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# INTERACTIONS BETWEEN DEMOGRAPHIC STOCHASTICITY AND GENETIC INTEGRITY OF LAKE STURGEON POPULATIONS

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AMY M. SCHUELLER

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# INTERACTIONS BETWEEN DEMOGRAPHIC STOCHASTICITY AND GENETIC INTEGRITY OF LAKE STURGEON POPULATIONS

By

Amy M. Schueller

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ABSTRACT

INTERACTIONS BETWEEN DEMOGRAPHIC STOCHASTICITY AND GENETIC INTEGRITY OF LAKE STURGEON POPULATIONS

By

Amy M. Schueller

Rehabilitation of lake sturgeon populations has become important because lake sturgeon were once abundant throughout the Great Lakes basin, but have been reduced to <1% of historic levels due to habitat degradation and overexploitation. Objectives of this study were to 1) determine which lake sturgeon population parameters have the greatest influence upon demographic and genetic characteristics, 2) determine the minimum viable population size (MVP) for lake sturgeon and how inbreeding depression may affect MVP, and 3) determine strategies for supplementation stocking in order to maintain long-term persistence of populations while maintaining the smallest genetic impact. An individual based modeling approach that represented demographic processes in a stochastic manner and genetic processes was used to address these objectives for this long-lived species. Sensitivity analyses were performed by holding all parameters at a nominal value and changing one parameter at a time across a range of plausible values. All responses were hypersensitive to YOY mortality, post YOY mortality, and age at first maturation and probability of mating for females, and were relatively insensitive to age at first maturation and probability of mating for males. The effects of inbreeding depression on MVP were incorporated under two scenarios: 1) individuals with inbreeding coefficients above a threshold experienced reduced fitness and 2) individuals experienced reduced fitness at a rate related to their inbreeding coefficient. Three mechanisms for

inbreeding depression were explored: YOY viability, post YOY viability, and progeny number. Minimum viable population size was defined as a population size with ~5% chance of extinction over 250 years and was estimated at 80 individuals without inbreeding. With inbreeding depression, MVP estimates ranged from 80-1,800, depending upon the scenario. Thus, both demographic stochasticity and inbreeding contributed to extinction risk. The model was used to explore supplementation scenarios which included three initial population sizes, two time frames, varying sex ratios, variance in family size, and different percentages of the adult population contributing progeny. All supplementation scenarios that I considered resulted in reduced extinction risk, increased population sizes, increased gene retention, and reduced inbreeding over time. Within the range of conditions that I explored, supplementing larger populations over longer time frames and capturing the greatest number of adults from the population for producing progeny were the most important considerations for maintaining genetic integrity in lake sturgeon.

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TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

# INTRODUCTION

The lake sturgeon *Acipenser fulvescens* is one of nine sturgeon species found on the North American continent and is one of 27 sturgeon species worldwide (Birstein 1993; Auer 1996a; Billard and Lecointre 2001). Lake sturgeons, a long-lived and late maturing species, spawn from late April to mid-May (Hay-Chmielewski and Whelan 1997). After reaching maturity at 12 to 22 years, male sturgeon spawn every other year, and after reaching maturity at 14 to 33 years, female sturgeon spawn once every 3 to 7 years (Roussow 1957; Harkness and Dymond 1961). Lake sturgeons are a potamodromous fish which spawn in freshwater river systems and spend their entire lives solely in freshwater systems (Rochard et al. 1990; Auer 1996a; Hay-Chmielewski and Whelan 1997). Lake sturgeon populations are often delineated by the river of spawning for management purposes (Hay-Chmielewski and Whelan 1997), whereby they spawn in natal streams, but mixing of populations commonly occurs in the Great Lakes during the non-spawning season.

Lake sturgeons were once found throughout Great Lakes drainage basin in the United States and Canada (Birstein et al. 1997; Hay-Chmielewski and Whelan 1997; Smith and Baker 2005). Lake sturgeons were initially an unwanted by-catch in the early commercial fisheries of the Great Lakes; however, by the year 1885, lake sturgeon became a highly sought after, commercially fished species (Kelso et al. 1996; Hay-Chmielewski and Whelan 1997). In 1885, commercial catch was near peak in the United States waters of the Great Lakes and ranged widely from 82,000 kg harvested in Lake Superior waters to 2.1 million kg harvested in Lake Erie waters (Auer 1996a). Catches of lake sturgeon diminished rapidly in all of the Great Lakes in the early 1900's (Auer

1996a). In 1977, all commercial fishing of the lake sturgeon ceased in waters of the United States, however, a small tribal harvest still occurs (Hay-Chmielewski and Whelan 1997). Currently, only a few water bodies in Michigan are open to sport fishing catch-and-release and limited harvest of lake sturgeon.

Because lake sturgeon have been reduced to less than 1% of their historic levels due to habitat degradation, overharvest, and fragmentation of spawning populations, lake sturgeon restoration and protection have become a high priority throughout the Great Lakes basin (Johnson et al. 1998; Auer 1999; Holey et al. 2000; McQuown et al. 2003). Factors that have contributed to the decline of lake sturgeon in the past continue to contribute to declines in abundance, and impede restoration where populations have been extirpated. Therefore, actions aimed at restoration and protection of the imperiled lake sturgeon have been developed and implement in many areas of the Great Lakes. For example, stocking and habitat restoration have been suggested, and stocking has been implemented for some populations in the state of Michigan (Hay-Chmielewski and Whelan 1997). Lake sturgeon restoration plans have been completed by Michigan (Hay-Chmielewski and Whelan 1997), Wisconsin (WDNR 2008), and Ontario (OMNR 2006), although considerable uncertainty exists as to the best course of action for lake sturgeon restoration.

Although lake sturgeon populations are greatly reduced, genetic diversity of these populations hasn't been depressed yet (DeHaan et al. 2006). Hope remains that genetic integrity of the lake sturgeon populations in the Great Lakes basin can be maintained, but actions need to be taken to minimize the risk of extinction and the effects of inbreeding due to current low levels of abundance. Conserving the genetic integrity (defined here as

both the retention of genes and reduced inbreeding accrual) is believed to be important for conserving this species (Hay-Chmielewski and Whelan 1997; McQuown et al. 2003; Keller and Waller 2002). Inbreeding occurs when individuals who are closely related mate, and most readily occurs in small populations where random mating can more readily result in breeding among related individuals (Hedrick and Kalinowski 2000; Brook et al. 2002; Keller and Waller 2002). Inbreeding is often thought to result in a decrease in an individual's fitness relative to non-inbred offspring, resulting in what is called inbreeding depression. Inbreeding depression can be manifested in any traits related to reduced fitness (e.g., poor survival (viability), lower fecundity; Crnokrak and Roff 1999; Hedrick and Kalinowski 2000; Amos and Balmford 2001), but has been difficult to demonstrate empirically (Newman and Pilson 1997).

Much debate has occurred over the past decades as to which process is most important for the risk of extinction for small population sizes: demographic stochasticity or genetic stochasticity, specifically inbreeding and inbreeding depression. Some have argued that demographic stochasticity is more important than genetic composition for small population sizes (Lande 1988; Young 1991; Harcourt 1991). Arguably, if you have no animals, you have no genes to conserve. However, others have demonstrated that inbreeding depression can lead to reduced population viability at small population sizes. Frankham (1995a) concluded that the risk of extinction increased with inbreeding. Keller and Waller (2002) found that many studies are now available whereby inbreeding depression has been found in the wild and can be detrimental to long-term persistence. Many argue that while inbreeding depression may not be the driving force towards extinction, it still has an impact and increases the risk of extinction (Mills and Smouse

1994). Therefore, a need exists to explore the relationship between demographics and genetics in regards to the long-term persistence of populations (Boyce 1992), specifically for long-lived species such as the lake sturgeon

Demographic stochasticity is a factor in the extinction process but has rarely been considered for a long-lived species such as the lake sturgeon (Higgins 1999). Small populations suffer from demographic stochasticity and inbreeding and for some of the population sizes, rehabilitation may be unlikely to be successful (Pimm et al. 1988; Tracy and George 1992; Lande 1993; Lynch and Walch 1998; Amos and Balmford 2001; Keller and Waller 2002). Therefore, identifying those situations where rehabilitation efforts will be most successful will be beneficial to the restoration and protection of lake sturgeon populations in the Great Lakes basin. Because of the longevity of this species, empirical tests of restoration strategies are impractical. Modeling is a useful tool because of the flexibility available, and it can also be used to integrate both population dynamics and genetics information in order to inform management decisions and determine the relative contributions of demographics and genetics to extinction risk (Brook et al. 2002).

An individual based model, which tracks individuals through time, was developed that incorporated both demographic stochasticity and inbreeding. This model was then used to address three main topics: 1) what population parameters are important for lake sturgeon persistence and genetic integrity and how sensitive the parameters are to perturbation, 2) the likely fate of lake sturgeon populations with no management actions with and without inbreeding depression, and 3) the impact of management intervention (supplementation) on the demographics and genetics of this species.

A sensitivity analysis was run across a broad range of parameter inputs to determine the importance and how perturbation of parameters affects the persistence and genetic integrity of lake sturgeon populations. Sensitivity analyses have rarely explored uncertainty effects on genetic factors (Beissinger and Westphal 1998), even though these may be crucial to long-term population sustainability. The objective of the first chapter of the dissertation was to determine which lake sturgeon population parameters have the greatest influence upon demographic characteristics including rates of extinction and percentage of populations increasing above the initial population size, and genetic characteristics including percentage of unique alleles retained and average inbreeding coefficient for a 250 year or approximately a 10 generation period.

The minimum viable population size (MVP) with and without inbreeding depression was estimated in order to explore the fate of populations with no management actions. Minimum viable population size is defined as a population of sufficient size to persist with a given probability over a given time frame (Shaffer 1981; Boyce 1992). Minimum viable population sizes are specific to each study or species and vary depending upon the species' life history parameters and the tolerance of extinction risk for the species' management and conservation (Shaffer 1981; Lindenmayer et al. 1993). Modeling the influence of genetic changes on demography has proven to be difficult in many situations because translating negative genetic impacts into demographic impacts is not straightforward and because genetic data are often unavailable (Beissinger and Westphal 1998; Kirchner et al. 2006). However, a need exists to explore the relationship between demographics and genetics in regards to the long-term persistence of populations (Boyce 1992; Shaffer 1980; Jager et al. 2000; Kirchner et al. 2006). Thus,

the objective of the second chapter of the dissertation was to determine the minimum viable population size for lake sturgeon, incorporating both demographic and genetic stochasticity through the potential impacts of inbreeding (Mills and Smouse 1994).

In the last chapter, I explored the fate of populations when various stocking strategies were implemented for several population scenarios. Stocking potentially results in trade-offs between population growth rate and maintaining genetic integrity of a species (Hansen et al. 2001). While supplementation is often focused on increasing population abundance, supplementation can result in the loss of genetic variability and increased inbreeding in a population (Ryman and Laikre 1991; Lynch and O'Hely 2001) thereby reducing genetic integrity (Tessier et al. 1997; Hansen et al. 2000). However, supplementing over multiple generations could lead to increased genetic integrity if the population size is larger in the long-term (Wang and Ryman 2001). Thus, while demographic stochasticity has been argued to be a more influential driving force with respect to probability of extinction than genetic factors, including both demographic stochasticity and genetics in population management strategies, has been advocated (Lande 1988). As such, the objective of this section of the dissertation was to determine the number of individuals that should be stocked in order to achieve population abundance goals while maintaining the smallest genetic impact.

Each of these main topics has tangible management implications for lake sturgeon populations in the Great Lakes. Estimating population parameters of importance will help to determine which management actions will have the largest impact on increasing the long-term persistence of populations (e.g., reducing harvest). Determining risks for extinction for different sized populations will help managers to rank populations for

rehabilitation purposes. Finally, after choosing populations for rehabilitation, the analysis of stocking strategies will provide guidance on which options are best to maintain population abundance and genetic integrity.

# SENSTIVITY OF LAKE STURGEON POPULATION DYNAMICS AND GENETICS TO DEMOGRAPHIC PARAMETERS

ABSTRACT.-Uncertainty in population parameters can make managing fisheries difficult, especially for long-lived species such as lake sturgeon. Models can be used to explore population parameter uncertainty and how uncertainty affects demographic and genetic population outputs through the use of sensitivity analyses. The objective of this study was to determine which lake sturgeon population parameters have the greatest influence upon demographic characteristics including rates of extinction and percentage of populations increasing above initial population size, and population genetic characteristics including percentage of unique alleles retained and average inbreeding coefficient. An individual based modeling approach that represented demographic and genetic processes was used to address this objective. Individual lake sturgeon were tracked throughout the modeling process with unique identifiers, allowing for the determination of parentage, degree of inbreeding, and number of unique alleles retained. Sensitivity analyses were performed by holding all of the parameters at a nominal value and changing one parameter at a time across a range of plausible values. All responses were hypersensitive to young of the year mortality, post young of the year mortality, age at first maturation for females, and the probability of mating for females. Post young of the year mortality rate was the most sensitive of all of the population parameters. The outputs were relatively insensitive to changes in age at first maturation for males and probability of mating for males. Sensitivity was dependent upon initial population size

with population parameters having differing sensitivities with respect to other parameters for smaller and larger population sizes. The demographic and genetic outputs were related to one another via similar relationships for each of the population sizes. These analyses should be used to target rehabilitation efforts on altering population parameters with the largest influence on population persistence and genetic integrity.

# INTRODUCTION

One species where the evaluation of demographic and genetic integrity is critically needed is lake sturgeon in the Great Lakes basin. Lake sturgeon were once found throughout the Laurentian Great Lakes, spawning in many tributary streams throughout the basin (Birstein et al. 1997; Hay-Chmielewski and Whelan 1997; Smith and Baker 2005). However, lake sturgeon have been reduced to less than 1% of historic levels due to habitat degradation, overharvest, and fragmentation of spawning populations (Johnson et al. 1998; Auer 1999; Holey et al. 2000; McQuown et al. 2003). Factors causing the decline of lake sturgeon in the past continue to contribute to declines in abundance and impede restoration where populations have been extirpated. Currently, lake sturgeon restoration is a priority throughout the Great Lakes basin (Hay-Chmielewski and Whelan 1997). Therefore, extensive management efforts aimed at restoration and protection of the imperiled lake sturgeon have been developed. While lake sturgeon restoration plans have been completed by Michigan (Hay-Chmielewski and Whelan 1997), Wisconsin (WDNR 2008), and Ontario (OMNR 2006), considerable uncertainty exists as to the best course of action for restoration because of the unique life history of the lake sturgeon.

Identifying those situations where rehabilitation efforts will be most successful will be beneficial to the restoration and protection of lake sturgeon populations in the Great Lakes basin. Uncertainty in demographic parameters and the genetic integrity of a population are important factors in the extinction process that have rarely been considered for a long-lived species such as the lake sturgeon (Higgins 1999). Small populations suffer from increased risks of extinction due to demographic stochasticity

(random births and deaths), environmental stochasticity (random environmental factors), catastrophes, and inbreeding, and for some population sizes, rehabilitation may be unlikely to be successful (Pimm et al. 1988; Tracy and George 1992; Lande 1993; Lynch and Walch 1998; Amos and Balmford 2001; Keller and Waller 2002).

Given the logistical difficulties in empirically studying such a long-lived species, the best tactic to integrate both population dynamics and genetics information to inform management decisions and guide current restoration efforts is through the use of modeling. Both demographic and genetic factors contribute to extinction risk and population decline, and should be incorporated into the modeling process (Mills and Smouse 1994; Frankham 1995). Therefore, modeling should be used as a tool to help understand the uncertainty surrounding population parameters and the influence those parameters have on extinction risk.

Modeling, in general, has been used to explore and quantify parameter uncertainty and how that uncertainty affects population outcomes such as extinction risk through the use of sensitivity and elasticity analyses (Bart 1995; Letcher et al. 1996; Beissinger and Westphal 1998; Reed et al. 1998; Caswell 2000; Ellner and Fieberg 2003). Sensitivity analysis is a method whereby baseline parameter values are altered, usually one at a time or independently, to see how the parameter alteration influences specified population outcomes within a simulation model (Bartell et al. 1986; Cross and Beissinger 2001; Ellner and Fieberg 2003). Sensitivity analyses explore responses within a limited frame of possible parameter values, generally with changes between ±1% to ±10% of nominal values (McCarthy et al. 1995; Essington 2003). Exploring parameters across a broader range of values is not typically done, but could have important management implications.

