model for 100 years to test age  
380 of senescence and maximum age, and 200 years to test quasiextinction probability.

381 Quasiextinction (Morris and Doak 2002) rate here is the percentage of replicate iterations where  
382 the population dropped below a threshold of 50 females. We chose 50 females as the threshold  
383 for quasiextinction following Jarić et al. (2010) who used 50 individuals as a measure of

384 pseudoextinction with European sturgeon. For senescence and maximum age, the longer time  
 385 horizon was necessary because the ranges of these variables could have no effect in only 38  
 386 years. One hundred years was chosen because it was long enough for multiple generations to  
 387 pass within the model, and not so long as to produce 95% percentile intervals of  $\lambda$  or population  
 388 size that were so wide as to be meaningless. For quasiextinction, the need for more years was a  
 389 result of the fact that our model was developed to produce a stable population for the 38 year  
 390 simulation time horizon used.

391

### 392 2.2.3. Hierarchical Inclusion of Uncertainty

393

394 Following the suggestions of McGowan et al. (2011a), we incorporated different  
 395 components of parameter uncertainty at different levels of the simulation. For each parameter we  
 396 separated the total variation into parameter and temporal variance (Gould and Nichols 1998).  
 397 Parameter variance is variance about the parameter itself while temporal variance is variation in  
 398 a parameter over time caused by environmental stochasticity (Gould and Nichols 1998, Morris  
 399 and Doak 2002, McGowan et al. 2011a). Generalizing from Gould and Nichols (1998) equation  
 400 for total variance in survival estimates, the total variance  $S^2$  in a parameter  $A$  sampled at  $n$   
 401 occasions is

402

$$403 \quad (6) \quad S^2 = \frac{1}{n-1} \sum_{i=1}^n (\hat{A}_i - \hat{\bar{A}})^2$$

404

405 where  $\hat{A}_i$  is the estimate of  $A$  at occasion  $i$ , and  $\hat{\bar{A}}$  is the mean of all  $\hat{A}_i$ . The temporal variance  $\hat{\tau}^2$   
 406 in  $A$  is the total variance  $S^2$  minus the parameter variance:

407

$$408 \quad (7) \quad \hat{\tau}^2 = S^2 - \frac{1}{n} \sum_{i=1}^n [Var(\hat{A}_i)]$$

409

410 It is worth noting that  $\hat{\tau}^2$  can be negative if the parameter variance is large. For those variables  
 411 where we found a negative temporal variance ( $\phi_{larva}$ ,  $\phi_0$ ,  $\phi_1$ ,  $\phi_{2+}$ , fecundity-at-length for fork  
 412 lengths  $\leq 774$  and  $> 1046$  mm, length-at-age for ages  $\geq 28$  years, age of first spawn, and

413 proportion spawning), we assigned the total variance to parameter variance (Gould and Nichols  
414 1998). At the replicate level, we sampled a mean for the replicate  $\mu_i$  as

415

$$416 \quad (8) \quad \mu_i \sim \text{TruncatedNormal}(\mu, \sigma_{param}, \mu \pm 1.96\sigma)$$

417

418 where  $\mu$  is the global mean for the parameter and  $\sigma_{param}$  was the parameter standard deviation,  
419 i.e., the square-root of the variance remaining after temporal variance was removed ( $\sigma_{param} =$   
420  $\sqrt{S^2 - \hat{\tau}^2}$ ). We sampled for replicate-level values from distributions of means and variances for  
421 each parameter of the model based on the combination of available estimates that exist. We  
422 sampled a temporal variance for the replicate using the estimated  $\hat{\tau}$  as the mean and a 5%  
423 coefficient of variation (McGowan et al. 2011a); i.e.,  $\tau_i \sim \text{Normal}(\hat{\tau}, 0.05\hat{\tau})$ . We then sampled a  
424 parameter value for each year within a replicate as

425

$$426 \quad (9) \quad A_{i,t} \sim \text{TruncatedNormal}(\mu_i, \tau_i, \mu_i \pm 1.96\tau_i)$$

427

428 with the parameter draw truncated to the replicate mean  $\mu_i \pm 1.96$  temporal standard deviations.  
429 If there was no temporal variance for a parameter, then  $\tau_i$  was 0 and there was no variability  
430 from year-to-year within a replicate. Parameters were additionally restricted to mathematically  
431 possible intervals (e.g., probabilities could not have values outside of [0,1] even if  $\mu_i \pm 1.96\tau_i$   
432 was not fully contained in that interval). This approach ensured that different contributions to  
433 parameter uncertainty were applied at appropriate levels. Every year within a replicate we drew  
434 parameters from the same underlying distribution, with parameter uncertainty expressed as  
435 changes in the distribution from replicate to replicate.

436 No series of age-specific, year-specific estimates of pallid sturgeon survival rates, which  
437 were required to partition the variance in survival rates, have been published. In order to obtain  
438 age-specific, year-specific estimates for Pallid Sturgeon survival rates, we combined the age-  
439 specific estimates presented by Steffensen et al. (2010, 2013) and year-specific estimates using a  
440 Bayesian-based approach (King et al. 2009) from the same PSPAP dataset used by Steffensen et  
441 al. (2013). For each age, we calculated a series of composite age-specific, year-specific survival  
442 rates as the square root of the product of an age-specific rate and a year-specific rate (i.e., the  
443 survival rate  $\phi_{a,y}$  for age  $a$ , year  $y$ , was the geometric mean of those two rates:  $\phi_{a,y} = \sqrt{\phi_a \phi_y}$ ; A.

444 Arab, Department of Mathematics and Statistics, Georgetown University, Washington, DC  
445 20057, *personal communication*). We calculated the variance of each composite estimate as the  
446 square root of the product of the variance of the age-specific estimate and the year-specific  
447 estimate (i.e., the variance of the survival rate  $\sigma_{a,y}^2$  for age  $a$  and year  $y$ , was the geometric mean  
448 of the variances of the age-specific and year-specific rates:  $\sigma_{a,y}^2 = \sqrt{\sigma_a^2 \sigma_y^2}$ ). We then used the  
449 methods of Gould and Nichols (1998) and McGowan et al. (2011a) to partition the variance in  
450 survival rates based on this series of composite estimates and their associated variances. To  
451 estimate parameter and temporal variance in overall age-0 survival, we assumed that its  
452 coefficient of variation was the same as for larval survival (i.e.,  $\sigma_{\phi_0}/\hat{\phi}_0 = \sigma_{\phi_{larva}}/\hat{\phi}_{larva}$ ), which  
453 was what was actually estimated by Steffensen et al. (2010). Though there are concerns about  
454 combining MLE and Bayesian estimates, it can be argued that this approach can be used because  
455 the inclusion of non-informative priors in the latter often results in estimates that closely match  
456 the MLE estimates (Bayarri and Berger 2004).

457 For length-at-age, fecundity-at-length, proportion spawning, sex ratio, and spawn age, we  
458 used available annual data [PSPAP, Albers et al. (2013), unpublished data] to estimate annual  
459 values for each parameter so that temporal variation could be estimated. To estimate parameter  
460 and temporal variability in length-at-age and fecundity-at-length, we fit the VBG equation to  
461 data from each year for which adequate data existed from 2004 to 2010, and the linear fecundity  
462 model to data from years 2008 to 2011 to obtain a series of annual estimates for each model  
463 parameter, respectively. We then generated prediction intervals for each year for length-at-age  
464 using a Delta method approximation (Spiess 2014) and for fecundity-at-length using the standard  
465 method for a linear model. We then applied the variance partitioning method of Gould and  
466 Nichols (1998) to the annual estimates and variances for length-at-age from age 0 to age 66 and  
467 for fecundity-at-length from length 0 mm to length 3000 mm. We could then sample iteration-  
468 level means and year-level values for length-at-age and fecundity-at-age using age-specific and  
469 length-specific overall means, parameter variances, and temporal variances.

470 We ran three versions of the model to investigate the effects of different variance  
471 components on population dynamics. The deterministic model had no parameter or temporal  
472 variance. The unpartitioned variance model had the total variance not partitioned and added to  
473 the time-step loop as temporal variance (McGowan et al. 2011a). The partitioned variance model



474 had the total variance partitioned as described above and the parameter variance (if any) added to  
475 the iteration loop and the temporal variance (if any) added to the time-step loop.

476 When we ran the deterministic model that had no variance, the survival and spawning  
477 probabilities used in the binomial processes above (equations 1 and 2) were treated as rates that  
478 determined the number of individuals that survived and reproduced in that time step. Without  
479 binomial trials for survival and reproduction, the model behaves as a standard Leslie matrix  
480 model. When the model was run without binomial trials, the expression for number of females in  
481 age class  $i$  surviving to the current year,  $t$ , ( $N_{i,t}$ ) becomes (abbreviations same as equation 1):

482

$$483 \quad (10) \quad N_{i,t} = N_{i-1,t-1} \times \phi_{i-1,t-1}$$

484

485 and the expression for yearly age-specific fertility becomes (abbreviations same as equation 2):

486

$$487 \quad (11) \quad F_{i,t} = E_{i,t} \times k \times N_{i,t} \times z_{i,t}.$$

488

489 We assessed extinction risk out to 200 years covering multiple generations as the  
490 quasiextinction rate, or the percentage of replicate iterations where the population dropped below  
491 the threshold of 50 females.