Often, managers are more uncertain about population parameters than ±10%, and sensitivities have been shown to be good predictors of population outcomes even with large parameter changes (Caswell 2000). Also, as the range of parameter values is expanded, the importance of each population parameter with respect to other population parameters may change. These differences in population outcomes could have large impacts on the ability of managers to influence population level responses if the change in a parameter due to management actions is large.

Sensitivity analyses have rarely explored uncertainty effects on genetic factors (Beissinger and Westphal 1998), even though these are crucial to long-term population sustainability. For example, genetic factors such as inbreeding can contribute to increased risks of extinction at small population sizes (Newman and Pilson 1997). Individual based models are a type of model which allows for representation of individual genetic characteristics and population processes, yet also allow for population level responses to be evaluated (Chambers 1993; Van Winkle et al. 1993a). Individual based models follow individuals through time during simulations, and outputs can be obtained on both the individual and population level. The flexibility available with an individual based model has led to this type of model being used to research populations of fish, plants, birds, mammals, and invertebrates (Rose and Cowan 1993; Beissinger and Westphal 1998; Grimm 1999). For example, dispersal in a metapopulation (Travis and Dytham 1998), fish responses to environmental change, pollution, and individual characteristics (Van Winkle et al. 1993b; Madenjian and Carpenter 1993; Letcher et al. 1996), management options for invasive plant species (Buckley et al. 2003), and effects of environmental and demographic stochasticity on red-cockaded woodpecker *Picoides*

*borealis* populations (Walters et al. 2002) have all been explored using individual based models. Individual based models have been used to explore inbreeding for the southern bluefin tuna *Thunnus maccoyii* and 19 other threatened species (Brook et al. 2002). The flexibility available and the ability to track individuals within a population make individual based models a good choice of model for assessing the sensitivity of population genetics to population dynamics parameters.

A key goal of conserving genetic integrity is to maintain the distribution of genes within a population. Many processes influence a population's genetic integrity, but a major factor is inbreeding (Hay-Chmielewski and Whelan 1997; McQuown et al. 2003). Inbreeding occurs when individuals who are closely related mate, and most easily occurs in small populations where random mating can more readily result in breeding among related individuals (Brook et al. 2002; Keller and Waller 2002). Inbreeding does not result in the loss of alleles, but does result in an increase in homozygotes and a decrease in heterozygotes (Conner and Hartl 2004). Thus, inbreeding does not reduce genetic diversity, but causes a redistribution of genes within the population. Inbreeding is often thought to result in a decrease in a species' fitness, termed inbreeding depression (Crnokrak and Roff 1999; Amos and Balmford 2001). Genetic integrity of a species has been shown to be positively related to population size (Secor et al. 2002). Therefore, the genetic integrity of small populations may be reduced through inbreeding, leading to an increased risk of extinction (Frankham 1995). However, inbreeding is thought to have less of an impact when accruing at a slower rate such as in long-lived species. Selection is better able to remove deleterious alleles in these situations, and thus extinction rates are also thought to be lower at slower rates of inbreeding accrual (Reed et al. 2003).

The parameters most important to the long-term persistence and genetic integrity of lake sturgeon populations are unknown. This study will use sensitivity analyses to address which population parameters for lake sturgeon are most influential for population outcomes. The objective of this study is to determine which lake sturgeon population parameters have the greatest influence upon demographic characteristics including rates of extinction and percentage of populations increasing above the initial population size, and genetic characteristics including percentage of unique alleles retained and average inbreeding coefficient for a 250 year or 10 generation period. Probability of extinction and percentage of populations increasing above the initial population size are population outcomes indicative of long-term population persistence. Percentage of unique alleles retained and average inbreeding coefficient are genetic outcomes which relate to long-term persistence and genetic variability. This research will help to inform management of lake sturgeon within the Great Lakes basin by determining which population parameters have the greatest impact on population features related to the likelihood of population persistence. This information could then be used to focus management efforts on rehabilitating lake sturgeon populations by altering those population parameters.

## METHODS

### *Model Development*

An individual based model was developed that incorporated demographic and genetic processes (Figure 1.1). Lake sturgeon exhibit a polygamous mating system which was represented based on available data whereby female lake sturgeon mature at approximately 20 years of age and spawn approximately once every 3 years, and male lake sturgeon mature at approximately 15 years of age and spawn approximately every

other year (Auer 1999; Bruch 1999; Billard and Lecointre 2001; DeHaan 2003; Nichols et al. 2003). Once an individual reached the minimum age for maturity then the individual was assigned a random number distributed Uniform(0,1). If that random number was less than the probability of mating each year, then that individual returned to the river to mate that year. Empirical data from Black Lake, Michigan, lake sturgeon suggest that reproductive success is not related to the length or weight of the adult sturgeon, therefore, the size of individual fish wasn't included in this individual-based model (DeHaan 2003). For each fish returning to spawn, the number of potential mates or batches of offspring, *B*, for each spawning male and female was based on empirical data from Black Lake, MI (Figure B.1; DeHaan 2003). Random numbers of batches were generated using a discrete form of the exponential distribution by:

$$B = 1 + \text{integer}(-2 * \ln(1 - U(0,1)).$$

This distribution represents the number of mates from empirical data (Figure B.1; DeHaan 2003). The batches for the males and females were randomly shuffled, and female batches were paired with male batches. This process allowed random mating between individuals, and allowed individuals to mate with multiple other individuals as has been observed in lake sturgeon. In this model, any batches produced by a male or female without a pair, or mate, were deleted. This distribution allows for a large number of mates as the uniform distribution approaches one; however, the number of mates is decreased based on how the batches are paired with mates. Thus, extremely large numbers of mates is unlikely. The number of progeny, *P*, created (at the end of the summer) from each mating pair, or batch, was generated using an exponential equation of the form:

$$P = \text{integer}(1 * (-\ln(1 - U(0,1))))$$

producing a distribution of numbers of offspring similar to that seen in Black Lake, MI (DeHaan 2003). This distribution was based on the empirical number of progeny per adults as reported by DeHaan (2003; Figure B.2). The empirical distribution was based on a parentage analysis whereby progeny in a sample were assigned to parents. Only about 25% of progeny were assigned to parents, however. Because of this, the empirical number of progeny per parent should be treated cautiously. Because the number of progeny was modified by varying the YOY mortality rate to match observed population sizes and trajectories, this distribution was judged to be appropriate.

The sex of offspring was randomly determined with an equal probability. Following birth, age-specific mortality rates were applied to each individual sturgeon. Mortality rates were set up in the model such that a random number between 0 and 1 was generated for each individual and if that random number was less than the specified level of mortality, then that individual suffered mortality. As such, demographic stochasticity was implicitly incorporated into the model because the death of each individual was randomly determined. The mortality rate from the end of the summer through the winter to the end of the first year is unknown. Therefore, this mortality rate was varied to produce population growth rates that mimic observed growth rates for existing populations. This technique has proven useful in previous studies and provides a means to develop management advice even though parameter values are uncertain (Vaughn and Saila 1976; Hayes and Taylor 1990; Heppell et al. 2000). All parameter values were developed from literature review and further review by local Great Lakes sturgeon experts. Mortality after the first year was set to 0.05 based on Baker (1980). Henceforth,

young of the year mortality will be referred to as such, and mortality after the first year will be referred to simply as "mortality." Young of the year and post young of the year mortality rates have been treated this way by past elasticity studies for other sturgeon species (Gross et al. 2002).

The effects of inbreeding on mortality rates of lake sturgeon are currently unknown. For this sensitivity analysis, inbreeding was assumed not to reduce the fitness of individual sturgeon. Also, the inbreeding at the start of the simulations was assumed to be zero; therefore, the model was only concerned with the net accrual of inbreeding.

Individual inbreeding coefficients were determined using path analysis of the individual's pedigree implemented in the INBREED procedure available in SAS® (SAS Institute Inc., 2003). From a pedigree, the inbreeding coefficient ($f_x$) for an individual was determined by summing all of the unique paths ($P$) through a common ancestor ($A$) as

$$f_x = \sum_{i-1}^{P} \left[\frac{1}{2}\right]^n (1 + f_A)$$

where n was the number of ancestors in the path and $f_A$ was the inbreeding coefficient of ancestor A (Wright 1922). Lake sturgeon are polyploid with a ploidy level of eight (Blacklidge and Bidwell 1993). Polyploidy is thought to mask inbreeding depression; however this effect has not been shown for other polyploid species such as salmon species *Oncorhynchus sp.* (Wang et al. 2002). Therefore, I assumed polyploidy of lake sturgeon did not affect the accrual of inbreeding or inbreeding depression. This approach allowed for the tracking of overall individual inbreeding levels and accrual of inbreeding rather than specifying certain alleles as deleterious.

Gene retention from the founding population was tracked based on a one locus system whereby each individual at the start of the simulations had two unique, hypothetical alleles at one locus (MacCluer et al. 1986). The hypothetical locus was assumed to be inherited as a Mendelian trait. As mating occurred between individuals, some alleles were lost from the population before they could be passed on to offspring. Random loss of unique alleles results in genetic differentiation among populations and determines the percentage of founders that have contributed genes to the population. The loss of unique alleles can be described through a technique called gene drop analysis (MacCluer et al. 1986; Hedrick and Miller 1992), which tracks all unique alleles that are retained or lost from the population through time (Haig et al. 1993). Thus, the percent of remaining alleles at the end of each simulation can then be expressed as the number of remaining alleles over the number of unique alleles at the beginning of the simulation which is two times the initial population size.

*Sensitivity Analysis*

A sensitivity analysis was performed by holding all of the parameters at a nominal value (Table 1.1), as identified from the literature and sturgeon biologists, and changing one parameter at a time across a range of plausible values to determine which parameters most strongly influenced model predictions and to evaluate how model predictions changed with changes in the population parameters (McCarthy et al. 1996; Essington 2003). The sensitivity of the model ($S$) to a parameter change was expressed as the difference in the output when the parameter was changed, compared to the associated output when all of the parameters were set at their nominal value:

$$S = \frac{(R_a - R_n)/R_n}{(P_a - P_n)/P_n}$$

where $R_a$ was the model response for the altered parameter, $R_n$ was the model response for the nominal or unaltered parameter, $P_a$ was the altered parameter, and $P_n$ was the nominal or unaltered parameter (Haefner 2005). If the percent deviation of the parameter caused a similar percent change (absolute value of $S = 1.00$) in the results of the simulation model, then the parameter was linearly related to the output (Letcher et al. 1996). If the percent deviation of the parameter caused less of a percent change (absolute value of $S < 1.00$) in the results of the simulation model, then the parameter was classified as an insensitive parameter. If the percent deviation of the parameter caused a greater change (absolute value of $S > 1.00$) in the results of the simulation model, then the parameter was classified as a highly sensitive parameter. This type of sensitivity analysis where proportional parameter changes are compared to proportional output changes is often called elasticity (Caswell 2000). The model was run 500 times per sensitivity analysis for 250 years to determine which population parameters had the greatest impact on the population outcomes of interest. Sensitivity analysis is often conducted across parameter space close to nominal values (e.g., Essington 2003); I term this local sensitivity. In the local sensitivity analysis, parameters were varied ± 10% about their nominal values. In addition to a local sensitivity analysis, I also determined sensitivity across a broader range of values (i.e., parameters were varied ± 30% about their nominal values) to determine if model responses were maintained beyond a local parameter space. Sensitivities, both local and broad, were presented as average sensitivities over the range

of parameter perturbation (±10% or ±30%). Thus, the sensitivities for both the negative and positive perturbations were averaged.

*Simulations*

Simulations were run with two initial population sizes, 50 and 200 individuals. The initial population size of 200 was used because this population size allowed for the exploration of parameter values with minimal risk of extinction due to demographic stochasticity. The initial population size of 50 was also chosen in order to explore population outcomes with a heightened risk of extinction in order to compare the effects of extinction on sensitivity of model outcomes. Simulations were assumed to have current environmental and demographic conditions, which remained constant into the future.

Based on preliminary analyses, a simulation duration of 250 years was used as this appeared to allow time for transient responses to dissipate. For each scenario, 500 simulations were run to provide precise estimates of the mean response and variance. A yearly time step was used in all simulations. The percent of populations extinct, population abundance (summarized as percentage of populations increasing above the initial population sizes of 50 and 200), average individual inbreeding coefficient in the final year, and percent of unique alleles retained were recorded for each simulation run of 250 years. The mean final abundance was the average abundance including zeroes for those populations that went extinct. The average individual inbreeding coefficient was the average inbreeding coefficient for progeny produced in the final year. No uncertainty estimates could be provided for the inbreeding coefficients because only the mean was an output for the model. The average percent of unique alleles retained was the average

percent of genes retained including zeroes for those populations that went extinct. For the percent of populations extinct, the percent of populations increasing, and the average percent of genes retained, confidence intervals were calculated as:

$$(\text{estimate} \pm 2*SE)*100$$

where the SE = (pq/n) ^ (1/2), p = (percent of extinct populations or genes retained/100), q = 1-p, and n=number of simulations.

Outputs from models are able to show responses for demographic and genetic questions, but those responses are also often related to one another. The relationship between model outputs can allow exploration of joint sensitivity of model parameters. To explore the relationship between the outputs for this model, all outputs were graphed against each other. Extinction was excluded in this comparison because of the low number of extinctions for the initial population size of 200. Both initial population sizes were included in these graphs in order to see where different initial population sizes fell on the relationship and if the same relationship existed for both initial population sizes.

## RESULTS

Baseline simulation conditions resulted in different levels of population persistence, gene retention, and inbreeding accrual for the initial population sizes simulated. Nominal parameters were chosen such that populations were approximately stable for an initial population size of 200. This is evident in the percent of populations increasing (46.2%) in baseline simulations for an initial population size of 200 (Table 1.2). With an initial population size of 200, no extinctions were observed, and approximately 9.5% of initial genes present were retained. Mean inbreeding was 0.0413 for progeny at the end of the simulation for an initial population size of 200. Extinction

occurred in nearly 35% of simulations for the initial population size of 50 (Table 1.2), and the percent of populations increasing was likewise much lower than for simulations with an initial population of 200. The percent of genes retained for an initial population size of 50 was about half (4.62%) of the initial population size of 200, but the mean inbreeding coefficient was nearly three times higher (f=0.1388).

The overall sensitivities were often asymmetrical in shape and the parameter with the highest sensitivity varied depending upon the degree of perturbation away from nominal values (Figure 1.2). Model outputs were fairly symmetrical and linear for the local sensitivities with small parameter deviations (Figure 1.3). However, sensitivities were generally asymmetrical with larger parameter deviations (Figure 1.2), and the outputs generally trended toward an asymptote or declined towards zero (Figure 1.3). For example, as parameter values were increasingly perturbed, the percent of populations increasing tended to either 100% or 0%, resulting in declining sensitivities toward an asymptote of zero (Figure 1.3). When comparing local versus broad sensitivity, the parameter of most importance changed across the range of plausible parameter values. For example, young of the year mortality, mortality, and age at maturation for females, in that order, were the most sensitive parameters locally, but broadly, mortality and age at maturation for females became more sensitive than young of the year mortality (Figure 1.3). Lastly, the impact of parameter values on the model outputs varied with the direction from the baseline the parameter was altered. For example, when parameter values were decreased, mortality was the most important parameter both locally and broadly; however, when parameters were increased, mortality was of less importance and young of the year mortality was more important locally (Figure 1.2).

The population and genetic response variables were hypersensitive to most of the input parameters with the exception of age at first maturation for males and probability of mating for males in some situations (Table 1.3; Table 1.4). When hypersensitivity was exhibited locally, hypersensitivity was also observed broadly in all cases except age at first maturation for males for the initial population size of 50 for the percent of populations extinct (Table 1.3; Table 1.4). In general, mortality rate was the most sensitive parameter both locally and broadly for all response variables. Young of the year mortality, probability of mating for females, and age at first maturation for females all had similar patterns of sensitivity across response variables. Parameters related to age at first maturation for males and probability of mating for males were least sensitive. Some response variables were hypersensitive to male reproductive parameters (e.g., percent of populations increasing to probability of mating for males); whereas most response variables were relatively insensitive.

The direction of response for each hypersensitive outcome varied between parameters but was fairly consistent for both local and broad sensitivities across both initial population sizes. For the initial population size of 50, as young of the year mortality rate, mortality rate, age at first maturation for females, and age at first maturation for males were increased, the percent of populations extinct increased both locally and broadly (Table 1.3; Table 1.4). For the initial population size of 50, as probability of mating for females and probability of mating for males were increased, the percent of populations extinct decreased both locally and broadly. Both locally and broadly, as young of the year mortality rate, mortality rate, age at first maturation for females, and age at first maturation for males increased, the percent of populations

increasing and average percent of genes retained decreased for both initial population sizes. Both locally and broadly, as the probability of mating for females and probability of mating for males increased, the percent of populations increasing and average percent of genes retained increased for both initial population sizes. As young of the year mortality rate, mortality rate, and age at first maturation for females increased, final mean inbreeding increased for both initial population sizes, and as the probability of mating for females increased, final mean inbreeding decreased for both initial population sizes both locally and broadly.

The pattern in the relationship among outputs was similar for both initial population sizes. Graphs of these relationships show that the outputs were not independent and exhibited joint sensitivity. As the average percent of genes retained decreased, the final mean inbreeding increased for both initial population sizes (Figure 1.4). Both initial population sizes exhibited an exponentially decreasing relationship between the average percent of genes retained and the final mean inbreeding. Final mean inbreeding increased more rapidly as the average percent of genes retained decreased for the smaller initial population size, however. As the percent of populations increasing decreased, the mean final inbreeding increased for both initial population sizes (Figure 1.5). Both initial population sizes exhibited a decreasing S-shaped relationship between the percent of populations increasing and the mean final inbreeding, but for the initial population size of 50, the final mean inbreeding increased at a quicker rate as the percent of populations increasing decreased. As the percent of populations increasing increased, the average percent of genes retained increased for both initial population sizes (Figure 1.6). Both initial population sizes exhibited an increasing S-shaped relationship between

the percent of populations increasing and the average percent of genes retained, but the smaller initial population size required a higher percent of genes retained to asymptote at 100%.

## DISCUSSION

The response of all measures of population performance and genetic integrity were hypersensitive to young of the year mortality, mortality, age at first maturation for females, and the probability of mating for females for both initial population sizes. Changes in all of these parameters have a large impact upon the long-term dynamics of the population and are driving the population outputs. Changing the parameters of young of the year mortality, age at first maturation for females, and probability of mating for females resulted in approximately equal sensitivity to changes for each of the outcomes of interest. The outcomes of interest were most sensitive to changes in the mortality rate for both initial population sizes. Gross et al. (2002) found population growth rate to be most sensitive to young of the year and adult mortality for other sturgeon species, and Marmontel et al. (1997) found mortality rates of various year classes to be the most sensitive parameters for population persistence for the Florida manatee *Trichechus manatus latirostris*, which is also a long-lived species.

The mortality rate was the most sensitive of all of the population parameters for the outcomes of interest. Because mortality rate was hypersensitive, changing this population parameter will have a large impact on long-term dynamics and population persistence. This finding is similar to Shaffer (1980) and Suchy et al. (1985) who found that mortality rate was the most sensitive parameter with the largest effects on grizzly bear *Ursus arctos* population dynamics and to findings of Cuthbert et al. (2001) for

Hutton's shearwater *Puffinus huttoni* conservation. Sutton et al. (2004) found that lake sturgeon mortality at older life stages was more influential on abundance and recruitment than mortality on younger life stages for a stage-structured model with respect to lampricide treatments. Long-lived organisms with life histories similar to lake sturgeon have been shown to have the largest sensitivities to adult mortality rates (Heppell et al. 2000). Reducing the mortality of lake sturgeon will thus have the largest impact on population persistence. Reductions in mortality can be accomplished through reducing and regulating harvest, both legal and illegal (Beamesderfer and Farr 1997). Reducing illegal harvest could be accomplished via protection of spawning adults, which is when adults are most vulnerable to illegal harvest.

The young of the year mortality rate was also hypersensitive for the outcomes of interest. Because of this, reducing young of the year mortality will also have a large impact on long-term dynamics and population persistence for lake sturgeon. Young of the year mortality could potentially be decreased through stocking or supportive breeding via stream-side rearing. Each of these practices have been suggested in past lake sturgeon rehabilitation strategies (Beamesderfer and Farr 1997; Hay-Chmielewski and Whelan 1997). Stocking and supportive breeding practices would lower mortality over the first year, which is when lake sturgeon are subject to the highest mortality rates, thus increasing long-term population growth rate (Ryman and Laikre 1991).

Although both the age at first maturation for females and the probability of mating for females were hypersensitive to changes, these lake sturgeon life history parameters would be difficult to change through current management practices. In theory, managers could alter these two parameters by selectively stocking offspring that

mature earlier and spawn more frequently. However, the change in the genetic characteristics of populations due to this direct, anthropogenic selection could be detrimental to long-term population dynamics because populations would likely loose adaptability and unique genes. Adaptability and unique genes allow species to survive during environmental extremes and in unique habitats (Kawecki and Ebert 2004). Also, the current life history strategy that lake sturgeon exhibit is likely a strategy that has evolved over a long time, and as such, negative impacts would likely occur if female reproductive strategy was artificially altered. Because many genes have been found to be linked to others, the loss of the genes associated with late maturation and more infrequent spawning could possibly result in the unexpected loss of other genes, which may be important for survival during environmental extremes and in unique habitats (Conner and Hartl 2004). My findings are similar to findings by Jager et al. (2002), who found the female parameters of average age at maturation and interval between spawning to be important for populations using an individual based model of demographics for white sturgeon *Acipenser transmontanus*.

Overall, the responses of the outputs of interest were relatively insensitive to changes in both the age at first maturation for males and the probability of mating for males. The percent of populations increasing for the initial population size of 50 was the only scenario that was hypersensitive to both the age at first maturation for males and the probability of mating for males. Thus, changes in these parameters have relatively little impact upon the long-term population dynamics of lake sturgeon and are not driving the population outputs. The lack of sensitivity for the male population parameters could be related to an excess of males available to mate with respect to the number of females

present in the spawning run each year. Male lake sturgeon mate at a younger age and more frequently than female lake sturgeon (Hay-Chmielewski and Whelan 1997), thus affording individual males more opportunities to contribute more progeny over a lifetime. Also, if larger numbers of males spawn each year, some males may not be able to find a female mate, but females will nearly always be able to find a male mate. These factors are likely the reason the outputs of the model are relatively insensitive to male mating characteristics.

Sensitivity was not linear for any of the output parameters across the range of plausible values explored. Many sensitivity analyses are conducted as local sensitivity analyses, whereby all of the parameters are held at a nominal value and one parameter at a time is changed by ±10% (or less) to determine which parameters most strongly influence model predictions (McCarthy et al. 1996; Essington 2003). However, in my sensitivity analyses, I varied model inputs across a broader range of values. These non-traditional sensitivity analyses delineated the shape of the sensitivity curve, depicting a richer picture of model sensitivity. Many of the sensitivity curves reached a maximum and then started to asymptote toward zero. This asymptote towards zero is due, in part, to increased extinctions or sufficiently large population sizes to overcome the effects of the change in the model input. This asymptotic behavior could also be exhibited because the output variables have a limited window of response (i.e., percent extinction is limited to 0 to 100%). Finally, this asymptotic behavior is also the result of a limiting parameter for the model output eventually being replaced by another limiting parameter. This type of non-traditional sensitivity analysis helps to determine which parameters are most

sensitive and in what range those parameters have the greatest influence on model outcomes.

The outputs for the model were found to have joint sensitivity, and the type of relationship between each set of the parameters was similar for both initial population sizes. Each output for the model describes a different aspect of the population (demographics or genetics), but each of the outputs was related to one another. Even though both initial population sizes had a similar relationship type, the relationships were not exactly the same. For example, the initial population size of 50 resulted in a quicker increase in mean final inbreeding with decreases in the average percent of genes retained and with decreases in the percent of populations increasing. However, the joint sensitivity between final mean inbreeding and percent of genes retained indicated that for a given level of inbreeding, the percent of genes retained for the initial population size of 200 was much less than for the initial population size of 50 (Figure 1.4). The initial population size of 50 also resulted in a slower increase in the percent of populations increasing with an increase in the average percent of genes retained. The differences in the functions for the two initial population sizes may be because the initial population size of 50 is more prone to extinction than the initial population size of 200. Generally, the differences observed between the two population sizes indicate that sensitivities are dependent upon initial population size. Thus, use of any sensitivity analysis information for species management and conservation is dependent upon the initial population sizes that are explored.

The relationship between percent of genes retained and inbreeding level is expected according to current theory (Conner and Hartl 2004). Gene retention was

similar for both initial population sizes, but the mean inbreeding coefficient was nearly three times higher for the smaller initial population size. Smaller populations are more prone to inbreeding, but inbreeding doesn't result in the direct loss of alleles (Conner and Hartl 2004); therefore, one would expect the two initial population sizes to have similar gene retention but differing inbreeding levels (Figure 1.4).

Assumptions with models and other factors could pose limitations and could result in differences in outputs for the model. First, constant environmental and demographic conditions were assumed into the future for these simulations, and environmental and demographic conditions were based on current conditions. Further degradations in habitat and exploitation could increase mortality rates for lake sturgeon. Increases in the mortality rates would increase the extinction risks and mean final inbreeding, and decrease the percent of populations increasing and the average percent of genes retained. Second, an Allee effect could cause a higher risk of extinction at low population densities because of predator-prey interactions, spawning behaviors, and other biotic factors not included in my model (Gascoigne and Lipcius 2004). An Allee effect could result in extinction risks being underestimated at small population sizes (Beissinger and Westphal 1998). Even with the assumptions required to model such as system, modeling is the most feasible option because field studies on long-lived organisms such as the lake sturgeon would be difficult due to time and money constraints.

Lake sturgeon populations have declined considerably in the past and rehabilitation efforts, such as reduced harvest and supplementation, have been implemented in the Great Lakes region (Hay-Chmielewski and Whelan 1997). Helping to foster sustainability of lake sturgeon populations has been a goal of many

rehabilitation strategies. The results of this study illuminate the potential value of various management practices to increase sustainability by reducing mortality sources. Some practices that could be valuable for lake sturgeon rehabilitation include stocking, stream-side rearing, reduced harvest, and protection from poaching. All of these practices lead to reduced mortality rates and thus increased probabilities of population persistence as well as lower levels of inbreeding and higher retention of unique alleles over time.

Table 1.1. Baseline parameter values as determined from the literature and from lake sturgeon biologists (Baker 1980; Hay- Chmielewski and Whelan 1997; Auer 1999; Bruch 1999; Billard and Lecointre 2001).

| | |
|---|---|
| Young of the year mortality rate | 0.47 |
| Mortality rate | 0.05 |
| Age at first maturation for females | 20 |
| Probability of mating for females | 0.33 |
| Age at first maturation for males | 15 |
| Probability of mating for males | 0.5 |

Table 1.2. Percent of populations extinct (±2 SE), percent of populations increasing (±2 SE), average percent genes retained (±2 SE), and final mean inbreeding for the baseline simulations for the initial populations sizes of 50 and 200.

| | N=50 | N=200 |
|---|---|---|
| Percent of populations extinct | 34.4 (30.2, 38.6) | 0 (0, 0) |
| Percent of populations increasing | 9.2 (6.61, 11.79) | 46.2 (41.74, 50.66) |
| Average percent genes retained | 4.64 (2.76, 6.52) | 9.5 (6.87, 12.11) |
| Final mean inbreeding | 0.1388 | 0.0413 |

Table 1.3. Local sensitivity (the average outcome for ±10% deviations), *S*, for each model parameter, each initial populations size, and each model output.

| | Population outputs | | | | Genetic outputs | | | |
|---|---|---|---|---|---|---|---|---|
| | Percent of populations extinct | | Percent of populations increasing | | Percent genes retained | | Mean inbreeding | |
| Input | N=50 | N=200 | N=50 | N=200 | N=50 | N=200 | N=50 | N=200 |
| YOY mortality rate | 6.99 | - | -16.94 | -11.46 | -6.91 | -3.21 | 1.58 | 1.74 |
| Mortality rate | 11.72 | - | -41.41 | -10.82 | -15.57 | -7.93 | 3.87 | 6.07 |
| Age at first maturation for females | 4.33 | - | -14.78 | -9.74 | -4.90 | -3.20 | 2.32 | 1.99 |
| Probability of mating for females | -5.35 | - | 14.67 | 10.02 | 5.82 | 3.48 | -2.06 | -2.46 |
| Age at first maturation for males | 0.60 | - | -5.10 | -0.63 | -1.28 | -0.04 | -0.09 | 0.08 |
| Probability of mating for males | -1.69 | - | 4.35 | 1.62 | 2.19 | 0.37 | 0.13 | -0.12 |

Table 1.4. Broad sensitivity (the average outcome for ±30% deviations), *S*, for each model parameter, each initial populations size, and each model output.

| | Population outputs | | | | Genetic outputs | | | |
|---|---|---|---|---|---|---|---|---|
| | Percent of populations extinct | | Percent of populations increasing | | Percent genes retained | | Mean inbreeding | |
| Input | N=50 | N=200 | N=50 | N=200 | N=50 | N=200 | N=50 | N=200 |
| YOY mortality rate | 5.44 | - | -16.12 | -7.64 | -6.15 | -3.14 | 1.18 | 2.16 |
| Mortality rate | 7.89 | - | -28.83 | -7.16 | -15.04 | -6.79 | 6.69 | 7.64 |
| Age at first maturation for females | 4.05 | - | -16.07 | -6.25 | -5.40 | -3.25 | 1.61 | 1.99 |
| Probability of mating for females | -4.65 | - | 14.87 | 6.34 | 5.58 | 3.37 | -1.61 | -2.77 |
| Age at first maturation for males | 1.11 | - | -4.64 | -0.77 | -1.48 | -0.11 | 0.00 | 0.05 |
| Probability of mating for males | -2.32 | - | 4.70 | 1.49 | 2.34 | 0.39 | -0.37 | -0.23 |

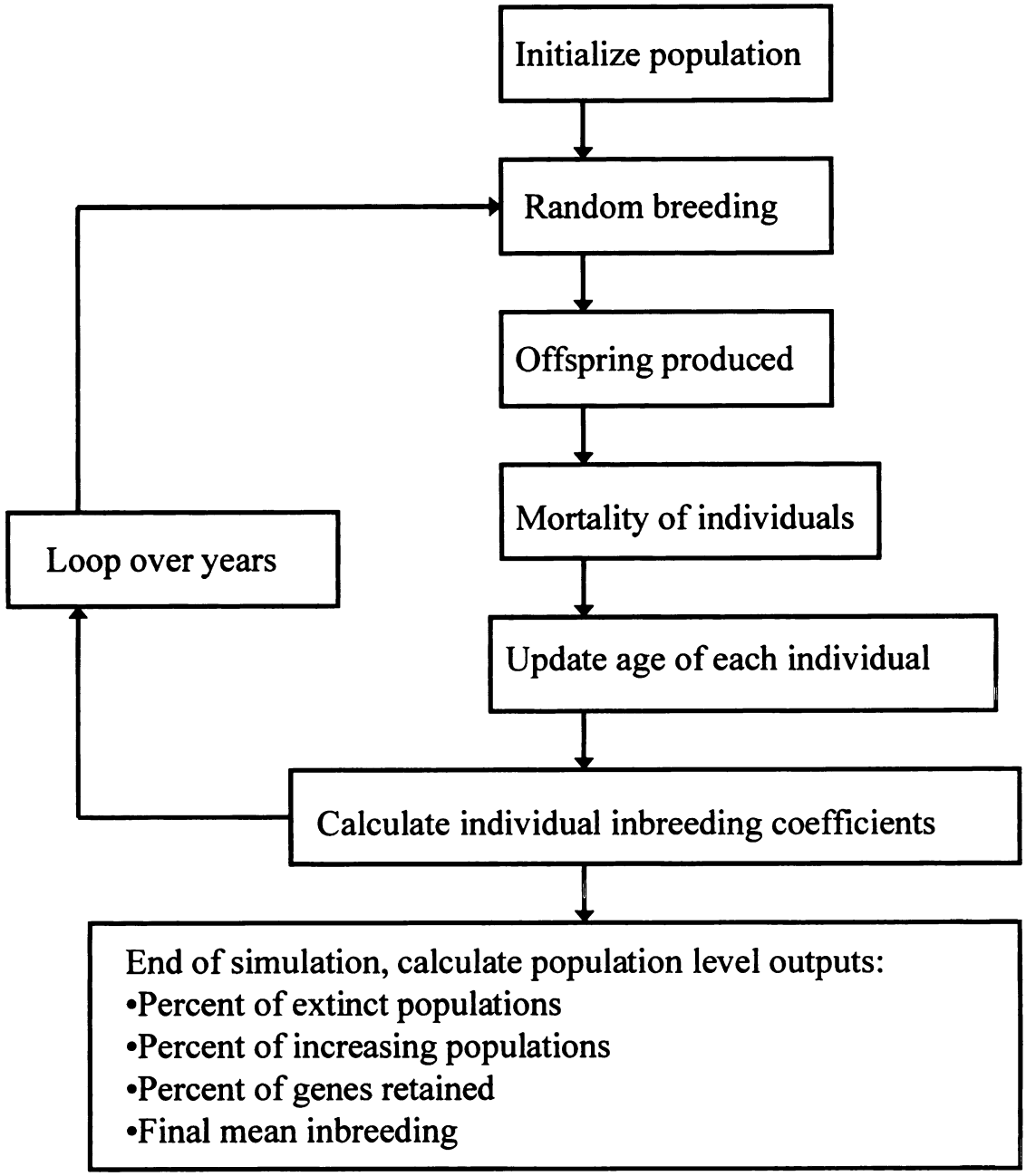


Figure 1.1. Basic model structure for simultaneous simulation of lake sturgeon demographics and genetics.