492

### 493 *2.3 Data analysis*

494

495 To test the effects of changing stochastic parameters, changing age-specific survival  
496 rates, age of first spawn, proportion spawning, reproductive senescence, and maximum age, we  
497 used population growth rate ( $\lambda$ ) as the measured response. We used the population size  $N_{\text{age}1+}$  at  
498 38 years as the measure of reproductive value of an age class. For all parameters tested, response  
499 variables failed either the Shapiro-Wilk test for normality, or the Levene test for homogeneity of  
500 variance, or both, so we used non-parametric tests (Wilcoxon rank-sum tests and Spearman rank  
501 correlation tests) to mitigate the assumption violations of ANOVA and linear regression. We set  
502  $\alpha = 0.05$  for all statistical tests, and applied Bonferroni corrections to account for multiple  
503 comparisons.

504 The population simulation program and all analyses were performed in R version 2.15.3

505 (R Core Team 2013). Within R we used package “msm” version 1.2 (Jackson 2011) for drawing  
506 from truncated normal distributions, package “lawstat” version 2.4.1 (Gastwirth et al. 2013) for  
507 Levene tests, and package “propagate” (Spiess 2014) for approximating the prediction intervals  
508 of the VBG equation.

509

## 510 **2. Results**

511

512 An initial run of the deterministic form of the pallid sturgeon population model using all  
513 current published parameter estimates and estimates based on the most recent data collected,  
514 resulted in pallid sturgeon population estimates of approximately 26,000 after only 38 years  
515 (number of years presented by Steffensen et al. 2013), not the expected stable population near  
516 the initial population of 7,122 that would have occurred using the Steffensen et al. (2013) model  
517 (Table 2). With nearly a 4-fold difference in population estimates, before any model simulations  
518 were done, we determined it was necessary to adjust our model to produce a stable population as  
519 was done in Steffensen et al. (2013) so that we could compare our results for sensitivity to model  
520 parameters. A stable population here means the mean population growth rate,  $\lambda$ , for years 21-38  
521 was 1. Survival estimates have been identified as the most sensitive parameters in pallid sturgeon  
522 population models (Bajer and Wildhaber 2007; Steffensen et al. 2013), supported by results of  
523 substituting Steffensen et al. (2013) parameters one at a time into our model (Table 2).  
524 Steffensen et al. (2013) noted their model was most sensitive to age  $\geq 1$  survival estimates and  
525 that age-1 survival estimates were the most uncertain (Steffensen et al. 2010). Given the results  
526 of the simulations using Steffensen et al.’s (2013) age-0 survival rate estimate of 0.00011 (Table  
527 2) necessary to produce a stable pallid sturgeon population under their model, we empirically  
528 estimated, in a fashion similar to Vaughan and Saila (1976), that an age-1 survival rate of 0.3674  
529 (replacing 0.686 presented by Steffensen et al. (2010)) was necessary to produce a stable  
530 population under our model (Table 2). Consequently, in all of our simulations we used a mean  
531 age-1 survival of 0.3674. Using the same set of survival rate estimates, we found that use of the  
532 Bajer and Wildhaber (2007) VBG equation resulted in a  $\lambda$  greater than 1 while the Shuman et al.  
533 (2011) equation resulted in a  $\lambda$  less than 1 and not a stable population as in our case. In addition,  
534 during decomposition of overall variance to parameter and temporal variance to fully

535 Table 2. Summary of differences caused by running our deterministic model using the values of  
 536 a previous pallid sturgeon PVA (Steffensen et al. 2013). We ran the model with our parameter  
 537 values, substituting in the values presented by Steffensen et al. (2013) one at a time to assess  
 538 each parameter's contribution to differences between the two models. The baseline for  
 539 comparison was our model run with our parameters and our empirically determined  $\phi_1 = 0.3674$ .  
 540 Measured response was population of age-1+ individuals after 38 years ( $N_{38}$ ) and difference in  
 541  $N_{38}$  from our baseline run. The difference between the baseline run and the run with all our  
 542 parameters and Steffensen et al.'s (2013)  $\phi_1$  (0.686) illustrates why their estimate of  $\phi_1$  cannot be  
 543 accurate if the population is stable or decreasing.  
 544

Parameter	Our values	Steffensen et al. (2013)	$N_{38}$	Difference	
Sex ratio (p(female))	0.4708	0.3333	4072	-3588	-46.8%
First spawn age	10	9	8143	+483	+6.3%
Proportion females spawning	0.281029	0.3333	10679	+3019	+39.4%
Fecundity (eggs/female)	0 to 205849.3	19064	2734	-4926	-64.3%
All Steffensen et al. (2013) parameter values, $\phi_1 = 0.686$			7416	-244	-3.2%
All Steffensen et al. (2013) parameter values, $\phi_1 = 0.3674$			2223	-5437	-70.9%
All our parameter values, $\phi_1 = 0.686$			25965	+18305	+238.9%
All our parameter values, $\phi_1 = 0.3674$			7660		

545  
 546 stochasticize the model as described by McGowan et al. (2011a), we found temporal variance to  
 547 be non-zero for only sex ratio, length-at-age for age classes 0 to 27 years, and fecundity-at-length  
 548 for lengths 775 to 1046 mm (Table 1).

549  
 550 *3.1 Model parameter sensitivities*  
 551

552 When assessing the sensitivity of the model to a 5% change in fecundity-at-length,  
 553 length-at-age, overall survival rate, proportion females, and proportion spawning, we found that  
 554 changing the majority of these parameters by 5% resulted in significant differences in  $\lambda$  from the  
 555 baseline using estimated means and variances (Table 1) in the deterministic, unpartitioned  
 556 variance, and partitioned variance models (Table 3); the only exceptions were age-0 and age-1  
 557 survival rates in the partitioned variance model (Table 4). Similar to Bajer and Wildhaber (2007),  
 558 the change in  $\lambda$  from the baseline was, essentially, symmetric for increases and decreases, except

559 Table 3. Results of Wilcoxon rank-sum tests for the effect on population growth rate of changing parameters by 5%; W is sum of  
560 ranks, effect is median difference from baseline,  $n$  for all tests was 4000, and all differences were significant at  $P < 0.0001$   
561 (Bonferroni-corrected  $\alpha = 0.0083$ ). Effect sizes for deterministic model are change in  $\lambda$ ; no test could be performed.  
562

Variable	Without stocking				With stocking			
	-5%		+5%		-5%		+5%	
	W	Effect	W	Effect	W	Effect	W	Effect
<b>Fecundity</b>								
Deterministic		-0.0024		0.0025		-0.0013		0.0014
Unpartitioned variance	1701241	-0.0021	2312280	0.0023	1802784	-0.0011	2231980	0.0014
Partitioned variance	1863976	-0.0023	2171263	0.0028	1860499	-0.0014	2149929	0.0015
<b>Growth</b>								
Deterministic		-0.0062		0.0057		-0.0033		0.0034
Unpartitioned variance	1363739	-0.0046	2674847	0.0050	1560222	-0.0026	2510711	0.0031
Partitioned variance	1740739	-0.0042	2345167	0.0059	1776660	-0.0022	2312820	0.0033
<b>Overall survival rate</b>								
Deterministic		-0.0561		0.0501		-0.0255		0.0400
Unpartitioned variance	117	-0.0473	3996143	0.0356	9226	-0.0242	3991252	0.0282
Partitioned variance	144517	-0.0480	3673480	0.0366	108800	-0.0223	3717084	0.0278
<b>Age-2+ survival rate</b>								
Deterministic		-0.0500		0.0455		-0.0236		0.0359
Unpartitioned variance	476	-0.0430	3983390	0.0307	18449	-0.0226	3968893	0.0239
Partitioned variance	229037	-0.0424	3496562	0.0306	195241	-0.0200	3550581	0.0226
<b>Proportion spawning</b>								
Deterministic		-0.0024		0.0025		-0.0013		0.0014
Unpartitioned variance	1604454	-0.0029	2378635	0.0027	1703112	-0.0018	2287836	0.0017
Partitioned variance	1876691	-0.0021	2153837	0.0025	1889963	-0.0011	2123136	0.0013
<b>Sex ratio</b>								
Deterministic		-0.0024		0.0025		-0.0018		0.0018
Unpartitioned variance	1670674	-0.0024	2330554	0.0024	1705543	-0.0017	2297798	0.0018
Partitioned variance	1870472	-0.0022	2126989	0.0022	1823044	-0.0018	2147878	0.0015

563

564 Table 4. Changes in population growth rate ( $\lambda$ ) from the baseline scenario ( $\lambda = 1.0000$ ) resulting  
565 from changing age-specific survival rates from age 0 to age 40 ( $\phi_0$  to  $\phi_{40}$ ) by 5% in the  
566 population without stocking. For models with variance, significance was determined by a  
567 Wilcoxon rank-sum test (see Methods); for tests shown in this table,  $\alpha = 0.0012$  (i.e., Bonferroni  
568 correction applied for each age). Nonsignificant results are not shown. Effect sizes for  
569 deterministic model are change in  $\lambda$ ; no test could be performed.  
570