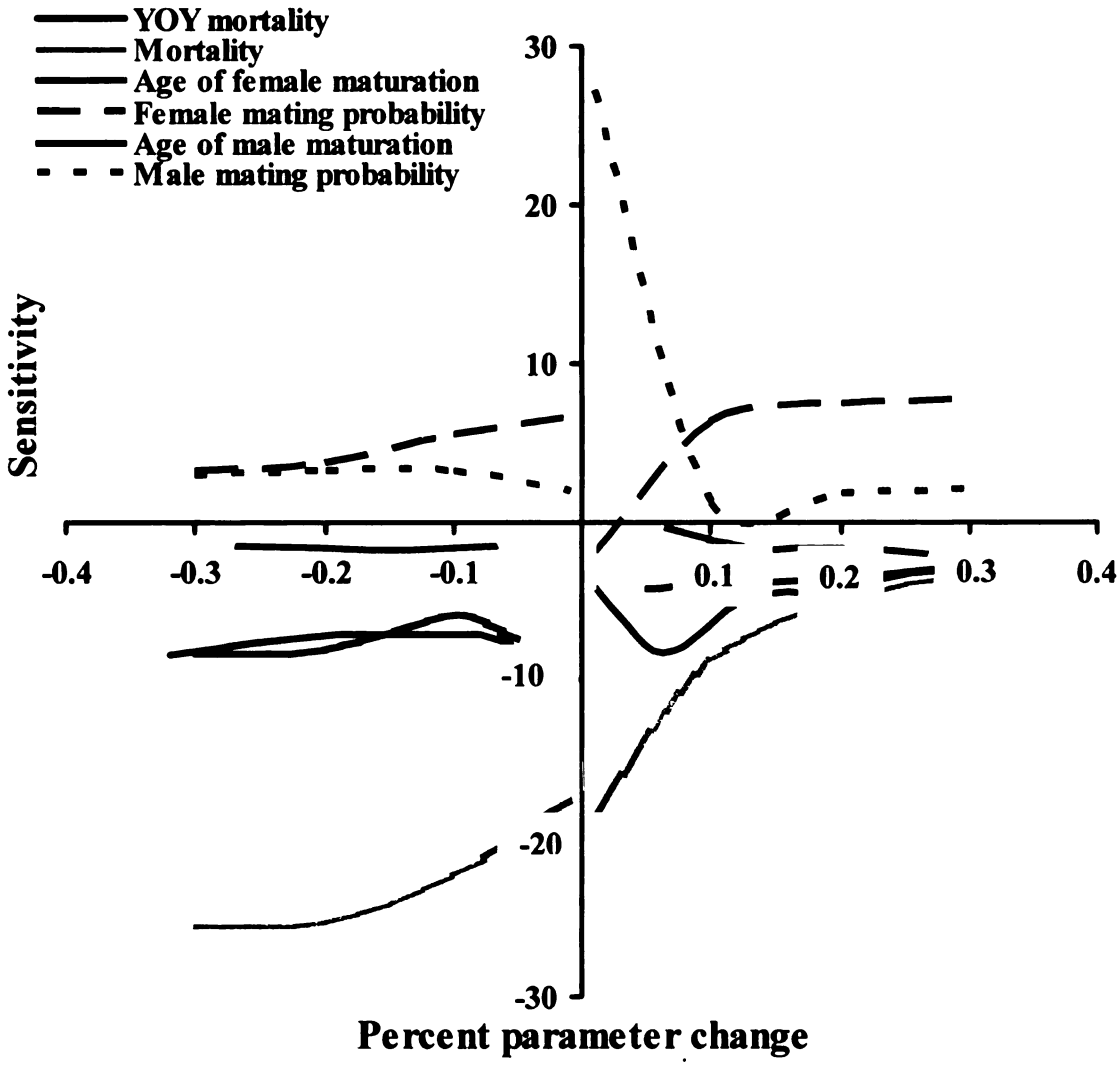


Figure 1.2. Percent change in parameter versus sensitivity, *S*, for average percent of genes retained for lake sturgeon with an initial population size of 50.

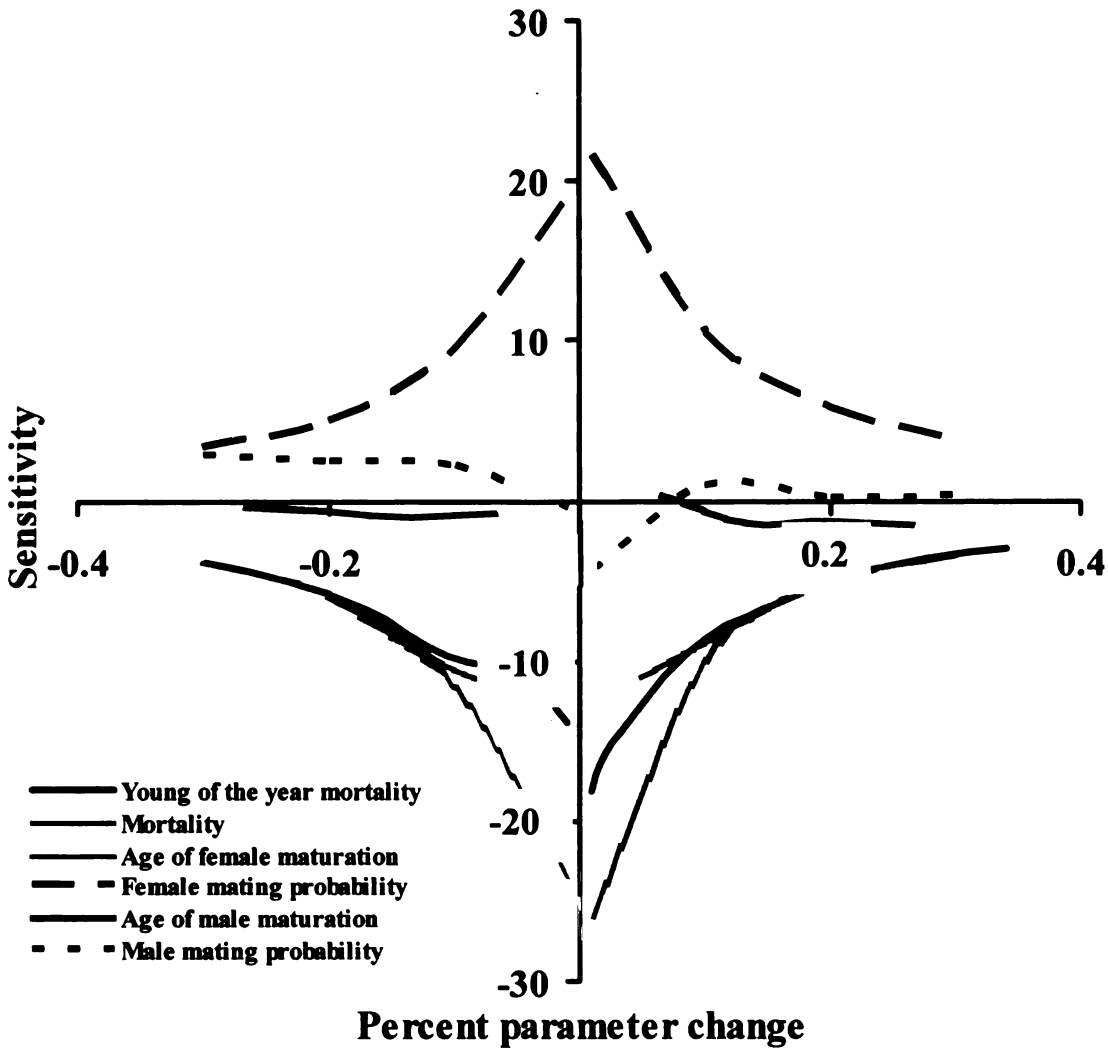


Figure 1.3. Percent change in parameter versus sensitivity, *S*, for the percent of populations increasing for lake sturgeon with an initial population size of 200.

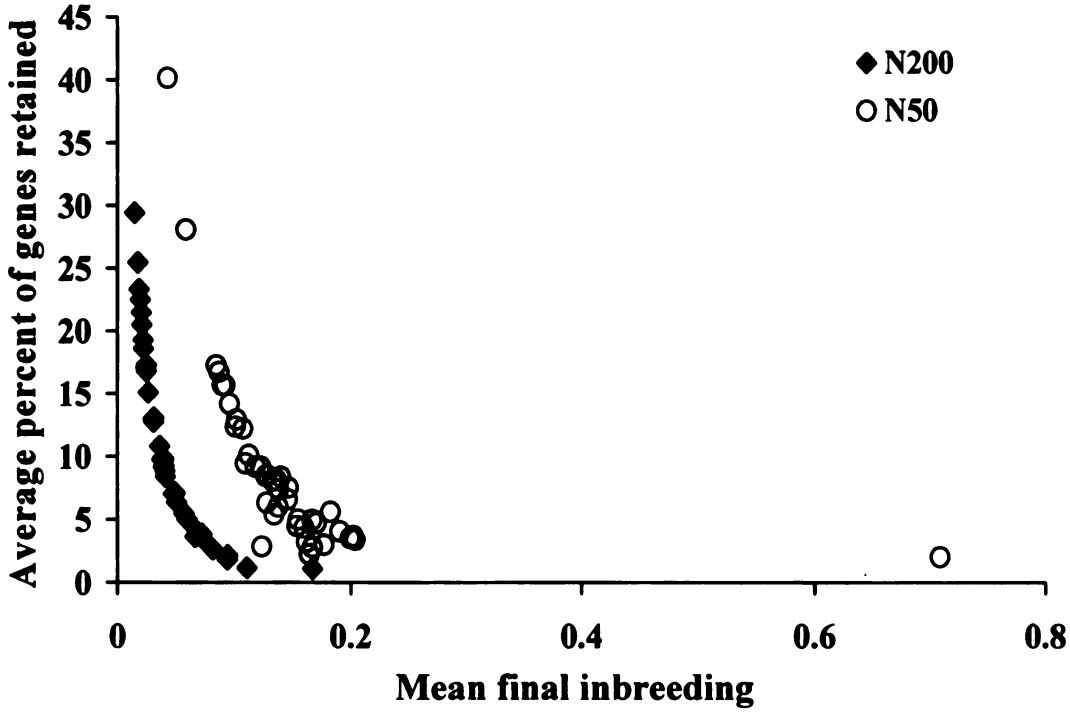


Figure 1.4. The average percent of genes retained versus final mean inbreeding for the initial population sizes of 200 and 50.

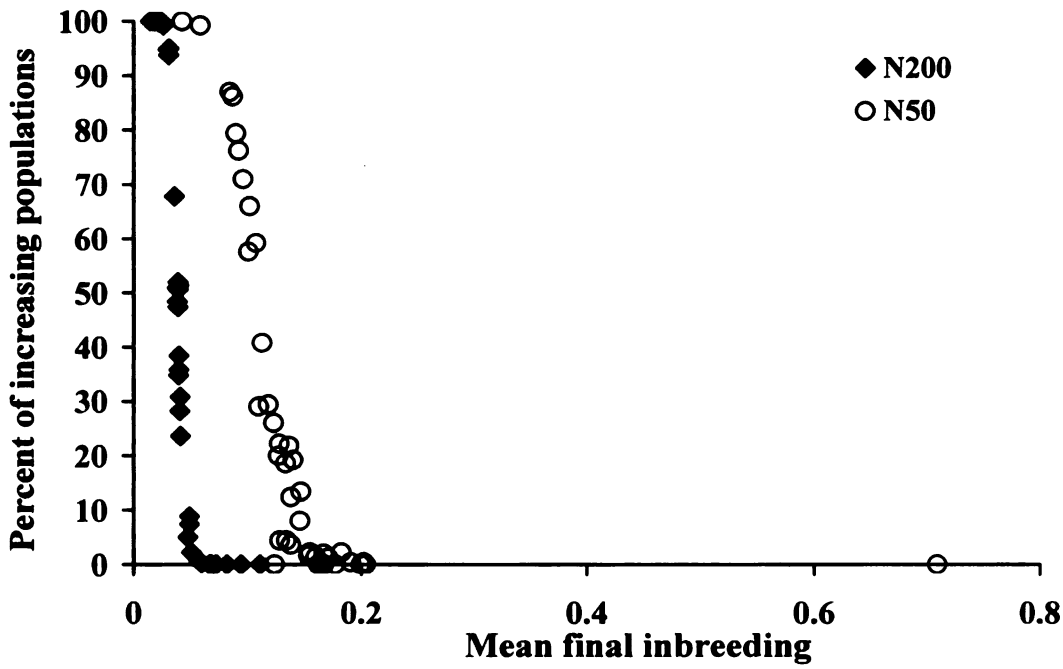


Figure 1.5. The percent of populations increasing versus the final mean inbreeding for the initial population sizes of 200 and 50.

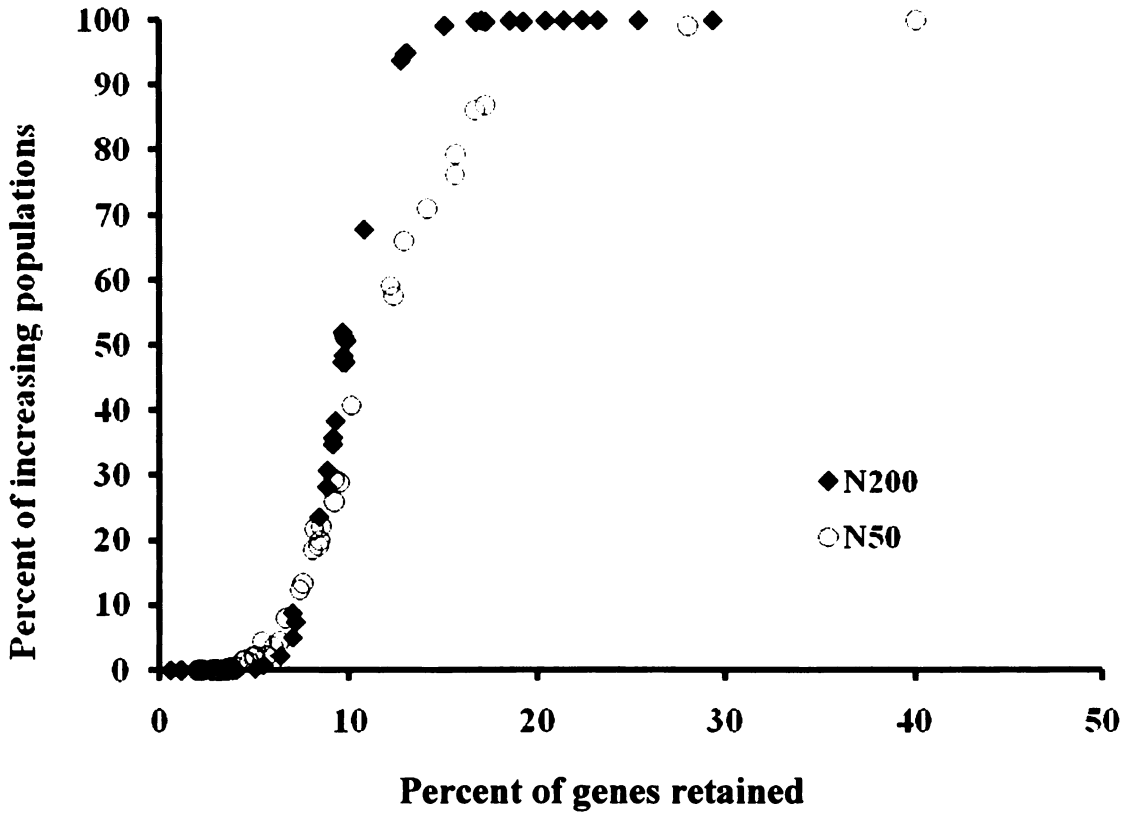


Figure 1.6. The percent of populations increasing versus percent of genes retained for the initial population sizes of 200 and 50.

# MINIMUM VIABLE POPULATION SIZE FOR LAKE STURGEON USING AN INDIVIDUAL BASED MODEL OF DEMOGRAPHICS AND GENETICS

ABSTRACT.-Lake sturgeon restoration is a priority in the Great Lakes basin, where sturgeon have been reduced to <1% of historic levels and have been extirpated from many areas. Population viability analysis is a useful tool to explore the relationship between extinction risk and population size over a specified time frame, but often doesn't include genetic factors. My objectives were to determine the minimum viable population size (MVP) for lake sturgeon, and to determine how inbreeding depression may affect MVP. An individual based model was developed incorporating inbreeding depression under two scenarios: where individuals with inbreeding coefficients above a threshold experienced inbreeding depression (threshold), and where individuals experienced inbreeding depression at a rate related to their inbreeding coefficient (gradual). Three well established mechanisms previously described relating inbreeding to fitness were explored (YOY viability, post YOY viability, and progeny number). Estimated MVP without incorporating inbreeding with ~5% chance of extinction over 250 years was 80 individuals. MVP was 150 under a reduced progeny number inbreeding model and 80 for decreased post YOY viability for all thresholds. MVP ranged from 80-125, with lower thresholds leading to increased MVP for YOY viability. For the gradual inbreeding depression scenarios, MVP was 85 for decreased YOY viability, 85 for reduced progeny number, and 1,800 for decreased post YOY viability. Results show that MVP can be influenced by particular types of inbreeding depression, but demographic stochasticity often dominated the process of extinction. This research will help to inform

lake sturgeon management within the Great Lakes basin by determining the minimum viable population size for lake sturgeon and how inbreeding, which is expected to accrue in remnant populations due to multiple generations of low population size, likely affects the minimum viable population size. This can then be used to prioritize populations for rehabilitation.

# INTRODUCTION

Lake sturgeon *Acipenser fulvescens*, a long-lived species, were once found throughout the five Great Lakes and the Great Lakes drainage basin in the United States and Canada (Birstein et al. 1997; Hay-Chmielewski and Whelan 1997; Smith and Baker 2005). Currently, lake sturgeon restoration is a priority throughout the Great Lakes basin, where sturgeon have been reduced to less than 1% of historic levels due to habitat degradation, overharvest, and fragmentation of spawning populations (Johnson et al. 1998; Auer 1999; Holey et al. 2000; McQuown et al. 2003). Factors that have contributed to the decline of lake sturgeon in the past continue to contribute to declines in abundance and impede restoration where populations have been extirpated. Therefore, extensive management goals, objectives, and actions aimed at restoration and protection of the imperiled lake sturgeon have been developed. For example, stocking and habitat restoration have been suggested and stocking has been implemented for some populations in the state of Michigan (Hay-Chmielewski and Whelan 1997). Lake sturgeon restoration plans have been completed by Michigan (Hay-Chmielewski and Whelan 1997), Wisconsin (WDNR 2008), and Ontario (OMNR 2006), although considerable uncertainty exists as to the best course of action for lake sturgeon restoration.

Lake sturgeon populations may be depressed in numbers, but the genetic diversity of these populations hasn't been depressed yet (DeHaan et al. 2006). Conserving the genetic integrity (defined here as both the retention of genes and reduced inbreeding accrual) of lake sturgeon should encompass maintaining the distribution of genes within a population, which is affected by inbreeding (Hay-Chmielewski and Whelan 1997;

McQuown et al. 2003; Keller and Waller 2002). Inbreeding occurs when individuals who are closely related mate, and most readily occurs in small populations where random mating can more readily result in breeding among related individuals (Hedrick and Kalinowski 2000; Brook et al. 2002; Keller and Waller 2002). Inbreeding is often thought to result in a decrease in an individual's fitness relative to non-inbred offspring, resulting in what is called inbreeding depression. Inbreeding depression can be manifested in any traits related to fitness (e.g., survival (viability), fecundity; Crnokrak and Roff 1999; Hedrick and Kalinowski 2000; Amos and Balmford 2001), but has been difficult to demonstrate empirically (Newman and Pilson 1997). The rate of inbreeding accrual is hypothesized to be important because natural selection is able to remove deleterious alleles at low rates of inbreeding, but high levels of inbreeding may result in an excess of deleterious genes in a homozygous state. Therefore, extinction rates are also thought to be lower at slower rates of inbreeding accrual (Reed et al. 2003a).

Small populations experience demographic and environmental stochasticity, catastrophes, and inbreeding; for some population sizes, rehabilitation efforts may be unlikely to be successful (Pimm et al. 1988; Tracy and George 1992; Lande 1993; Lynch and Walch 1998; Amos and Balmford 2001; Keller and Waller 2002). Therefore, identifying situations where rehabilitation efforts will be most successful will be beneficial to the restoration and protection of lake sturgeon populations in the Great Lakes basin. Because of their longevity, it is difficult if not impossible to empirically determine the MVP for lake sturgeon and to fully document interactions between demographic and genetic processes leading to extinction. Modeling is a useful tool, because of the flexibility available, and can be used to integrate both population

dynamics and genetics information in order to inform management decisions and determine the relative contributions of demographics and genetics to extinction risk (Brook et al. 2002).

Population viability analysis (PVA) is a useful model-based tool for conservation efforts for species like lake sturgeon because PVA allows for the exploration of the relationship between extinction risk and current population size (Shaffer 1981; Shaffer 1990; Boyce 1992; Brook et al. 2000). PVA has been used to explore the effects of environmental and demographic stochasticity on numerous species, such as the red-cockaded woodpecker *Picoides borealis* (Walters et al. 2002) and the long-lived Asian elephant *Elephas maximus* (Armbruster et al. 1999). PVA has also been used to explore the risk of extinction for spring Chinook salmon *Oncorhynchus tshawytscha* over two time frames and in the face of habitat degradation (Ratner et al. 1997). PVA and simulation models provide an important means to explore assumptions about uncertain parameter values, relationships, management actions, and feedback mechanisms within a population in order to determine a range of possible minimum viable population sizes (Shaffer 1981; Brook et al. 2000; Engen and Sæther 2000; Leech et al. 2008).

Generally, minimum viable population size is defined as a population of sufficient size to persist with a given probability over a given time frame, taking into account stochastic population processes (Shaffer 1981; Boyce 1992). Minimum viable population sizes are specific to each study or species and vary depending upon the species of interest, the species' life history, and the tolerance of extinction risk for the species' management and conservation (Shaffer 1981; Lindenmayer et al. 1993). Two important factors that need to be considered in a population viability analysis are demographic

stochasticity (random births and deaths of individuals) and genetic stochasticity (random genetic changes due to genetic events such as inbreeding or drift; Shaffer 1981; Lindenmayer et al. 1993; Reed and Bryant 2000; Reed 2005). Both demographic and genetic stochasticity become increasingly important to a population's viability as population size decreases (Lindenmayer et al. 1993), but determining whether demographic or genetic stochasticity is more important to long-term population persistence is difficult (Shaffer 1981). Also, modeling the influence of genetic changes on demography has proven to be difficult in many situations because translating negative genetic impacts into demographic impacts is not straightforward and because genetic data are often unavailable (Beissinger and Westphal 1998; Kirchner et al. 2006).

Much debate has occurred over the past decades as to which process is most important for the risk of extinction for small population sizes: demographic stochasticity or genetics, specifically inbreeding and inbreeding depression. Some have argued that demographic stochasticity is more important than genetics at small population sizes (Lande 1988; Young 1991; Harcourt 1991) based on the premise that if there are no animals surviving, there are no genes left to conserve. However, others have demonstrated that inbreeding depression can lead to reduced population viability at small population sizes. Frankham (1995a) concluded that the risk of extinction increased with inbreeding. Keller and Waller (2002) found that many studies are now available whereby inbreeding depression has been found in the wild and can be detrimental to long-term persistence. Many argue that while inbreeding depression may not be the driving force towards extinction, that it still has an impact and increases the risk of extinction (Mills and Smouse 1994). Therefore, a need exists to explore the relationship between

demographics and genetics in regards to the long-term persistence of populations (Boyce 1992; Shaffer 1980; Jager et al. 2000; Kirchner et al. 2006), specifically for long-lived species such as the lake sturgeon.

Despite this need, very few analyses have incorporated genetic factors into determinations of long-term population viability (Boyce 1992; Brook et al. 2002). Genetic factors such as inbreeding and genetic drift can contribute to increased risks of extinction at small population sizes (Boyce 1992) as was shown for the evening primrose *Clarkia pulchella* in Montana (Newman and Pilson 1997). Very little work has been completed addressing genetic stochasticity and how genetic stochasticity and the breeding system of an animal contribute to the minimum viable population size (Shaffer 1981). Among those studies that have been conducted, inbreeding has been shown to be a critical factor in the long-term persistence of species in the wild (Frankham 1995b). For example, demographic and genetic factors have been explored via population viability analysis and genetic factors were found to be important for the red-cockaded woodpecker (Haig et al. 1993), the plant species *Banksia cuneata* (Burgman and Lamont 1992), generic mammal species (Mills and Smouse 1994), and for 20 threatened species across many taxa including the southern bluefin tuna *Thunnus maccoyii* (Brook et al. 2002). Many of these studies are based on the concept of lethal equivalents (deleterious genes whose effect when totaled, results in one mortality when present in the homozygous form; Keller and Waller 2002) instead of individual inbreeding coefficients, and results are not consistent from study to study (Swindell and Bouzat 2006).

The objective of my study was to determine the minimum viable population size for lake sturgeon, incorporating both demographic and genetic stochasticity through the

potential impacts of inbreeding (Mills and Smouse 1994). This objective was addressed using an individual based model of demographic and genetic stochasticity. Of particular interest was modeled risk of extinction for different population sizes, but genetic population characteristics such as percentage of unique alleles lost, and levels of inbreeding were also critical outcomes that I evaluated. Results of this research will help to inform lake sturgeon management within the Great Lakes basin by estimating the minimum viable population size for lake sturgeon and how inbreeding affects the minimum viable population size, which should help inform objectives and management actions for rehabilitation of lake sturgeon populations.

## METHODS

### *Model Development*

An individual based model was developed that incorporated demographic and genetic processes (Figure 2.1). Lake sturgeon exhibit a polygamous mating system which was represented based on available data whereby female lake sturgeon mature at approximately 20 years of age and spawn approximately once every 3 years, and male lake sturgeon mature at approximately 15 years of age and spawn approximately every other year (Auer 1999; Bruch 1999; Billard and Lecointre 2001; DeHaan 2003; Nichols et al. 2003; Table 2.1). Once an individual reached the minimum age for maturity, then the individual was assigned a random number distributed Uniform(0,1). If that random number was less than the probability of mating, then that individual returned to the river to mate that year. Empirical data from Black Lake, Michigan, lake sturgeon showed that reproductive success was not related to adult length or weight (DeHaan 2003). Therefore, the size of individual fish wasn't included in this individual-based model. For

each fish returning to spawn, the number of potential mates or batches of offspring, *B*, for each spawning male and female was based on empirical data from Black Lake, MI (Figure B.1; DeHaan 2003). Random numbers of batches were generated using a discrete form of the exponential distribution by:

$$B = 1 + \text{integer}(-2 * \ln(1 - U(0,1)).$$

This distribution represents the number of mates from empirical data (Figure B.1; DeHaan 2003). The batches for the males and females were randomly shuffled, and female batches were paired with male batches. This process allowed random matings between individuals, and allowed individuals to mate with multiple other individuals as has been observed in lake sturgeon. In this model, any batches produced by a male or female without a pair, or mate, were deleted. This distribution allows for a large number of mates as the uniform distribution approaches one; however, the number of mates is decreased based on how the batches are paired with mates. Thus, extremely large numbers of mates is unlikely. The number of progeny, *P*, produced (at the end of the summer) from each mating pair, or batch, was generated using an exponential equation of the form:

$$P = \text{integer}(1 * (-\ln(1 - U(0,1))))$$

producing a distribution of numbers of offspring similar to that seen in Black Lake, MI (DeHaan 2003). This distribution was based on the empirical number of progeny per adults as reported by DeHaan (2003; Figure B.2). The empirical distribution was based on a parentage analysis whereby progeny in a sample were assigned to parents. Only about 25% of progeny were assigned to parents, however. Because of this, the empirical number of progeny per parent should be treated cautiously. Because the number of

progeny was modified by varying the YOY mortality rate to match observed population sizes and trajectories, this distribution was judged to be appropriate.

The sex of offspring was randomly determined with an equal probability. Following birth, age-specific mortality rates were applied to each individual sturgeon. Mortality rates were set up in the model such that a random number between 0 and 1 was generated for each individual and if that random number was less than the specified level of mortality, then that individual suffered mortality. As such, demographic stochasticity was implicitly incorporated into the model because the death of each individual was randomly determined. The mortality rate from the larval stage through the end of the first year is unknown. Therefore, this mortality rate was varied to produce population growth rates that mimic observed growth rates for existing populations. This technique has proven useful in previous studies and provides a means to develop management advice even though parameter values are uncertain (Vaughn and Saila 1976; Hayes and Taylor 1990; Heppell et al. 2000). All parameter values were developed from literature review and further review by Great Lakes sturgeon experts. Mortality after age 0 was set to 0.05 based on Baker (1980; Table 2.1). Henceforth, young of the year mortality will be referred to as YOY mortality, and mortality after the first year will be referred to as post YOY mortality. Young of the year and post young of the year mortality rates have been treated this way by past elasticity studies for other sturgeon species (Gross et al. 2002).

Individual inbreeding coefficients were determined using path analysis of the individual's pedigree implemented in the INBREED procedure available in SAS® (SAS Institute Inc., 2003). From a pedigree, the inbreeding coefficient ($f_x$) for an individual

was determined by summing all of the unique paths ($P$) through a common ancestor ($A$) as

$$f_x = \sum_{i-1}^{P} \left[\frac{1}{2}\right]^n (1 + f_A)$$

where n was the number of ancestors in the path and $f_A$ was the inbreeding coefficient of ancestor A (Wright 1922). Lake sturgeon are polyploid with a ploidy level of eight (Blacklidge and Bidwell 1993). Polyploidy is thought to mask inbreeding depression; however this effect has not been shown for other polyploid species such as salmon species *Oncorhynchus sp.* (Wang et al. 2002). Therefore, I assumed polyploidy of lake sturgeon did not affect the accrual of inbreeding. This approach allowed for the tracking of overall individual inbreeding levels and accrual of inbreeding rather than specifying certain alleles as deleterious.