Age $\phi$	-5%			+5%		
	Deterministic	Unpartitioned variance	Partitioned variance	Deterministic	Unpartitioned variance	Partitioned variance
$\phi_0$	-0.0024	-0.0023		0.0025	0.0026	
$\phi_1$	-0.0024	-0.0019		0.0025	0.0024	
$\phi_2$	-0.0024	-0.0019		0.0025	0.0020	0.0038
$\phi_3$	-0.0023	-0.0020		0.0025	0.0019	
$\phi_4$	-0.0023	-0.0022		0.0024	0.0016	
$\phi_5$	-0.0023	-0.0019		0.0024	0.0018	
$\phi_6$	-0.0023	-0.0018		0.0024	0.0016	
$\phi_7$	-0.0023	-0.0018		0.0024	0.0020	
$\phi_8$	-0.0023	-0.0021		0.0025	0.0018	
$\phi_9$	-0.0022	-0.0020	-0.0038	0.0025	0.0018	
$\phi_{10}$	-0.0021	-0.0018		0.0024	0.0019	0.0060
$\phi_{11}$	-0.0021	-0.0020		0.0023	0.0015	0.0035
$\phi_{12}$	-0.0020	-0.0017		0.0022	0.0017	
$\phi_{13}$	-0.0019	-0.0016		0.0021	0.0018	
$\phi_{14}$	-0.0018	-0.0017		0.0021	0.0015	
$\phi_{15}$	-0.0017	-0.0015		0.0019	0.0013	
$\phi_{16}$	-0.0016	-0.0011		0.0019	0.0014	
$\phi_{17}$	-0.0015	-0.0014		0.0019	0.0013	
$\phi_{18}$	-0.0014	-0.0014		0.0017	0.0010	0.0041
$\phi_{19}$	-0.0012	-0.0011		0.0015	0.0011	
$\phi_{20}$	-0.0011			0.0013	0.0009	
$\phi_{21}$	-0.0010	-0.0008		0.0011	0.0013	
$\phi_{22}$	-0.0009			0.0010	0.0010	
$\phi_{23}$	-0.0008			0.0009		
$\phi_{24}$	-0.0007			0.0008		
$\phi_{25}$	-0.0006			0.0007		0.0037
$\phi_{26}$	-0.0005			0.0006		
$\phi_{27}$	-0.0005			0.0006		
$\phi_{28}$	-0.0004			0.0005		
$\phi_{29}$	-0.0003			0.0005		
$\phi_{30}$	-0.0003			0.0004		
$\phi_{31}$	-0.0002			0.0003		
$\phi_{32}$	-0.0002			0.0003		
$\phi_{33}$	-0.0002			0.0002		
$\phi_{34}$	-0.0002			0.0002		

$\phi_{35}$	-0.0001	0.0001
$\phi_{36}$	-0.0001	0.0001
$\phi_{37}$	-0.0001	0.0001
$\phi_{38}$	-0.0001	0.0001
$\phi_{39}$	-0.0001	0.0001
$\phi_{40}$	0.0000	0.0001

---

571

572 for change in overall survival rate or age-2+ survival rate where the effect was greater for a  
573 decrease without stocking (Table 3 and 4).

574 A further break down of the sensitivity to survival of individual age classes (Table 4),  
575 produced a limited number of age classes that significantly changed  $\lambda$  relative to the baseline. All  
576 the age classes that significantly changed  $\lambda$  relative to the baseline were younger than 26 years of  
577 age. Only four age classes significantly changed  $\lambda$  relative to the baseline for both variance  
578 structures with an increase in survival rate. The number of individual age classes that  
579 significantly changed  $\lambda$  from the baseline was greater for an increase in survival rate than a  
580 decrease under both variance structures (Table 4). Similar results for changing individual age-

581 specific survival rates by 5% were observed occurred with and without stocking (Tables 3 and 4;  
582 stocking results for individual age classes 2+ not shown).

583         The correlations between age-0, age-1, and age-2+ survival rates and  $\lambda$  without stocking  
584 were highly significant with and without any form of variance (Table 5). Stocking had no effect  
585 on the correlation between survival rate and  $\lambda$  for ages 0 and 1, but eliminated the correlation for  
586 ages 2+ with and without variance (Table 5). With and without variance and without stocking, it  
587 took a smaller percent change in age-2+ survival rate from its mean to change  $\lambda$  by 5% than it  
588 took to change  $\lambda$  by the same amount by manipulating age-0 and age-1 survival rates (Table 5).

589         Age at first spawn correlations with  $\lambda$  were weaker in the presence of any form of  
590 variance, and were weakened by approximately one half with partitioned variance (Table 6).  
591 Stocking had no impact on the effects of variance on the correlation between age at first spawn  
592 and  $\lambda$  (Table 6). Proportion of females spawning correlations with  $\lambda$  weakened in the presence of  
593 any form of variance (Table 6). With stocking, the correlations between  $\lambda$  and proportion  
594 spawning were reduced more by either variance structure than without stocking (Table 6). Age  
595 of reproductive senescence correlations with  $\lambda$  weakened in the presence of any form of variance  
596 (Table 6). Stocking weakened the correlation between  $\lambda$  and age of reproductive senescence. The  
597 effect of variance was much greater on the correlation between  $\lambda$  and age at first spawn than it  
598 was for the correlation between  $\lambda$  and age of senescence or proportion spawning. Maximum age  
599 correlation with  $\lambda$  weakened in the presence of any form of variance (Table 6). Stocking further  
600 decreased the correlation between  $\lambda$  and maximum age with and without any form of variance.

601         Because no quasiextinctions were predicted by any of the three models at 38 years, we  
602 ran the model for a longer period of time to assess extinction risk. After 200 years, there were no  
603 quasiextinctions under the deterministic model or the model with unpartitioned variance. In the  
604 partitioned variance model, quasiextinction rate increased over time to approximately 10.25%  
605 after 200 years (Figure 1).

606

607 Table 5. Ranges of age-specific survival rates required to increase or decrease population growth rate ( $\lambda$ ) by 5% from the baseline  $\lambda$  of  
608 1.0000 for each model run mode. The percentage change from the parameter means represented by each range are shown in  
609 parentheses (age-0 mean = 0.00011; age-1 mean = 0.3674; age-2 mean = 0.922). Age-0 survival rate ( $\phi_0$ ) was tested from 0 to 0.001 in  
610 increments of 0.00005; age-1 and age-2+ survival rates ( $\phi_1$  and  $\phi_{2+}$ , respectively) were tested from 0 to 1 in increments of 0.05. Blank  
611 entries indicate that no value of  $\phi_0$ ,  $\phi_1$ , and  $\phi_{2+}$  tested would increase or decrease  $\lambda$  by 5%.

612

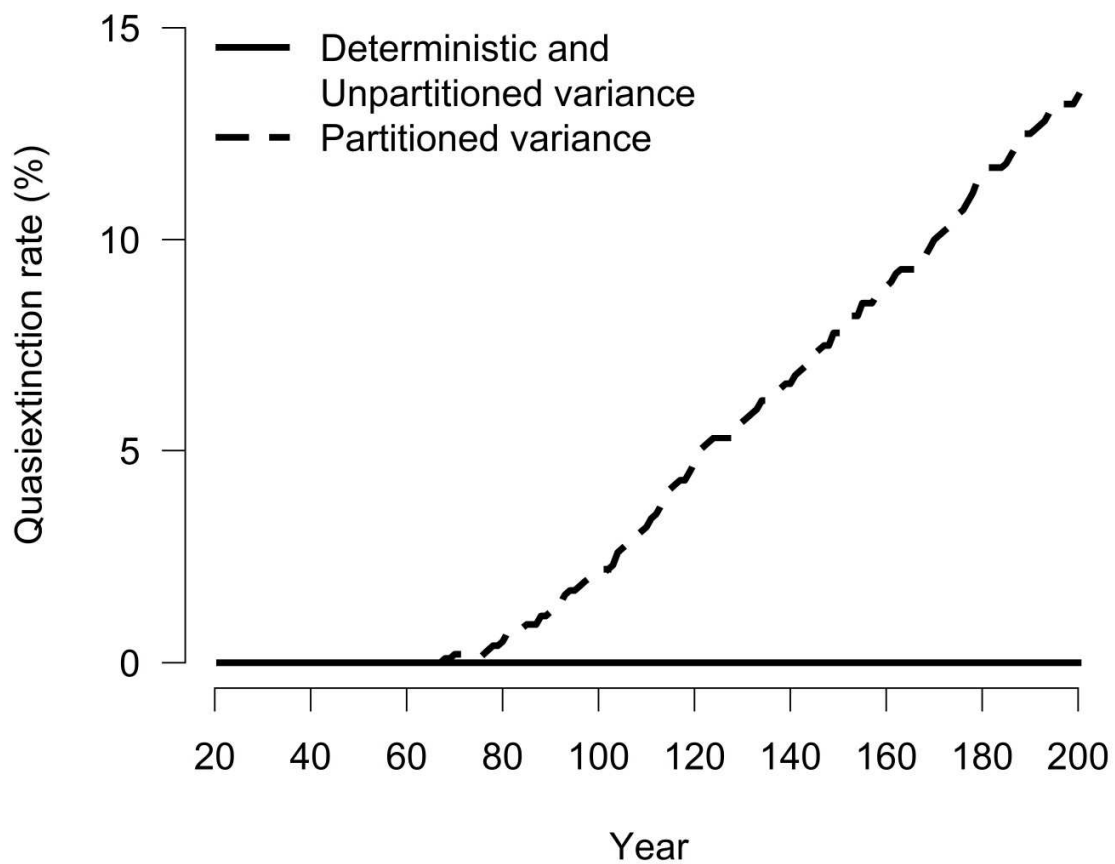
Model run type	Without stocking		With stocking	
	Change in $\lambda$		Change in $\lambda$	
	-5%	+5%	-5%	+5%
Age-0 survival( $\phi_0$ )				
Deterministic		$2.5 - 3 \times 10^{-4}$ (+127% - 172%)		$3.5 - 4 \times 10^{-4}$ (+218% - +263%)
Unpartitioned variance		$2.5 - 3 \times 10^{-4}$ (+127% - 172%)		$3.5 - 4 \times 10^{-4}$ (+218% - +263%)
Partitioned variance		$2.5 - 3 \times 10^{-4}$ (+127% - 172%)		$3 - 3.5 \times 10^{-4}$ (+218% - +263%)
Age-1 survival ( $\phi_1$ )				
Deterministic	0.05 - 0.1 (-86% - -73%)	0.95 - 1 (+158% - +172%)	0 - 0.05 (-100% - -86%)	
Unpartitioned variance	0.05 - 0.1 (-86% - -73%)	0.95 - 1 (+158% - +172%)	0 - 0.05 (-100% - -86%)	
Partitioned variance	0 - 0.05 (-100% - -86%)	0.85 - 0.9 (+131% - +145%)	0.05 - 1 (-86% - -73%)	0.95 - 1 (+158% - +172%)
Age-2+ survival ( $\phi_{2+}$ )				
Deterministic	0.8 - 0.85 (-13% - -8%)	0.95 - 1 (+3% - +8%)		0.95 - 1 (+3% - +8%)
Unpartitioned variance	0.8 - 0.85 (-13% - -8%)	0.95 - 1 (+3% - +8%)		0.95 - 1 (+3% - +8%)
Partitioned variance	0.8 - 0.85 (-13% - -8%)	0.95 - 1 (+3% - +8%)		0.95 - 1 (+3% - +8%)