Gene retention from the founding population was tracked based on a one locus system whereby each individual at the start of the simulations had two unique, hypothetical alleles at one locus (MacCluer et al. 1986). The hypothetical locus was assumed to be inherited as a Mendelian trait. As mating occurred between individuals, some alleles were lost from the population before they could be passed on to offspring. Random loss of unique alleles results in genetic differentiation among populations and determines the percentage of founders that have contributed genes to the population. This loss of unique alleles can be described through a technique called gene drop analysis (MacCluer et al. 1986; Hedrick and Miller 1992), which tracks all unique alleles that are lost from the population through time (Haig et al. 1993). Thus, the percent of remaining alleles at the end of each simulation can then be expressed as the number of remaining

alleles over the number of unique alleles at the beginning of the simulation which is two times the initial population size.

*Minimum Viable Population Size*

The minimum viable population size (MVP) was considered the population size whereby the probability of extinction was approximately 5% over a 250 year time frame (which is approximately 10 generations for lake sturgeon). A 5% risk of extinction is a common criterion for population viability analysis (e.g., grizzly bears *Ursus arctos*, Shaffer 1980; kaka *Nestor meridionalis*, Leech et al. 2008; capercaillie *Tetrao urogallus*, Marshall and Edwards-Jones 1998; Scott et al. 1995). MVP was determined for a scenario with no inbreeding effects which was then used for comparison to the scenarios which included inbreeding depression.

The impacts of inbreeding depression on individual fitness were incorporated into the demographic model by creating demographic feedbacks for specified inbreeding scenarios. Two types of scenarios were simulated. In the first set of scenarios, reduced fitness was implemented by choosing an inbreeding level above which all individuals experienced reduced fitness. I termed this a "threshold" scenario. In the next set of scenarios, reduced fitness was implemented as a linear decline in fitness with increasing individual inbreeding coefficient. I termed this a "gradual" scenario. Three mechanisms for possible inbreeding depression were explored: YOY viability (i.e., survival), progeny number, and post YOY viability. Each of these traits has been shown to be affected by inbreeding depression in many animal species including fish (Hedrick and Miller 1992; DeRose and Roff 1999).

Little work has been done on genetic impacts, including inbreeding and inbreeding depression, on persistence outside of a captive environment (Caughley 1994; Ralls et al. 1988). The fitness effects that inbreeding have on lake sturgeon are currently unknown; therefore, I evaluated different plausible scenarios given what has been found for other species. This is somewhat like a sensitivity analysis for inbreeding depression in order to see what effect fitness changes have on long-term population persistence. I choose to explore the effects of inbreeding depression with thresholds of 0.0625, 0.125, and 0.250. These coefficients represent levels of inbreeding which have been shown to have deleterious effects in natural populations. For example, increased levels of inbreeding were found to decrease survival of song sparrows *Melospiza melodia* whereby those individuals above an inbreeding level of approximately 0.06 all died during a population crash (Keller et al. 1994). At an inbreeding level of approximately 0.25 the probability of persistence was about 100% for all effective population sizes of *Drosophila melanogaster*, but above 0.25, extinction risk increased (Reed et al. 2003a). A captive wolf *Canis lupus* population, which demonstrated inbreeding depression, had an average F=0.25 (Laikre and Ryman 1991). Also, a wild Mexican jay population *Aphelocoma ultramarine* had reduced survival through the first year with related parents (Brown and Brown 1998).

We also explored the population effects of a gradual reduction in fitness with increases in inbreeding coefficient. Burgman and Lamont (1992) simulated 10% reductions in survival and reproduction for a 10% increase in the inbreeding coefficient for the plant species *Banksia cuneata*. DeRose and Roff (1999) found an 11% reduction in fitness related to life history traits such as fecundity and survival, at the inbreeding

level of 0.25 using data from several animal species. Inbreeding depression of ~2-6% for body weight and egg number was observed with a 10% increase in inbreeding coefficient for captive reared rainbow trout *Oncorhynchus mykiss* (Su et al. 1996). With a 10% increase in inbreeding coefficient, an 18.2% decrease in reproduction was found for a wild muskox *Ovibos moschatus* population (Laikre et al. 1997). Captive brown bears *Ursus arctos* had inbreeding coefficients ranging from 0 to 0.375 (Laikre et al. 1996), where an increase of $f$ by 0.1 equaled a 7% change in litter size. For captive Pacific white shrimp *Penaeus vannamei*, approximately a 2-4% reduction in growth was observed with a 10% increase in inbreeding (Moss et al. 2007). Finally, for the long-haired rat *Rattus villosissimus* inbreeding depression resulted in approximately a 3% decline in litter size with a 10% increase in the inbreeding coefficient (Lacy and Horner 1997). Given the observed range in inbreeding depression from ~1-19%, I used slopes representative of the observed relationships between the inbreeding coefficient and the fitness component, which is described below. These inbreeding coefficients and scenarios (threshold and gradual) were chosen because they represent a range of plausible values and scenarios from past studies, and because inbreeding has been found to affect different species with similar results (Crnokrak and Roff 1999; Reed et al. 2003a).

In total, twelve inbreeding scenarios were explored. Three scenarios were explored for YOY viability using a threshold (0.0625, 0.125, and 0.250) whereby all individuals above the threshold did not survive. Hence, if the individual's inbreeding coefficient was above the specified threshold level, then the individual had a 0% chance of survival. Three scenarios were explored for progeny number using a threshold (0.0625, 0.125, and 0.250) whereby all individuals above the threshold experienced a

10% reduction (on average per year) in the number of progeny produced. Three scenarios were explored for post YOY viability using a threshold (0.0625, 0.125, and 0.250) whereby individuals above the cutoff threshold had a reduced survival probability (a 10% increase in the post YOY mortality rate, which is a reduction in survival). One scenario was explored for YOY viability using gradual inbreeding whereby individuals were exposed to a reduced survival rate which was related to their inbreeding coefficient by the relationship:

$$y = 0.47x + 0.47$$

where $y$ was the individual YOY mortality rate, $x$ was the individual's inbreeding coefficient, and 0.47 was the baseline YOY mortality rate (Table 2.1). For every increase in the individual inbreeding coefficient of 0.10, the mortality rate increased by 10% from the baseline with a maximum mortality of 100%, which was the maximum for the threshold scenarios. A gradual change of 10% was used as it was within the range of observed changes. One scenario was explored for progeny number using gradual inbreeding depression whereby individuals had a reduced progeny number related to their inbreeding coefficient. The progeny number was on average reduced 10% for each 0.10 increase in inbreeding coefficient. A gradual change of 10% was used as it was within the range of observed changes. Finally, one scenario was explored for post YOY viability using gradual inbreeding whereby individuals had decreased survival which was related to their inbreeding coefficient by the relationship:

$$y = 0.0208x + 0.05$$

where $y$ was the individual post YOY mortality rate, $x$ was the individual's inbreeding coefficient, and 0.05 was the baseline post YOY mortality rate (Table 2.1). The post

YOY mortality rate was able to increase until *y* reached a maximum increase in mortality of 10%, which was the maximum mortality increase for the post YOY viability threshold scenarios. Because the gradual scenarios were limited by the minimum and maximum changes of the threshold scenarios, I was able to compare the threshold versus gradual scenarios.

*Simulations*

Simulations were run across a range of initial population sizes to determine MVP based on the specified criterion. Based on preliminary analyses, a simulation duration of 250 years was used as this allowed time for transient responses to dissipate. For each scenario, 500 simulations were run to provide precise estimates of the mean response and the variance across the factors explored. A yearly time step was used in all simulations. The percent of extinct populations, average individual inbreeding coefficient in the final year, and percent of unique genes retained were recorded for each simulation run of 250 years. The average individual inbreeding coefficient is the average inbreeding coefficient for progeny produced in the final year. No uncertainty estimates could be provided for the inbreeding coefficients because only the mean was an output for the model. The percent of unique genes was the average percent of genes retained where extinct simulations were included as zero genes retained. For the average percent of genes retained, confidence intervals were calculated as:

$$(\text{estimate} \pm 2*SE)*100$$

where the SE = (pq/n) ^ (1/2), p = (percent of genes retained/100), q = 1-p, and n=500. Confidence intervals for the percent of extant populations were also calculated for each scenario using proportions, but the error bars were not graphed because the bars fell

within the markers on the graphs. Simulations were assumed to have current environmental and demographic conditions, which remained constant into the future.

## RESULTS

The MVP with approximately a 5% risk of extinction over the 250 year time frame with demographic stochasticity but no inbreeding effects was approximately 80 individuals for lake sturgeon. The risk of extinction increased rapidly for smaller populations; initial populations of 40 had an approximately 50% extinction rate, and populations of 15 or less went extinct in virtually all cases (Figure 2.2). The final inbreeding coefficient averaged 0.0913 and the percent of genes retained was 7.63 (95% CI= 5.26 to 10.01) for simulations starting at the MVP of 80, and with demographic stochasticity but no inbreeding effects (Table 2.2).

For many of the scenarios, the MVP was not heavily influenced by inbreeding depression (Table 2.2), as the MVPs were the same as or close to the MVP with no inbreeding depression. MVP was 80 for decreased post YOY viability for all thresholds. For gradual inbreeding depression, MVP was 85 for decreased YOY viability and 85 for reduced progeny number. However, MVP increased when inbreeding depression was incorporated as a reduction in progeny number or YOY viability based on inbreeding thresholds, and when post YOY viability gradually decreased as a function of inbreeding. Minimum viable population size was 150 with reduced progeny number for all thresholds. Minimum viable population sizes ranged from 80-125, with lower thresholds leading to increased MVP for YOY viability. The only scenario where MVP was vastly different was with gradual inbreeding depression with a decrease in post YOY viability. Under this scenario, MVP was approximately 1,800.

Mean inbreeding and the percent of genes retained after 250 years were generally similar across all scenarios with and without inbreeding depression (Table 2.2). The final mean inbreeding coefficient and the percent of genes retained for all of threshold scenarios for post YOY viability were similar to the scenario with no inbreeding effects. The final mean inbreeding coefficient for all thresholds for reduced progeny was similar to the scenario with no inbreeding effects, but the percent of genes retained was approximately half. The final mean inbreeding coefficient and the percent of genes retained both increased with increasing thresholds for the inbreeding depression scenarios for YOY viability. The final mean inbreeding coefficient and the percent of genes retained were similar to no inbreeding effects for the gradual YOY viability scenario and slightly less for the gradual reduced progeny number scenario. The final mean inbreeding coefficient was similar to the no inbreeding scenario, but the percent of genes retained was greatly reduced when compared to the no inbreeding scenario for inbreeding depression via gradual post YOY viability.

When inbreeding depression resulted in a MVP different than 80, the persistence curve (the curve of percent of extant populations versus initial population size) changed when compared to the persistence curve with no inbreeding depression. Minimum viable population size is a point on the persistence curve with a given extinction risk, and as the initial population size increases or decreases, the risks of extinction change differently for the different scenarios (Figure 2.2). When the MVP changed, the persistence curves maintained high risk at small population sizes and lower risk at large populations sizes. However, at intermediate population sizes, the risk of extinction changed at different rates. For example, the rate at which the persistence curve reached 100% decreased as

the initial population size was increased with threshold inbreeding depression as reduced progeny number (Figure 2.2). Some of the curves maintained the same shape but simply shifted. For example, the persistence curve simply shifted causing an increase in the MVP for threshold inbreeding depression on YOY viability (Figure 2.2). The persistence curves were the same when compared to the persistence curve with no inbreeding depression when the MVP was not different (e.g., gradual inbreeding depression for progeny number). Therefore, not all persistence curves were graphed because of the large number of lines that would be necessary and because some MVPs didn't change, instead a representative sample was chosen for illustrative purposes.

When inbreeding depression increased the MVP, the percent of genes retained decreased, but the impact on the final mean inbreeding depended upon the scenario. The percent of genes retained decreased slightly for threshold inbreeding depression on YOY viability and decreased greatly for threshold inbreeding depression as reduced progeny number when compared to the scenario without inbreeding (Figure 2.3). The final mean inbreeding level increased for threshold inbreeding depression as reduced progeny number, and the final mean inbreeding level decreased for threshold inbreeding depression as decreased YOY viability (Figure 2.4). Finally, in scenarios where MVP was similar to the no inbreeding depression simulation, the percent of genes retained and the final mean inbreeding did not change when compared to the percent of genes retained and final mean inbreeding with no inbreeding depression. Therefore, not all scenarios were graphed.

# DISCUSSION

Minimum viable population size is important for identifying populations for conservation and for identifying extinction risks associated with differing population sizes (Shaffer 1981). Populations with extremely low abundance are often difficult to rehabilitate given the need to overcome demographic stochasticity. Traditionally, population viability analysis models which explore minimum viable population size focus on demographic and environmental stochasticity. Often, genetic components are not incorporated but can have a significant impact on a population's persistence (Boyce 1992; Shaffer 1980; Jager et al. 2000; Kirchner et al. 2006). Only one fish species included in the large meta-analysis by Traill et al. (2007) included inbreeding effects, and only one fish species of 102 vertebrate species were considered in another meta-analysis of MVP by Reed et al. (2003b). Thus, incorporating both demographics and genetics to determine the MVP may be important but has not been widely explored for fish species (Boyce 1992; Traill et al. 2007; Reed et al. 2003b). Therefore, I aimed to explore the MVP for different scenarios of inbreeding depression for a long-lived fish, the lake sturgeon.

The probability of extinction can never truly be zero for any wild population (Shaffer 1990), but managment can strive to minimize the risk of extinction by determining MVP and maintaining populations above that level. Based on the above described model, I estimated that the MVP for lake sturgeon populations in the Great Lakes basin was 80 individuals with approximately a 5% risk of extinction over 250 years. Few MVP's have been determined for fish species, only 9 of 287 MVP's were for fish species in the original dataset compiled for the meta-analysis by Traill et al. (2007)

and only 1 of 102 for a study by Reed et al. (2003b). Those MVP's that have been estimated for fish species are generally larger than for the MVP estimated for lake sturgeon, which could be related to different life history strategies between species or different time frames used to estimate MVP. For example, the MVP for white-spotted charr *Salvelinus leucomaenis* was estimated to be 250 with a 5% risk of extinction over 100 years (Morita and Yokota 2002), and Traill et al. (2007) predicted a standardized MVP using a general linear mixed effects model for eight fish species to range from approximately 200,000 to 2 million. The MVP for lake sturgeon was however comparable to MVP's for other long-lived species. The MVP was found to be 125 grizzly bears *Ursos arctus horribilis* for 100 years (Suchy et al. 1985), and about 100 for a Japanese black bear *Ursus thibetanus japonicus* population for 100 years with a 5% risk of extinction (Horino and Miura 2000). A population of approximately 120 Asian elephants *Elephas maximus* was determined to be the MVP with about a 5% risk of extinction over 1,000 years (Armbruster et al. 1999).

Little empirical evidence is available relating levels of inbreeding to MVP; therefore, modeling plausible scenarios is a useful strategy to explore possible effects. Theory suggests that MVP can be increased by inbreeding depression by increasing the population size needed to maintain viability, because individuals in an inbred population have lower fitness than individuals in a non-inbred population of the same size (Amos and Balmford 2001). For example, for red-cockaded woodpeckers, increased levels of inbreeding depression resulted in increased risks of extinction using VORTEX (Haig et al. 1993). Similarly, the MVP using VORTEX for the Atlantic Forest spiny rat *Trinomys eliasi* was higher when inbreeding was included than when inbreeding wasn't (Brito et al.

2003). Finally, population outputs were sensitive to inbreeding depression when modeling the long-furred woolly mouse opossum *Micoureus paraguayanus* using the program VORTEX which includes inbreeding depression via juvenile survival (Brito and Fonseca 2006). My study was unique because my study used a generalized individual based model instead of VORTEX.

When genetic factors have been incorporated in the past, they have often been incorporated using the program VORTEX (Caughley 1994). VORTEX uses lethal equivalents or heterozygosity to implement inbreeding depression on juvenile survival (rarely on any other fitness components; Marshall and Edwards-Jones 1998). Also, the defaults are often used in VORTEX because inbreeding depression hasn't been measured for a lot of different types of species (e.g., bird species; Marshall and Edwards-Jones 1998). An alternative to VORTEX is a more generalized individual based model. Individual based models (IBM) are useful because they track individuals through time and because results can be given at both the individual and population levels. For tracking inbreeding, using an IBM is more appropriate than a population model because each individual has an inbreeding coefficient. Thus, tracking inbreeding at the individual level allows for individual mortality instead of mortalities at the population level. Overall, studies using IBMs with pedigrees are rare (Overall et al. 2005), but could be very informative.

Some inbreeding depression scenarios explored in this analysis resulted in little or no change to the MVP required to maintain persistence when compared to the scenario without inbreeding depression. With inbreeding depression under the threshold scenario, the MVP was the same as the MVP with no inbreeding depression for post YOY viability

for all thresholds. With gradual inbreeding depression for both YOY viability and progeny number, the MVP increased only slightly to 85. Similar results were found in other studies. For example, increased probabilities of extinction were not predicted for the plant species *B. cuneata* with increased levels of inbreeding (Burgman and Lamont 1992). Inbreeding depression was thought not to increase extinction risks in Burgman and Lamont's model (1992) because of the random effects of environmental stochasticity.

However, some inbreeding depression scenarios explored did result in changes to the predicted MVP required to maintain persistence. With threshold inbreeding depression on progeny number, the MVP was 150, nearly twice the MVP with no inbreeding depression. This result is similar to other findings where small increases in inbreeding depression for survival and fecundity parameters consistent with mammal species increased the risk of extinction for populations above the extinction risk for simulations without inbreeding (Mills and Smouse 1994). Also, the probability of extinction increased when inbreeding depression in the form of lethal equivalents on juvenile mortality was included in simulation models of 20 species (Brook et al. 2002). For the bird capercaillie *Tetrao urogallus*, the MVP with a 5% extinction risk was about 150 individuals with inbreeding depression manifested for juvenile survival in VORTEX (Grimm and Storch 2000). Finally, the MVP including inbreeding depression on pup mortality was 400 individuals for wolves *Canis lupus* in Scandinavia (Nilsson 2003). Thus, I have predicted that inbreeding depression can increase extinction risk depending upon how inbreeding depression is incorporated.

We found that gradual inbreeding depression via post YOY viability resulted in a MVP of approximately ~1,800. Given the current lake sturgeon population sizes in the

Great Lakes basin, this scenario seems implausible because most populations are below 1,800 and have not spiraled to extinction during the recent generations at low abundance (Hay-Chmielewski and Whelan 1997). I feel that this large MVP is due to the longevity of lake sturgeon, and their ability to accumulate inbreeding over several generations. This longevity leads to lake sturgeon being exposed to higher mortality rates due to the accumulated inbreeding levels which results in high levels of extinction. In a sensitivity analysis of a lake sturgeon population model (Schueller and Hayes *in review*; Chapter 1), we found that post YOY mortality was the most sensitive parameter, whereby even small increases in the mortality rate led to increased extinction rates and reduced abundance. Sensitivity to post YOY survival has been found for other long-lived species (Boyce 1992). Thus, this model result makes sense given that even small increases in the post YOY mortality rate resulted in large increases in the probability of extinction.

For the scenarios which incorporated inbreeding depression gradually, the estimated MVP will be highly dependent on the slope of the fitness function. Because the model outputs were hypersensitive to changes in the population parameters related to survival (Chapter 1), the MVP for these scenarios will likely change with changes in survival. For example, the model was most sensitive to post YOY mortality and the MVP estimated with gradual inbreeding depression on post YOY mortality resulted in the largest MVP needed for persistence. This example illustrates that the slope chosen for these scenarios can greatly influence the outcome. Therefore, there is a critical need to obtain better empirical estimates of inbreeding depression on sensitive population parameters.

One important difference between my study and others is that I used an IBM and the individual inbreeding coefficients were calculated through path analysis. The inbreeding coefficient ($f_x$) calculated in my study via path analysis is a direct probability of inbreeding or of genes being identical by descent which is in contrast to studies using effective population size or other proxies (Su et al. 1996). This allowed for those individuals that were the most inbred to be subjected to reduced fitness instead of the population as a whole being subjected to reduced fitness.

With threshold inbreeding on YOY viability, the MVP increased with decreasing thresholds (Table 2.2). This outcome may be the result that purging would have on a population. Although inbreeding depression reduces fitness, mortality of inbred individuals prior to reproduction leads them to not contribute to the next generation. Thus, these inbred individuals are "purged" from the population. This process can lead to fitness levels being maintained or sometimes decreased in future generations (Hedrick and Kalinowski 2000; Crnokrak and Barrett 2002; Keller and Waller 2002). Purging thus can lead to situations where deleterious genes are lost and inbreeding depression is reduced in future generations (Leberg and Firmin 2007). I found that as the threshold increased, the final mean inbreeding coefficient increased as did the percent of genes retained. This is an example of purging where individuals with inbreeding coefficients above the threshold experience mortality as YOY. This results in the removal of those individuals with higher inbreeding coefficients, leading to lower mean inbreeding coefficients than what would be expected without purging (Crnokrak and Barrett 2002). My finding of purging is similar to findings from a meta-analysis where purging was found to affect fitness of organisms including plants, mammals, mollusks, and insects

(Crnokrak and Barrett 2002), and to findings by Swindell and Bouzat (2006) where inbreeding depression was likely reduced by purging for *Drosophila melanogaster* for small population sizes.

Neither the final mean inbreeding coefficient nor the percent of genes retained changed substantially for most of the scenarios which incorporated inbreeding depression when compared to the scenario without inbreeding depression. However, for the threshold scenarios for inbreeding depression affecting progeny number, the percent of genes retained was about halved when compared to the scenario of no inbreeding depression. Loss of abundance leads to the loss of genes generally, but the percent of genes retained was lowest for the inbreeding depression with the highest MVP required. Inbreeding depression via reduced progeny number means that fewer individuals are contributing progeny, and thus fewer individuals are passing their genes to future generations. This may explain why progeny number resulted in fewer genes being retained while still requiring a larger MVP.

Demographic stochasticity often dominated the process of determining MVP for lake sturgeon because the MVP was often the same or only slightly larger with inbreeding depression (Table 2.2). For example, with the addition of inbreeding depression for post YOY viability under threshold scenarios, the MVP was still 80. However, MVP was influenced by inbreeding depression depending upon the scenario. For example, with inbreeding under the threshold scenario, the MVP for progeny number was 150 or nearly twice the MVP with no inbreeding effects. Much discussion has occurred over whether demographic stochasticity or genetic stochasticity is more important or has a greater influence on long-term persistence (Lande 1988; Young 1991;

Frankham 1995a; Spielman et al. 2004). Based on the scenarios in my study, whether demographic or genetic stochasticity dominate the determination of MVP and extinction risk is dependent upon whether inbreeding depression was expressed as threshold or gradual and whether inbreeding depression affected viability or progeny number. Thus, my study doesn't provide a clear picture of whether demographic or genetic stochasticity dominates extinction risk. The focus, however, should not be on which factor "dominates" the extinction process. Rather, efforts should be made to understand and document how genetic and demographic factors jointly affect MVP.

Often, measuring inbreeding depression is difficult because of the many environmental factors that impact populations and individuals (Pimm et al. 1988; Reed and Bryant 2000). One factor I did not include was environmental stochasticity. When inbreeding depression and environmental stochasticity act simultaneously, an inbreeding vortex can occur whereby populations spiral to extinction at a quicker rate (Tanaka 2000). Thus, the incorporation of environmental stochasticity to this model could increase rates of extinction for smaller population sizes via the inbreeding vortex. Therefore, larger populations may need to be maintained for threatened and endangered species to protect against an extinction vortex which could result from demographic stochasticity, the plausible effects of inbreeding depression, and environmental stochasticity. Environmental stochasticity wasn't included in this model because of the longevity of the lake sturgeon, and because the year to year variation in population parameters would most likely not be large enough to cause differences in population persistence over the long run (Benton et al. 1995). This is likely true because the trajectory of the population parameters mimics the trajectory of the real world which

includes environmental effects. Moreover, Melbourne and Hastings (2008) showed that environmental stochasticity was less of a factor for extinction risk if demographic heterogeneity (random births and deaths) and stochasticity in sex ratio are included in the model. This was especially true when population sizes are small or declining (Melbourne and Hastings 2008). Thus, because my analysis explored smaller population sizes, the sex ratio was allowed to vary, and demographic heterogeneity was included, including environmental stochasticity would likely not have increased extinction risk substantially.

As a final caveat, as shown in Chapter 1, the outputs of the model were hypersensitive to changes in the population parameters (e.g., YOY mortality and post YOY mortality). Thus, if the baseline parameter values vary, then the minimum viable population size as estimated above would likely change, potentially significantly. For example, if either of the mortality rates are increased or decreased, the minimum viable population size would increase or decrease, respectively. Thus, the estimate of minimum viable population size is dependent upon the baseline parameters used, but can still be a useful for management purposes if this aspect of uncertainty is taken into account.

## RECOMMENDATIONS

Because this work looks at the plausible role that inbreeding depression may play in the extinction process, this work should be used to guide experimental research looking to measure the effects of inbreeding depression. Thus, if inbreeding depression is manifesting itself in lake sturgeon or other long-lived species, inbreeding depression should be most readily measured by reduced progeny number. Finally, if inbreeding depression is resulting in purging of a population, then YOY viability should be investigated.

Given that in some inbreeding depression scenarios the MVP was increased, I recommend increasing the MVP to account for the possibility of inbreeding depression for other threatened and endangered species in order to overcome both demographic stochasticity and maintain genetic integrity. Because lake sturgeon are long-lived and because of their life history characteristics (e.g., iteroparous), a much lower MVP may have resulted when compared to most other species. Shorter life spans (e.g., those of insects) most likely require populations of greater size to maintain population persistence through time (Pimm et al. 1988; Boyce 1992). Therefore, other threatened and endangered species, which don't have long life spans, should have their populations maintained at much higher levels, and those populations that are long-lived, with similar population parameters to the baseline parameters used here, at least need populations maintained above 80-150 individuals. Given the uncertainty in these parameter estimates, larger population sizes may still be required for persistence.

Lake sturgeon long-term dynamics and persistence are dependent upon maintaining populations which are above the minimum viable population size while also maintaining genetic integrity. Thus, I recommend that populations should be maintained above 80 to 150 individuals, for the given baseline parameters explored. These recommendations should help to foster the protection of sustainable lake sturgeon populations for the future by minimizing extinction risks due to both demographic stochasticity and inbreeding depression. Also, estimation of MVP should help lake sturgeon managers prioritize populations for future rehabilitation efforts, given extinction risks. Given populations are below the MVP level, management efforts such as some

form of supplementation may be necessary to overcome demographic stochasticity and maintain persistence.

Table 2.1. Baseline parameter values as determined from the literature and from lake sturgeon biologists.

| Parameter | Parameter Value |
|---|---|
| Young of the year mortality rate | 0.47 |
| Mortality rate | 0.05 |
| Age at first maturation for females | 20 |
| Probability of mating for females | 0.33 |
| Age at first maturation for males | 15 |
| Probability of mating for males | 0.5 |

Table 2.2. Minimum viable population size for no inbreeding depression, threshold inbreeding depression, and gradual inbreeding depression for several fitness components, and the final mean inbreeding coefficient and percent of genes retained at MVP for each of the scenarios. For the percent of genes retained, simulations which went extinct were assigned a zero. Means (±2 SE) are provided for percent of genes retained.

| Inbreeding scenario | Manifestation | MVP | Final mean inbreeding coefficient | Percent genes retained |
|---|---|---|---|---|
| No inbreeding depression | Na | 80 | 0.0913 | 7.63 (5.26, 10.01) |
| YOY viability | 0.0625 | 125 | 0.0376 | 5.78 (3.69, 7.86) |
| | 0.125 | 100 | 0.0574 | 6.92 (4.65, 9.19) |
| | 0.25 | 80 | 0.0822 | 7.53 (5.17, 9.89) |
| | Gradual | 85 | 0.0902 | 7.28 (4.96, 9.60) |
| Post YOY viability | 0.0625 | 80 | 0.0912 | 7.33(5.00, 9.66) |
| | 0.125 | 80 | 0.0951 | 7.49 (5.13, 9.84) |
| | 0.25 | 80 | 0.0921 | 7.43 (5.08, 9.77) |
| | Gradual | 1,800 | 0.0942 | 0.29 (-0.19, 0.78) |
| Progeny number | 0.0625 | 150 | 0.0834 | 4.12 (2.34, 5.90) |
| | 0.125 | 150 | 0.0809 | 4.13 (2.35, 5.90) |
| | 0.25 | 150 | 0.0894 | 4.03 (2.27, 5.79) |
| | Gradual | 85 | 0.0877 | 7.28 (4.96, 9.61) |

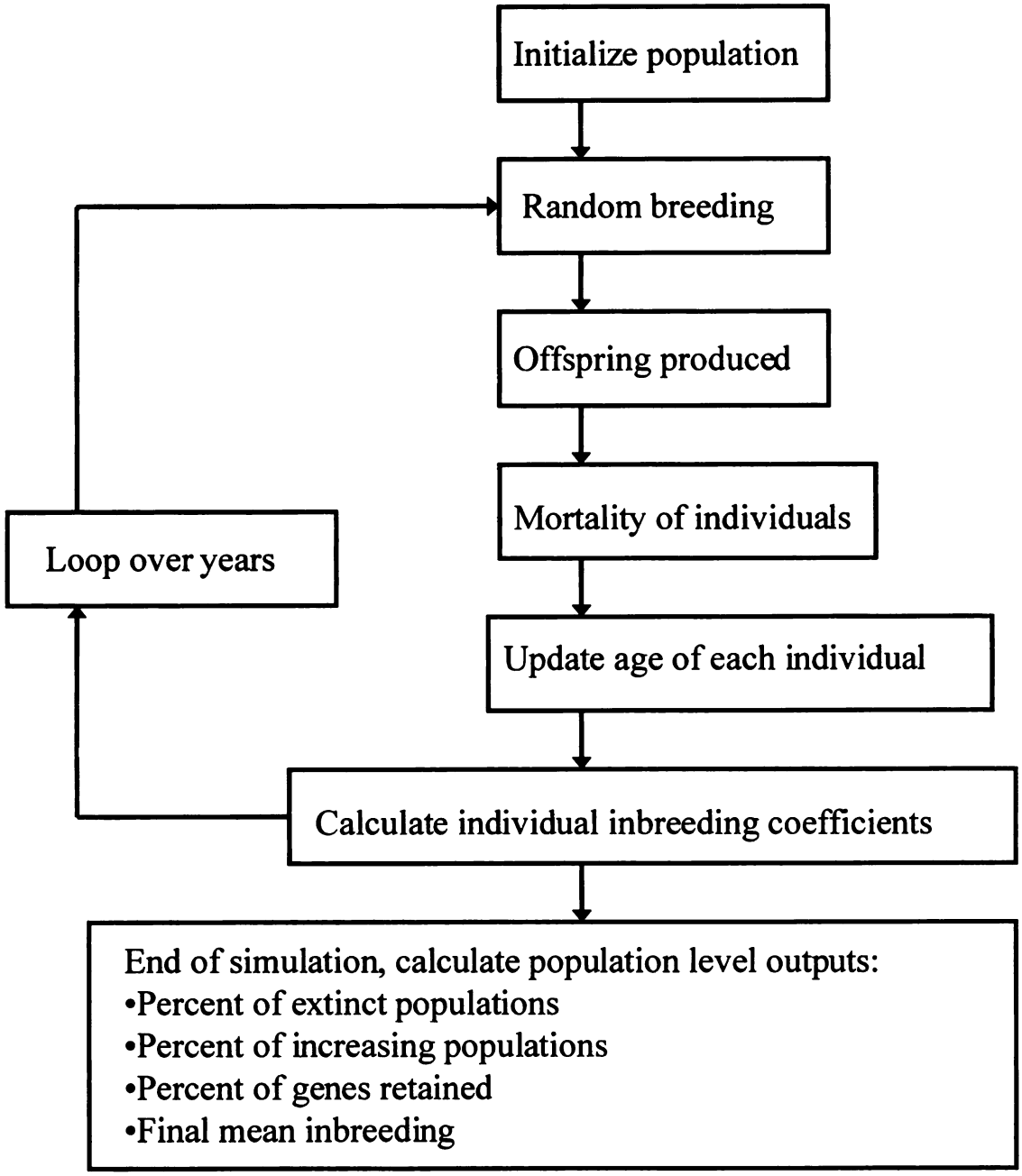


Figure 2.1. Model structure for simulations of lake sturgeon demographic and genetic parameters.