613 Table 6. Results of Spearman rank-correlation tests for correlations between population growth  
614 rate ( $\lambda$ ) and age-0 survival rate, age-1 survival rate, age-2+ survival rate, age of first spawn, age  
615 of reproductive senescence, maximum age, and proportion of females spawning in all three  
616 models (deterministic, unpartitioned variance, and partitioned variance), with and without  
617 stocking. Total sample size ( $n$ ) is reported once for each independent variable.  $S$  is the sum of  
618 squared rank differences,  $\rho$  is the correlation coefficient. Unless otherwise indicated, all  
619 correlation coefficients were significant at  $P < 0.0001$ .

Variable	Without Stocking		With Stocking	
	$S$	$\rho$	$S$	$\rho$
Age-0 survival rate ( $n = 42000$ )				
Deterministic	0	1.0000	0	1.0000
Unpartitioned variance	$3.0158 \times 10^{11}$	0.9756	$3.0410 \times 10^{11}$	0.9754
Partitioned variance	$1.9634 \times 10^{11}$	0.9841	$1.9757 \times 10^{11}$	0.9840
Age-1 survival rate ( $n = 42000$ )				
Deterministic	0	1.0000	0	1.0000
Unpartitioned variance	$1.4271 \times 10^{11}$	0.9884	$1.1888 \times 10^{11}$	0.9904
Partitioned variance	$7.0935 \times 10^{10}$	0.9943	$6.2241 \times 10^{10}$	0.9950
Age-2+ survival rate ( $n = 42000$ )				
Deterministic	247923.6	0.8394	1667861	-0.0806 <sup>a</sup>
Unpartitioned variance	$1.0739 \times 10^{12}$	0.9130	$1.2434 \times 10^{13}$	-0.0070 <sup>b</sup>
Partitioned variance	$1.0722 \times 10^{12}$	0.9132	$1.2330 \times 10^{13}$	0.0017 <sup>c</sup>
Age of first spawn ( $n = 32000$ )				
Deterministic	1364778	-0.9993	1364778	-0.9993
Unpartitioned variance	$9.9060 \times 10^{12}$	-0.8138	$9.6116 \times 10^{12}$	-0.7599
Partitioned variance	$7.8594 \times 10^{12}$	-0.4391	$8.0860 \times 10^{12}$	-0.4806
Age of reproductive senescence ( $n = 60000$ )				
Deterministic	18019.82	0.9960	0	1
Unpartitioned variance	$1.9463 \times 10^{12}$	0.9459	$5.1021 \times 10^{12}$	0.8583
Partitioned variance	$8.2049 \times 10^{12}$	0.7721	$1.7060 \times 10^{13}$	0.5261
Maximum age ( $n = 102000$ )				
Deterministic	34012.95	0.9984	1402534	0.9366
Unpartitioned variance	$3.1660 \times 10^{13}$	0.8210	$5.0148 \times 10^{13}$	0.7165
Partitioned variance	$8.6047 \times 10^{13}$	0.5115	$1.1012 \times 10^{14}$	0.3774
Proportion spawning ( $n = 24000$ )				
Deterministic	0	1.0000	0	1.0000
Unpartitioned variance	$1.8235 \times 10^{11}$	0.9209	$4.8737 \times 10^{11}$	0.7885
Partitioned variance	$5.7812 \times 10^{11}$	0.7491	$7.3413 \times 10^{11}$	0.6814

<sup>a</sup> Not significant ( $P = 0.2449$ ); <sup>b</sup> Not significant ( $P = 0.7333$ ); <sup>c</sup> Not significant ( $P = 0.2074$ )



620

621 Figure 1. Although the model did not predict quasiextinctions (population dropping below 50  
 622 individuals) at 38 years, quasiextinctions did occur when the model was run for a longer time  
 623 horizon (200 years) with partitioned variance. No quasiextinctions were observed with either the  
 624 deterministic model or the unpartitioned variance model. There were no quasiextinctions when  
 625 the model was run without variance (deterministic) because we empirically estimated the age-1  
 626 survival rate to make the population stable.

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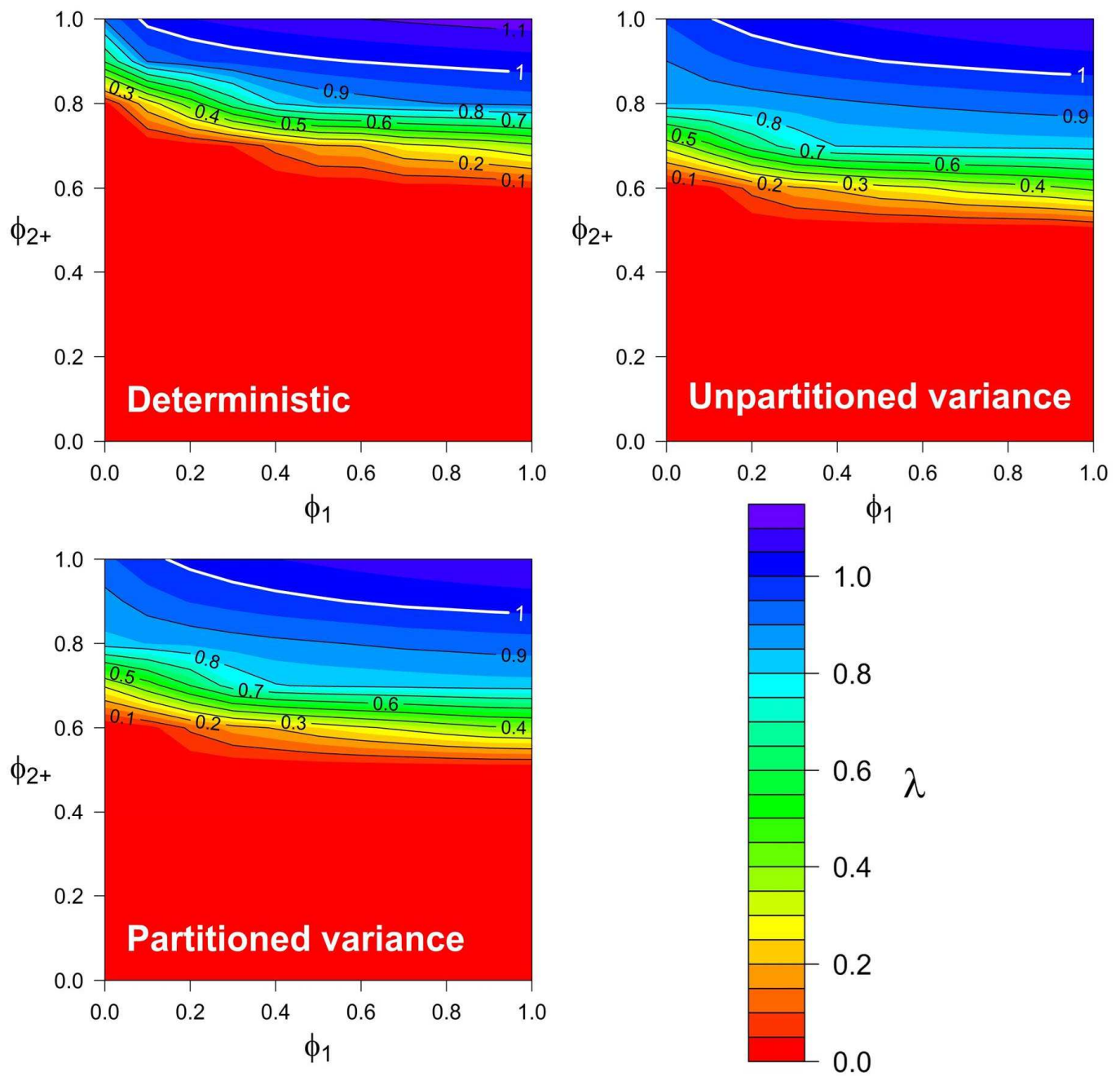
629

### 630 3. Discussion

631

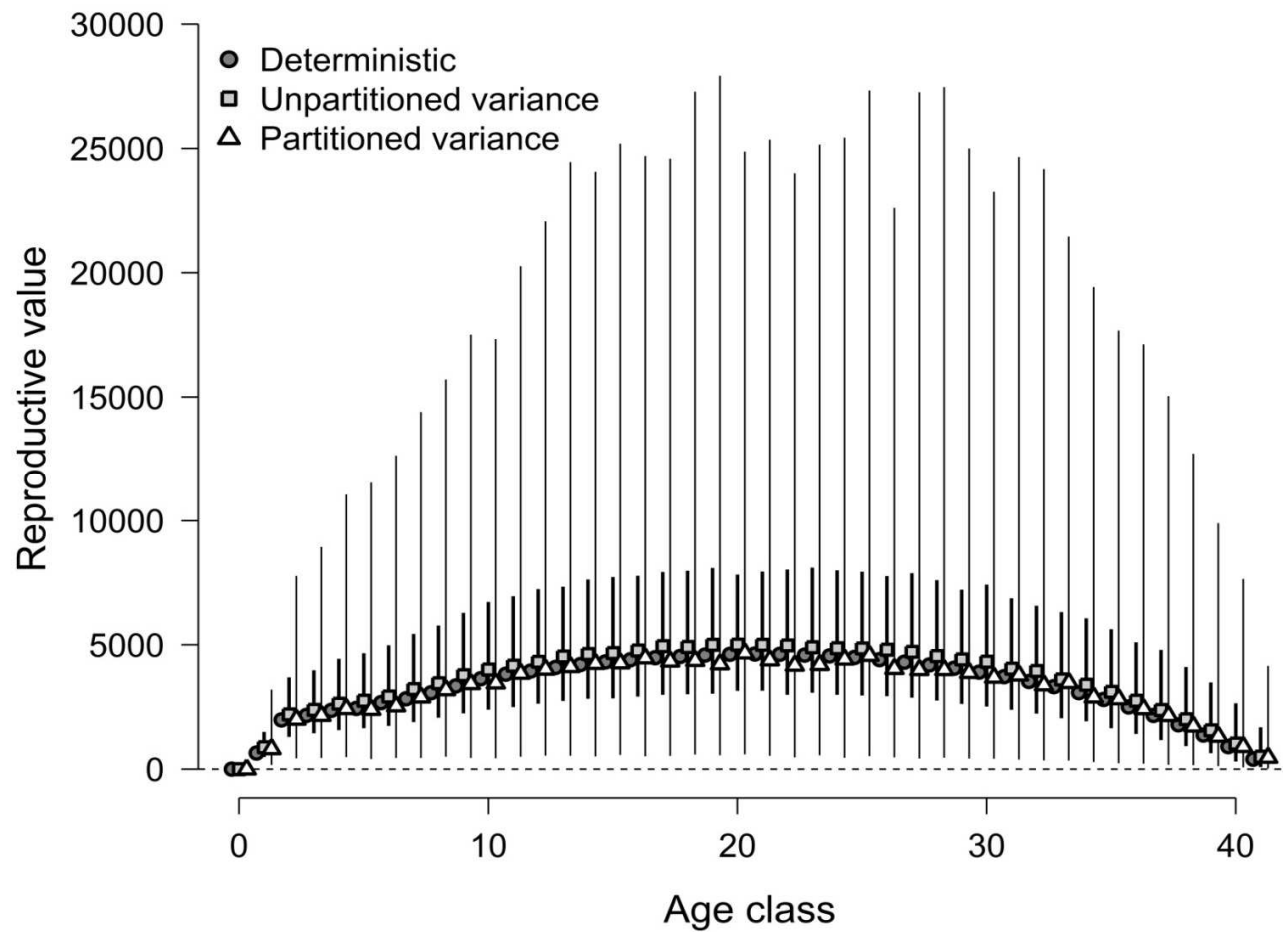
632 As would be expected, the form and parameterization of the various components of the  
633 pallid sturgeon population model, especially without variance included, determined whether the  
634 predicted future populations would be increasing, stable, or decreasing. Even without variance in  
635 parameter and function estimates present, survival estimates for age-1 pallid sturgeon had to be  
636 set to about half the reported estimate for the Lower Missouri River (Steffensen et al. 2010) to  
637 produce a stable population using our parameters in favor of those used by the previous pallid  
638 sturgeon PVA (Steffensen et al. 2013). Apart from our treatment of uncertainty about  
639 parameters, the key difference between our model and that of Steffensen et al. (2013) was the use  
640 of a VBG length-at-age equation in concert with a fecundity-at-length equation to estimate age-  
641 specific fecundity rather than using a single fecundity for all female pallid sturgeon. Relative to  
642 the results from our model (i.e., a stable population), the use of the VBG model of Bajer and  
643 Wildhaber (2007) predicted an increasing Pallid Sturgeon population while the VBG of Shuman  
644 et al. (2011) predicted a decreasing population in the Lower Missouri River. Our model also  
645 differed from Steffensen et al. (2013) in its age at first spawn, proportion of females spawning,  
646 and sex ratio of the population, but all of these parameters had less of an impact on the model  
647 than did fecundity (Table 2).

648 The population of pallid sturgeon was very sensitive to survival rates. The model was  
649 most sensitive to age-2+ survival. A change in age-2+ survival alone produced a change in  $\lambda$   
650 from the baseline similar to a change in all age classes (Table 3, Table 4). The sensitivity to age-  
651 2+ survival rate is also shown by the rapid change in population growth rate associated with  
652 changing age-2+ survival by a small amount regardless of the age-1 survival rate (Figure 2) and  
653 by the small changes in age-2+ survival rate necessary to change  $\lambda$  by 5% (Table 1, Table 5). The  
654 highly non-linear response to age-2+ survival seen in Figure 2 suggests that there may be a  
655 threshold value of  $\phi_{2+}$  below which the population cannot sustain itself. Significant effects of  
656 individual age-class survival on  $\lambda$  ceased as of age 26. This is likely because fewer individuals  
657 overall survive to older ages, so changing those survival rates has a smaller effect than changing  
658 the survival rate of earlier, more populous age classes. This paralleled reproductive value  
659 peaking between 19 and 21 years of age (Figure 3) and age of reproductive senescence effects



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Figure 2. Contour plots of the population growth rate ( $\lambda$ ) resulting from different combinations of age-1 survival rate ( $\phi_1$ ) and age-2+ survival rate ( $\phi_{2+}$ ), where both  $\phi_1$  and  $\phi_{2+}$  were varied independently from 0 to 1 in increments of 0.1.



666

667 Figure 3. Reproductive value peaked around age 20 for all model run types. Here the reproductive value of any age class is the  
 668 population of recruited individuals, age-1+ after 38 years resulting when the population is initialized with 3000 individuals in only that  
 669 age class. For runs with variance, the median  $\lambda$  and the 2.5% to 97.5% percentile interval of  $\lambda$  are shown. Points for unpartitioned  
 670 variance are centered on the appropriate age class; points for deterministic and partitioned variance are offset slightly to the left and  
 671 right, respectively.

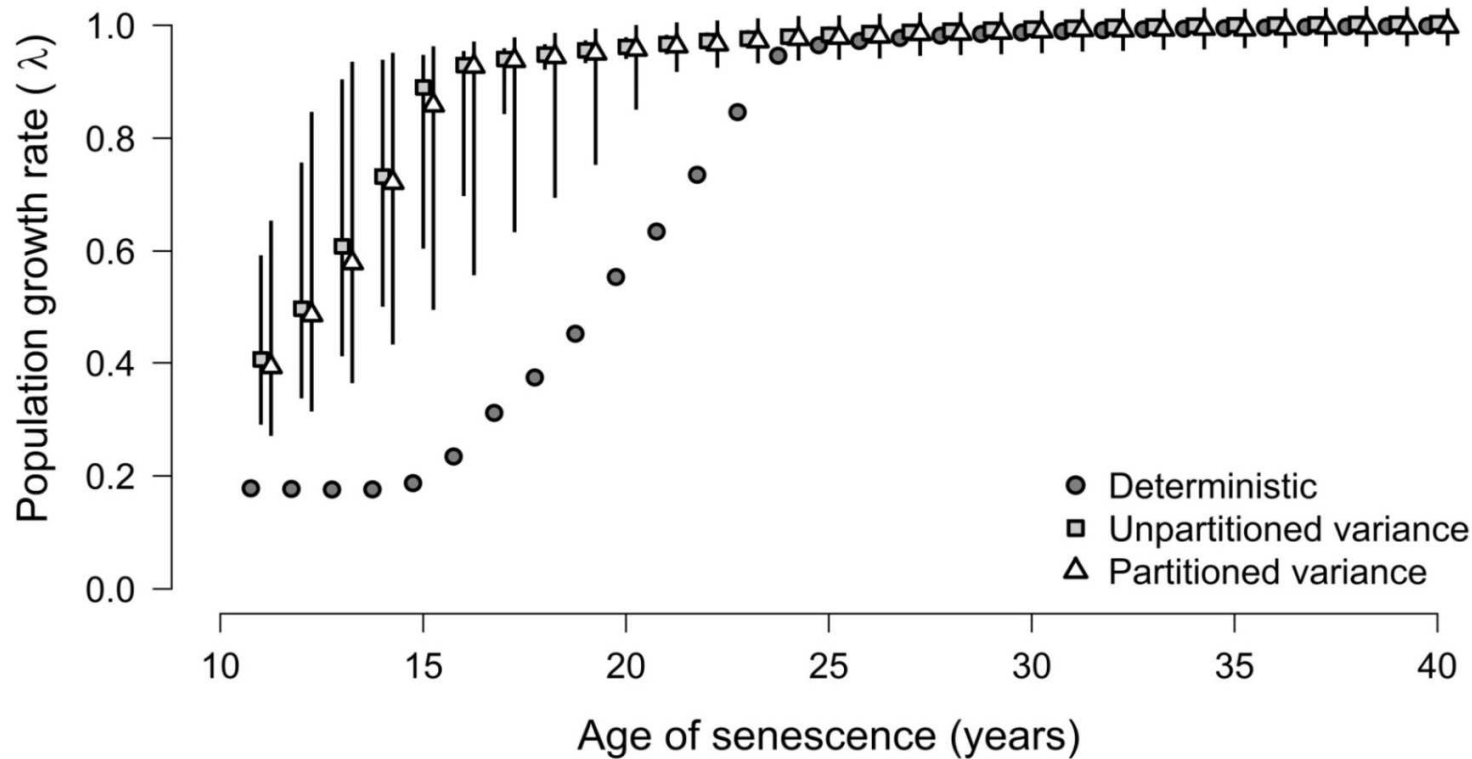
672 dramatically declining when pallid sturgeon were in their late teens and early 20s (Figure 4). In  
673 addition, the effects of survival of any one age-class on  $\lambda$  occurred more often for an increase in  
674 survival rate than a decrease. Comparison of  $\lambda$  across all combinations of ages 1 and 2+ survival  
675 rates indicates there is a minimum survival rate necessary for each age class in the presence of no  
676 mortality for the other in order for a stable population to occur (age-1 deterministic,  
677 unpartitioned variance, and partitioned variance 0.081, 0.111, and 0.147, respectively; age-2+  
678 0.8779, 0.8469, and 0.8684, respectively; Figure 2). These thresholds may result from the long  
679 delay between recruitment and age of first spawn: if essentially no individuals survive to  
680 reproductive age, then the population is doomed without allochthonous recruitment.

681

#### 682 4.1 *Effects of uncertainty*

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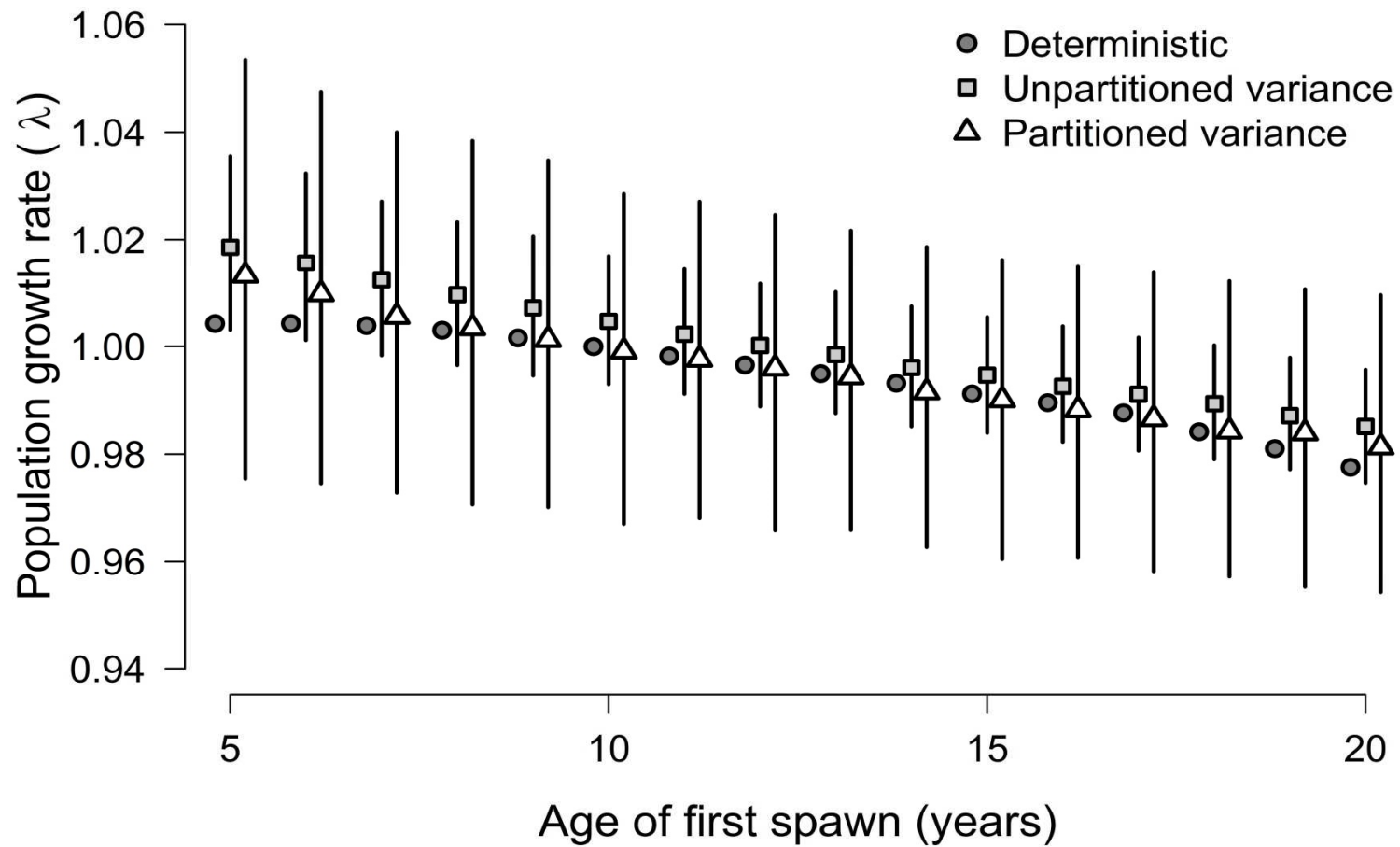
684 The effects of fecundity-at-length, length-at-age, all age-specific survival rates, proportion  
685 females, proportion spawning and age-0, -1, and 2+ survival rates on  $\lambda$  were similar across the  
686 deterministic, unpartitioned variance, and partitioned variance models. The effect of age at first  
687 spawn and maximum age on  $\lambda$  decreased in the presence of variance while the effect of variance  
688 was less for age of reproductive senescence or proportion spawning. Population growth rate was  
689 consistently higher for the unpartitioned variance model than the deterministic or partitioned  
690 variance model (Figures 3, 4, and 5). When age at first spawn was 5 through 8 and greater than  
691 17 years  $\lambda$  was less for the deterministic model than it was in the partitioned variance model  
692 (Figure 5). The uncertainty in model predictions (i.e., the width of the 95% percentile interval)  
693 was greater in all cases with the partitioned variance model (Figures 3, 4, and 5). The increased  
694 uncertainty may partly explain why most individual parameters had a smaller influence on  $\lambda$   
695 when variance in the model was partitioned (Tables 3, 4, and 6). Because we empirically  
696 estimated the age-1 survival rate that would produce a stable population, the deterministic model  
697 predicted no quasiextinctions at any time horizon tested (Figure 1). The addition of variance  
698 to the model introduced quasiextinctions only if the variance was partitioned. In the partitioned  
699 variance model, the quasiextinction rate was approximately 0.5% after 100 years and  
700 approximately 10.25% after 200 years. This should not be misconstrued as a prediction of the  
701 probability of extinction of pallid sturgeon within 100 or 200 years. Instead, what we show is that  
702 properly partitioned variance increases the predicted probability of quasiextinction and that



703

704 Figure 4. Population growth rate ( $\lambda$ ) tended to increase as the age of reproductive senescence increased in the deterministic model and  
 705 the models with either variance structure for 100 years. The increase in  $\lambda$  slowed down as reproductive senescence occurred later; the  
 706 greatest gains in  $\lambda$  were seen as the age of senescence increased up to approximately age 25. For runs with variance, the median  $\lambda$  and  
 707 the 2.5% to 97.5% percentile interval of  $\lambda$  are shown. Points for unpartitioned variance are centered on the appropriate age class;  
 708 points for deterministic and partitioned variance are offset slightly to the left and right, respectively.

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Figure 5. Population growth rate ( $\lambda$ ) was negatively correlated with age of first spawn without variance and with both variance structures. For runs with variance, points show median  $\lambda$  and error bars show the 2.5% to the 97.5% percentile interval of  $\lambda$ . Points for unpartitioned variance are centered on the appropriate age class; points for deterministic and partitioned variance are offset slightly to the left and right, respectively.



717 that probability increases over time. A population model with unpartitioned variance might  
718 underestimate the risk of quasiextinction or worse, misleadingly imply that the risk was zero.

719

#### 720 4.2 *Stocking*

721

722 The effect of changing overall survival rate was greatest for a decrease in the presence of  
723 annual stocking. Without stocking, when survival rates for all age classes were increased or  
724 decreased simultaneously the change in  $\lambda$  from the baseline ranged from near 10 to over 20 times  
725 that of changes in all other parameters with length-at-age the next most influential parameter  
726 (Table 3). With stocking, the effect of each parameter on the change in  $\lambda$  from the baseline was,  
727 generally, less than half the effect each had without stocking. Stocking had, essentially, no effect  
728 on the correlation between survival rate and  $\lambda$  for ages 0 and 1, a limited effect on the correlation  
729 for age at first spawn, maximum age, age of reproductive senescence, and proportion spawning,  
730 decreased the correlation between  $\lambda$  and age of reproductive senescence but essentially  
731 eliminated the correlation for age-2+ survival rate. Therefore, continued annual stocking of  
732 individuals that are immediately recruited to the population could mitigate the effects of a highly  
733 influential survival rate falling below some threshold value. This would imply that some limiting  
734 effect is occurring to individuals in the wild before the age of stocking.

735

#### 736 4.3 *Model formulation and full stochasticity*

737

738 A common theme in sturgeon population assessments, and PVA for long-lived species  
739 overall, is the importance of survival rates to population sustainability (Heppell et al. 2000).  
740 Previous studies have shown that overall or age-0 survival are the most influential parameters in  
741 sturgeon population models (Pine et al. 2001; Schueller and Hayes 2010; Vélez-Espino and  
742 Koops 2009; Jager et al. 2010; Jarić et al. 2010, 2011; Doukakis et al. 2010; Heppell 2007; Gross  
743 et al. 2002). The importance of age-0 survival is further emphasized by observation of Lv and  
744 Pitchford (2007) that fish larvae that survive tend to be larger, from the right tail of the size  
745 distribution. Results from this and previous studies (Bajer and Wildhaber 2007; Steffensen et al.  
746 2013) indicate pallid sturgeon are typical in that survival of young individuals is paramount to a  
747 sustainable population. Increasing survival of all age groups by 5% caused population growth

748 rate to increase by 3 to 5%, depending on the variance structure, similar to Bajer and Wildhaber  
749 (2007) deterministic model results. Our observations parallel those of Bajer and Wildhaber  
750 (2007) in that changing survival rates after age 25 had little impact on population growth; they  
751 indicated a drop off in importance between 20 and 25 years of age.

752 An important consideration when determining the influential nature of each parameter  
753 and its importance to management of the species is whether one is considering recovery or  
754 limiting harm. For instance, a vital rate (e.g., adult survival) may have a large influence on  
755 population growth such that any harm or reduction in this vital rate would be expected to  
756 produce large relative reductions in population growth. However, the average value of this vital  
757 rate can be so high (e.g., 0.93) that there is very little room for improvement, such that trying to  
758 recover a population through improvements in adult survival alone would be very difficult.  
759 Concurrently, there may be other vital rates (e.g., age-0 survival) that have a much lower relative  
760 influence on population growth (i.e., lower elasticity) but a much lower average value (e.g., 0.3),  
761 and therefore, a greater potential for improvement. In such a case, management  
762 recommendations as part of a recovery plan could be to avoid any reductions to adult survival  
763 while trying to increase age-0 survival.

764 Parameters other than survival, though not as influential, also played a role in  
765 determining pallid sturgeon population dynamics. This is similar to previous sturgeon PVAs  
766 which found that an increase in fecundity due to increased egg production per each female (Bajer  
767 and Wildhaber 2007; Heppell 2007; Jarić et al. 2011), reduced age at maturation (Schueller and  
768 Hayes 2010, Jarić et al. 2010 and 2011), or increased proportion spawning (Pine et al. 2001; Jarić  
769 et al. 2010 and 2011) may improve population growth rate by less than one-twentieth of the  
770 change in  $\lambda$  caused by a similar increase in overall survival. Our results differed from those of  
771 Bajer and Wildhaber (2007) and Steffensen et al. (2013) in that our model had similar sensitivity  
772 to proportion females as it did to the other non-survival parameters. In addition, Bajer and  
773 Wildhaber (2007) indicated a much older age range of maximum reproductive value of 25-35  
774 years, whereas we found the range of maximal reproductive value of 19-21 years, suggesting  
775 protection of the ages above these age classes may not be necessary for recovery and  
776 conservation to be successful. Consequently, given a mean age at maturation of 10 years and  
777 mean spawning interval of females of 3.6 years (Table 1) and 19-21 years for maximal  
778 reproductive value, we would suggest that additional mortality before the age of maximum

779 reproduction should be minimized to allow females the opportunity to spawn a minimum of three  
780 to four times in their life span (i.e.,  $10 \text{ years} + 2 \times 3.6 \text{ years} = 17.2 \text{ years}$ ;  $10 + 3 \times 3.6 = 20.8$   
781 years).

782         The model developed here included recruitment rates for Pallid Sturgeon in the Lower  
783 Missouri River greater than currently suspected recruitment rates, which are near zero  
784 (Steffensen et al. 2013). The observations from our model of limited need for protection of older  
785 age classes of pallid sturgeon is predicated on non-zero recruitment rates. The simulation results  
786 presented are only applicable after the species has recovered and the population is naturally  
787 sustaining. However, virtually no recruitment has been observed in the Lower Missouri River  
788 pallid sturgeon population (Steffensen et al. 2013). Even with habitat improvement that may  
789 increase recruitment, the current endangered state of the species and the nature of its life history  
790 (e.g., delayed maturity) would suggest it may be decades before the Missouri River habitat  
791 restoration efforts result in such recruitment. Until Lower Missouri River conditions improve to  
792 the point where successful recruitment of pallid sturgeon is occurring, any single spawning event  
793 may be as important as another, independent of fecundity or the number of previous spawns by  
794 an individual female. Furthermore, the model suggests older age classes collectively contribute  
795 fewer offspring because fewer fish survive to old age than reproduce at young ages; however, if  
796 recruitment is not occurring or lower than the rates assumed in this model then every  
797 reproductive fish and each spawning event is as important as any other spawning event for the  
798 continuation of the species.

799         The fact that inclusion of partitioned variance into the model increased the rate of  
800 quasiextinction means that having a reasonably accurate estimate of the initial population is  
801 critical. For instance, Steffensen et al. (2013) estimated there were 6000 wild and 42000 hatchery  
802 pallid sturgeon in Lower Missouri River as of 2012 based on extrapolation of Steffensen et al.  
803 (2012) from one river segment. Similar extrapolation of Winders and Steffensen (2014) pallid  
804 sturgeon estimates from a different segment of the Lower Missouri River produced a total  
805 population estimate of 7122 for the Lower Missouri River. Steffensen et al. (2013) argue  
806 population size was not important based on a 5% change in population estimate. That may be  
807 true for mean population growth rates, but their estimates were nearly 7 times that of Winders  
808 and Steffensen (2014), the number we used in our simulations. Under the 38 year simulation  
809 conducted by Steffensen et al. (2013) and ours based on a stable population model, the likelihood

810 of quasiextinction occurring would, essentially, be eliminated if the higher, initial population  
811 estimate is assumed. However, using the lower of the two pallid sturgeon population estimates  
812 and including partitioned variance resulted in quasiextinction not only occurring, but rapidly  
813 increasing over time while no quasiextinction occurred using unpartitioned variance. This  
814 follows McGowan et al. (2011a) who indicated that the importance of the incorporation of  
815 uncertainty is not in the mean estimates given, since they found their mean results were  
816 essentially the same with and without uncertainty, but in the increased probability of the  
817 populations becoming extinct in the presence of uncertainty. As suggested by McGowan et al.  
818 (2011a), we observed that while the central tendency of the population trajectory was similar for  
819 the deterministic model and both variance models, the 95% percentile interval was much wider  
820 (and thus the model more uncertain) when variance was partitioned into sampling and temporal  
821 components.

822         The various life history parameters of a long-lived fish species, such as the pallid  
823 sturgeon, can be impacted by human activities to various degrees. For parameters that represent  
824 more of a direct, acute population measure, such as survival, identification of management  
825 practices that support recovery and conservation of the species is simpler. For parameters that  
826 represent a more indirect, long-term or innate population measure, such as age at first spawn,  
827 identification of management practices that support recovery and conservation of a species is  
828 much more complex. Just like survival, age at first spawn has been identified as an important  
829 parameter in sturgeon population models (Schueller and Hayes 2010; Jarić et al. 2010 and 2011).  
830 However, identification of factors that drive age at first spawn and the management activities  
831 that alter it is a much more complex set of questions than what directly affects survival of  
832 various age classes of a long-lived fish species.

833         Parameter uncertainty has often been ignored or not fully accounted for in population  
834 viability analyses (e.g., Heppell 2007), one of the tools most commonly used by resource  
835 managers (McGowan et al. 2011a). Similar to McGowan et al. (2011a), we found that without  
836 parameter uncertainty, extinction risk was underestimated. Numerous parameters exhibited no  
837 temporal variance and therefore the model was no different than using the overall variance  
838 estimate alone: survival for ages 0, 1, 2+ as a whole, age at first spawn, and proportion spawning.  
839 However, we found temporal variance up through age 27 for length at age, from 775 to 1046 mm  
840 FL for fecundity at length, and proportion spawning. This mixed result in the presence of

841 temporal variability is likely due to the nature of the life history of the pallid sturgeon and the  
842 part the parameter represents and/or lack of adequate data to estimate temporal variability. The  
843 lack of data observation is supported by the fact the length at ages after age 27 and fecundity at  
844 length outside 775 to 1046 mm FL could all be attributed to lack of data for those ages and  
845 lengths, respectively. For the more direct and acute population parameters such as survival and  
846 proportion spawning, there would be more of any expectation for the presence of temporal  
847 variance (i.e., annual variability) because of how quickly changes in environmental conditions  
848 can change such rates. For the more indirect and long-term innate population parameters such as  
849 age at first spawn, there would be less of any expectation for temporal variability because  
850 changes in such rates would be expected to occur much slower in the presence of changes in  
851 environmental conditions.

852

#### 853 4.4 *Conclusions*

854

855 The current model was developed and tested assuming a stable, recruiting pallid sturgeon  
856 population as was presented in a previously published pallid sturgeon model (Steffensen et al.  
857 2013). Our primary goal was to develop a fully-stochasticized modeling approach for fish  
858 populations based on pallid sturgeon. The assumption of population stability was to facilitate the  
859 evaluation of the importance of life history parameters; currently, the pallid sturgeon population  
860 in the Lower Missouri River is neither stable or recruiting (Steffensen et al. 2013). Without  
861 recruitment, any model would predict a rapidly declining population where stochasticity of  
862 survival estimates enhances extinction probability. Until the limiting factors for this population  
863 are determined and these limitations are removed so that recruitment occurs, this non-recruiting  
864 population will continue to decline without stocking. Under the current state of knowledge and  
865 conditions, stocking is the only current management option available for the prevention of the  
866 extinction of pallid sturgeon, whether stocking larger numbers of young fish or smaller numbers  
867 of older fish. Ultimately, a fully stochasticized model, such as presented here, can be a very  
868 valuable tool for natural resource managers involved in recovery and conservation efforts, but its  
869 parameterization and implementation may be very limited without the data necessary to inform  
870 it. Here we did not include structural uncertainty or systems dynamics in the form of carrying  
871 capacity; however, carrying capacity and its uncertainty could easily be incorporated through

872 addition of a population cap with some given distribution or a density-dependence function such  
873 as the Ricker or theta-logistic model (Morris and Doak 2002). By sampling from distributions of  
874 demographic and model parameter estimates on an annual basis, we also address temporal  
875 variance. Also, additional mortality from any source (e.g., fishing, high water, etc.) can easily be  
876 incorporated into our model through additional survival multiplier. For instance, if 15% of age  
877 20 fish are lost to fishing, then age 20 survival can be multiplied by 0.85. Additionally, stochastic  
878 events that affect mortality such as floods can be included with a given probability to occur each  
879 year with a concomitant proportional effect on survival rates.

880 The model presented here, unlike previous pallid sturgeon population models (Bajer and  
881 Wildhaber 2007; Steffensen et al. 2013), to the extent the data exists to inform them, tries to  
882 address key components of uncertainty in forecasting population trends. Using a more realistic  
883 approach, such as presented here, is especially critical when dealing with species that are already  
884 classified as in danger of extinction. Though not the same as changing estimates by a full  
885 standard error as was done by Goldwasser et al. (2002), our change of 5% in demographic and  
886 parameter estimates does address the question of how important such changes are to projections  
887 in the presence of the multiple forms of uncertainty.

888

### 889 **Supporting Information**

890

891 Details on the methods used to select run characteristics such as number of years in  $\lambda$   
892 calculation, number of years before  $\lambda$  calculation could begin, number of iterations used, and  
893 initial population size (Appendix A). The authors are solely responsible for the content and  
894 functionality of these materials. Queries (other than absence of material) should be directed to  
895 the corresponding author.

896

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898

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905 does not imply endorsement by the U.S. Government.

906

## 907 **Appendix A. Details on the methods used to select run characteristics**

908

909 This document contains additional information about how run characteristics such as  
910 number of years in population growth rate ( $\lambda$ ) calculation, number of years before  $\lambda$  calculation  
911 could begin, number of iterations used, and initial population size were determined before  
912 running simulations. The authors are solely responsible for the content and functionality of these  
913 materials. Queries (other than absence of material) should be directed to the corresponding  
914 author.

915

### 916 *Introduction*

917

918 As we developed our model it became clear that the outcomes might depend, at least in  
919 part, on the characteristics of the simulations themselves rather than on any biological parameter.  
920 For example, if we were to use the central tendency (e.g., mean or median) of population growth  
921 rate ( $\lambda$ ) as a response variable, it might matter how many years were included in the calculation  
922 of that central tendency. Or, which years were included in that calculation. Therefore, before  
923 conducting any of the simulation experiments reported in this paper, we took steps to ensure that  
924 any results we obtained were driven by manipulation of biological parameters and not by  
925 artifacts of the simulation process.

926

927 The four run characteristics we investigated *a priori* were:

928

- 929 1. *Years in  $\lambda$  calculation*: the number of years in the simulation included in calculating the  
930 central tendency for population growth rate for each iteration.
- 931 2. *Spin-up period for  $\lambda$  calculation*: the number of years at the beginning of each simulation  
932 that were not included in the calculation of  $\lambda$ . The purpose of waiting before beginning  $\lambda$   
933 calculation was to allow the model dynamics to stabilize. Without a spin-up period, the

934 chaotic first few years of the simulation, which are highly dependent on initial conditions,  
935 might disproportionately influence the representation of the dynamics in later years.

936 3. *Number of iterations*: Because our model contains numerous stochastic components,  
937 many realizations might be necessary for the model to explore enough of the parameter  
938 space so that we could be confident that our estimates of the shape of response variable  
939 distributions were valid.

940 4. *Initial population size*: In preliminary runs of the model we noticed that the size of the  
941 initial population would influence population growth rate and the absolute population  
942 size by the end of the population. We wanted to be confident that the simulations were  
943 initialized with a starting population that would have a minimal influence on later  
944 dynamics.

945

#### 946 *Years in $\lambda$ calculation and spin-up period*

947

948 We first investigated the number of years necessary to calculate  $\lambda$  and the minimum  
949 number of years to allow the model to “spin up” before  $\lambda$  calculation began. The model was run  
950 with an initial population of 7122 individuals (see Methods). We ran all three models  
951 (deterministic, unpartitioned variance, and partitioned variance) for 150 years and for 2000  
952 iterations. We assumed that the model would require at least 5 years for dynamics to stabilize;  
953 therefore the earliest year that could potentially have been included in  $\lambda$  calculation was year 6.  
954 For each iteration, mean  $\lambda$  was calculated for as many years as possible including 10, 18, 20, 30,  
955 40, 50, 60, 70, 80, 90, and 100 years in the calculation window (e.g., a 10 year window could  
956 begin at any year from 6 to 141; a 100 year window could begin at years 6 to 51). For each  
957 window length we calculated the empirical rate of change in  $\lambda$  from each year to the subsequent  
958 year ( $\Delta\lambda/\Delta t$ ). The slope  $\Delta\lambda/\Delta t$  measured the effect of allowing the model to run and the  
959 population dynamics to stabilize for an additional year before beginning  $\lambda$  calculation. We  
960 considered the earliest year for which  $\Delta\lambda/\Delta t$  was  $\leq 0.001$  to be the earliest year at which  $\lambda$   
961 calculation could begin. Because  $\lambda$  stabilized after that year,  $\lambda$  calculation could begin any time  
962 after that without affecting the results. When the model was run for 38 years, as was done by  
963 Steffensen et al. (2013), the earliest year  $\lambda$  calculation could start was year 6 in all three models.



964 Therefore the selected spin-up period of 20 years surpassed the minimum number of years  
965 required for model dynamics to stabilize.

966

#### 967 *Number of iterations*

968

969 We also evaluated number of iterations necessary to achieve consistent results from run  
970 to run, without requiring so many iterations as to make the model computationally unwieldy. The  
971 model was run for 38 years, with a spin-up period of 20 years, with both variance structures  
972 (unpartitioned and partitioned variance) for 20000 iterations. We tested iteration counts from  
973 1000 to 20000 in increments of 1000. For each iteration count  $I$ , we constructed 1000  
974 subsamples of  $I$  iterations from the 20000 iterations and calculated the median and 95% quantile  
975 interval (i.e., the interval from the 2.5 to the 97.5 percentiles) for  $\lambda$  of the  $I$  subsamples because  
976 those measures of central tendency and the distribution of  $\lambda$  were to be measured later as the  
977 response to experimental manipulations. We required that the width of the 95% quantile interval,  
978  $W$ , change less than 0.001 for each additional 1000 iterations (i.e., absolute value of  $\Delta W/\Delta I \leq 10^{-6}$ )  
979 and assumed that the model would require  $>1000$  iterations. Therefore we selected 2000 as the  
980 number of iterations because it was  $>1000$  and smallest multiple of 1000 iterations for which the  
981 absolute value of  $\Delta W/\Delta I \leq 10^{-6}$  (at 2000 iterations, unpartitioned variance:  $\Delta W/\Delta I = -6.6514 \times$   
982  $10^{-7}$ ; partitioned variance:  $\Delta W/\Delta I = -7.4409 \times 10^{-7}$ ).

983

#### 984 *Initial population size*

985

986 To determine the minimum initial population size required to achieve consistent results,  
987 we ran the population model with a range of initial population sizes and calculating a minimum  
988 population size where the finite rate of population growth  $\lambda$  ( $N_t/N_{t-1}$  where  $N_t$  is the total number  
989 of females in the population age 1 and older and  $N_{t-1}$  is the number during the previous year) was  
990 changing less than 0.001 with the addition of one individual per age class. We ran the population  
991 model for 38 years with initial population sizes ranging from 2 to 200 per reproductive ages 10  
992 to 41 in increments of 2 per age class. We empirically determined the slope between each pair of  
993 adjacent points in the  $\lambda$ - $N$  relationship (i.e., as  $\Delta\lambda/\Delta N$ ) and selected the minimum number of  
994 individuals per age class that produced a  $\Delta\lambda/\Delta N \leq 0.001$ . The slope  $\Delta\lambda/\Delta N$  was used as a

995 measure of the effect on  $\lambda$  of adding another individual at each age class from 1 to 41 to the  
996 initial population. Initial runs of the models without stocking showed that this minimum N was  
997 26 individuals per age class without stocking (deterministic) and 6 individuals per age class  
998 (unpartitioned or partitioned variance) corresponding to a total population size of 1066 and 246  
999 total individuals, respectively. Therefore, our initial population size of 7122 individuals, recently  
1000 reported by Winders and Steffensen (2014), was large enough to ensure that the effect of initial  
1001 population size on  $\lambda$  in simulation scenarios was negligible. This population was spread over  
1002 ages 1 to 41, with 174 females in age classes 1 to 29 and 173 females in age classes 30 to 41 (i.e.,  
1003 after 173 fish were put into each age class, the remaining 29 fish were seeded starting with the  
1004 youngest age class).

1005

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