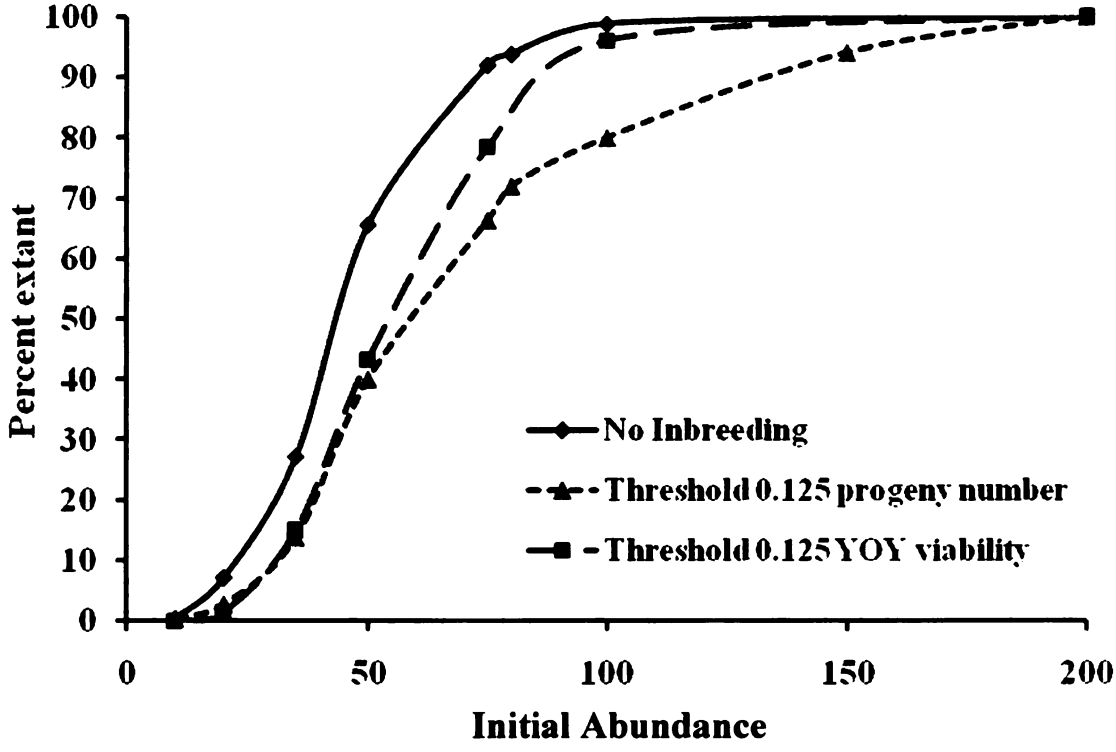


Figure 2.2. Percent of extant populations across a range of initial population sizes (persistence curves) under the scenarios of no inbreeding, threshold inbreeding depression as reduced progeny number at the threshold 0.125, and threshold inbreeding depression as decreased YOY viability at the threshold 0.125.

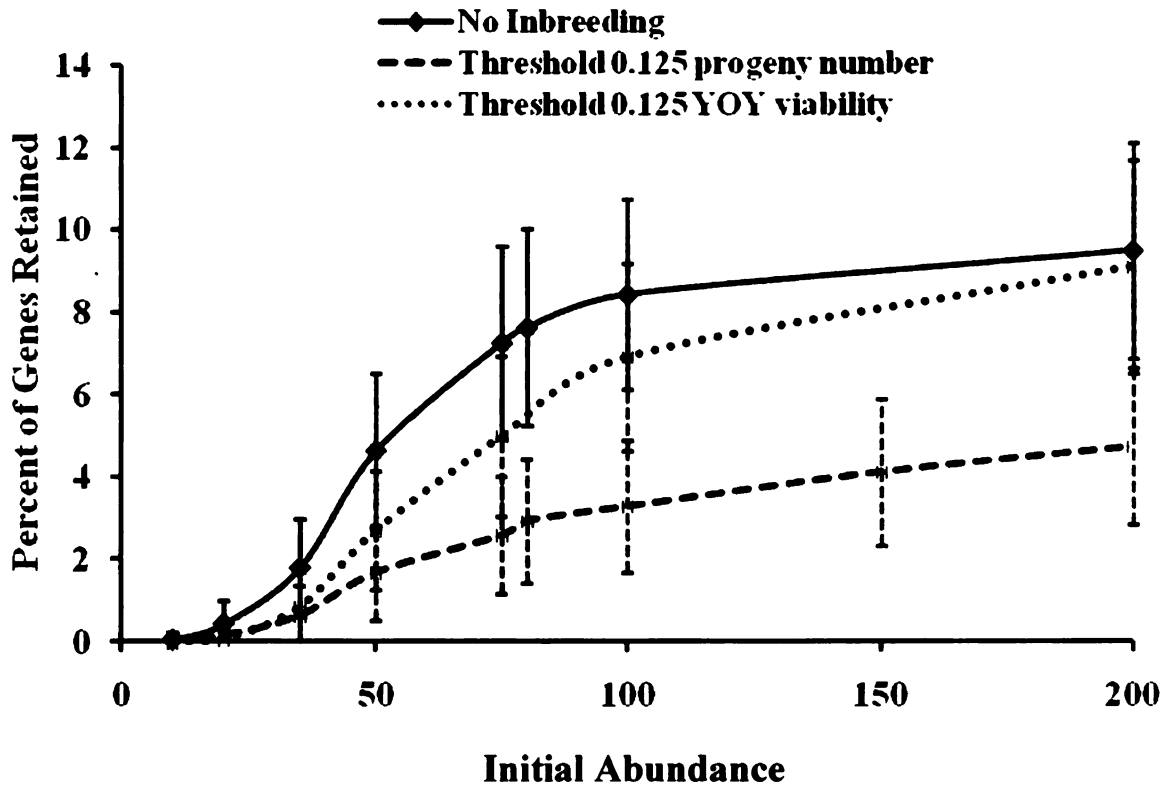


Figure 2.3. Percent of genes retained across a range of initial population sizes under the scenarios of no inbreeding, threshold inbreeding depression as reduced progeny number at the threshold 0.125, and threshold inbreeding depression as decreased YOY viability at the threshold 0.125. Percent of genes retained represent all simulations, including populations with no survivors. Error bars (±2 SE) for each scenario are represented in the same line type for each scenario. Simulations with no survivors were considered to have no genes retained.

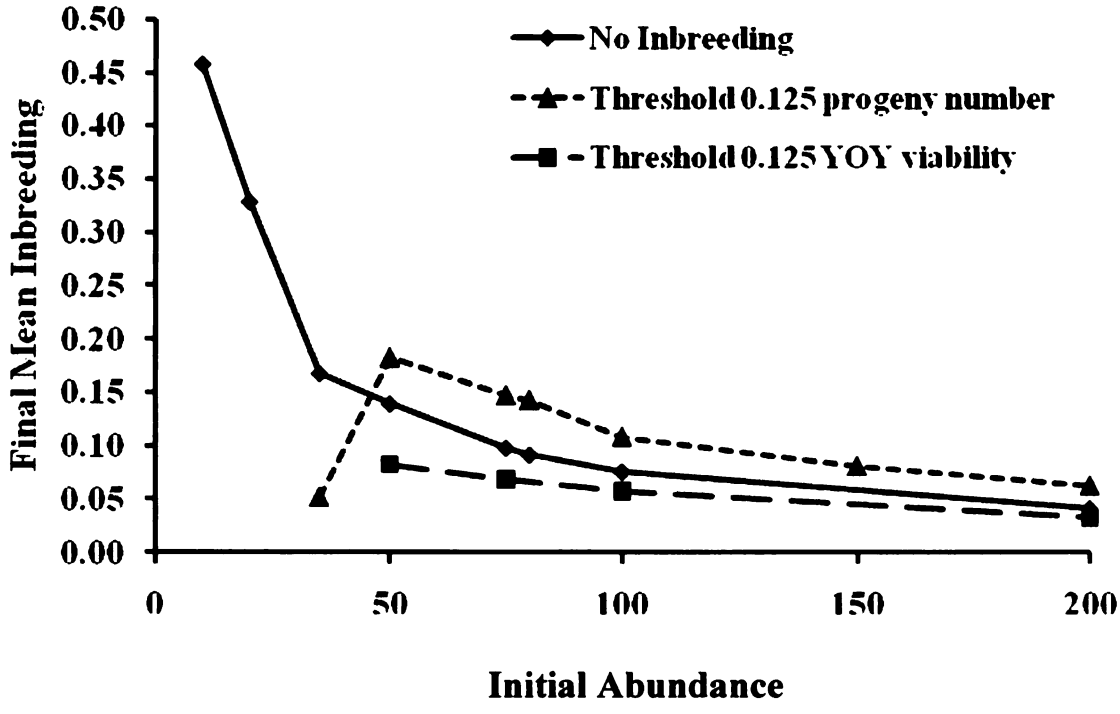


Figure 2.4. Final mean inbreeding across a range of initial population sizes under the scenarios of no inbreeding, threshold inbreeding depression as reduced progeny number at the threshold 0.125, and threshold inbreeding depression as decreased YOY viability at the threshold 0.125. Final inbreeding coefficients only represent extant populations at the end of the 250 year simulation duration; populations with no survivors were not assigned an inbreeding coefficient.

# EVALUATION OF STOCKING STRATEGIES FOR LAKE STURGEON: TRADEOFFS BETWEEN DEMOGRAPHIC STOCHASTICITY AND GENETIC INTEGRITY

ABSTRACT.-Lake sturgeon were once abundant throughout the Great Lakes basin, but have been reduced to less than one percent of historic levels due to habitat degradation and overexploitation. Current management strategies suggest stocking as a tool to increase abundance, but this strategy also has genetic implications. The objective of this study was to determine the number of individuals that should be stocked in order to maintain long-term persistence of population abundance while maintaining the smallest genetic impact. An individual based model of demographics and genetics was used to explore scenarios which included three initial population sizes, two different supplementation time frames, varying sex ratios, variance in family size, and different percentages of the adult population contributing progeny for supplementation. All stocking scenarios resulted in reduced extinction risk, increased population sizes, increased gene retention, and reduced inbreeding over time. Stocking over long time frames was only necessary for larger population sizes. A skewed sex ratio and unequal family size had little impact on the genetics of populations. Reduced numbers of adults contributing progeny reduced the proportion of genes retained and increased inbreeding. To the extent logistically possible, supplementing larger populations over longer time frames and capturing the greatest number of adults from the population for supplementation purposes are the most important considerations for maintaining genetic integrity.

# INTRODUCTION

Lake sturgeon *Acipenser fulvescens* are a long-lived species that was once abundant throughout the five Great Lakes and the Great Lakes drainage basin in the United States and Canada (Birstein et al. 1997; Hay-Chmielewski and Whelan 1997; Smith and Baker 2005). Currently, lake sturgeon restoration is a priority throughout the Great Lakes basin, where sturgeon have been reduced to less than 1% of historic levels due to habitat degradation, overharvest, and fragmentation of spawning populations (Johnson et al. 1998; Auer 1999; Holey et al. 2000; McQuown et al. 2003). Factors that have contributed to the decline of lake sturgeon in the past continue to contribute to declines in abundance and impede restoration where populations have been extirpated. Therefore, extensive management efforts aimed at restoration and protection of the imperiled lake sturgeon have been developed. Lake sturgeon restoration plans have been completed by Michigan (Hay-Chmielewski and Whelan 1997), Wisconsin (WDNR 2008), and Ontario (OMNR 2006), although considerable uncertainty exists as to the best course of action for lake sturgeon restoration. Stocking, habitat improvement, and reduced exploitation are all part of the overall strategy for lake sturgeon management. However, stocking is often the only option available for rehabilitation; because exploitation is already reduced and habitat improvement is unlikely in the short-term given dams are one of the major habitat impediments. In addition, stocking can result in relatively rapid achievement of population abundance goals as outlined in lake sturgeon management plans.

Stocking is a management tool which has been used for lake sturgeon rehabilitation, either through the use of traditional hatchery methods or through stream-

side rearing practices, a form of supportive breeding (Hay-Chmielewski and Whelan 1997). Supportive breeding generally refers to using local, wild adults to produce progeny (Ryman and Laikre 1991; Ruzzante et al. 2001; Duchesne and Bernatchez 2002). Those progeny are then released back into the wild population from which they came, as opposed to traditional hatchery rearing which involves domesticated brood stock. Supportive breeding increases survival (Ryman and Laikre 1991), and is the type of supplementation generally used for lake sturgeon populations given that adults are much too large and long-lived to easily house in a traditional hatchery setting.

As supportive breeding programs are implemented for lake sturgeon, rehabilitation efforts need to consider reducing genetic risks such as inbreeding (Waples 1994) or loss of unique alleles. Inbreeding occurs when individuals who are closely related mate, and most readily occurs in small populations where random mating often results in breeding among related individuals (Hedrick and Kalinowski 2000; Brook et al. 2002; Keller and Waller 2002). Inbreeding is often thought to result in a decrease in an individual's fitness relative to non-inbred offspring, resulting in inbreeding depression. Inbreeding depression can be manifested in any traits related to fitness (e.g., survival, fecundity; Crnokrak and Roff 1999; Hedrick and Kalinowski 2000; Amos and Balmford 2001), but has been difficult to demonstrate empirically (Newman and Pilson 1997). Lake sturgeon populations in the Great Lakes basin are greatly reduced in numbers, but the genetic diversity of these populations has not yet been depressed (DeHaan et al. 2006). As such, care must be taken when stocking in order to avoid an accrual of inbreeding.

Supportive breeding is thought to result in tradeoffs between abundance, or demographics, and genetic integrity such as inbreeding and gene retention of a population. While supplementation is often focused on increasing population abundance, supplementation can result in the loss of genetic variability and increased inbreeding in a population thereby reducing genetic integrity (Ryman and Laikre 1991; Tessier et al. 1997; Hansen et al. 2000; Lynch and O'Hely 2001; Brown and Day 2002). However, supplementing over multiple generations could lead to increased genetic integrity, increased gene retention and reduced inbreeding accrual, if the population size is larger in the long-term (Wang and Ryman 2001; Jager 2005). Thus, while demographic stochasticity has been argued to be a more influential driving force with respect to probability of extinction than genetic factors, inclusion of both demographic stochasticity and genetics in population management strategies has been advocated (Lande 1988; Lande 1998).

When supplementing a population, several recommendations have been made to minimize genetic impacts. Some of these recommendations include supplementing over long time frames, maintaining a 1:1 sex ratio of males to females contributing progeny, equalizing progeny contributions from families or matings, and using large numbers of adults selected from the population for breeding purposes (Frankham 1995b; Wang et al. 2002; Miller and Kapuscinski 2003; Fraser 2008). Supplementing a population over a longer time frame is thought to result in greater genetic integrity and less generational change in allele frequencies and diversity (Miller and Kapuscinski 2003; Page et al. 2005) because more adults will have the opportunity to contribute genes to progeny. A sex ratio varying from an equal number of males and females has been shown to reduce

the effective population size and increase relatedness (Miller and Kapuscinski 2003; Page et al. 2005) which could lead to increased inbreeding among progeny and an increased risk of losing alleles (Fraser 2008). For example, a skewed sex ratio resulted in increased inbreeding for the Japanese flounder *Paralichthys olivaceus* (Oota and Matsuishi 2005) and reduced genetic diversity for Atlantic salmon *Salmo salar* L. in Spain (Machado-Schiaffino et al. 2006). Unequal family size or high levels of variance in the number of progeny produced per mating pair has been shown to reduce genetic diversity (Allendorf 1993; Page et al. 2005; Fraser 2008). If one family contributes most of the progeny that are released, then relatedness is increased and genes will be lost. Finally, using the largest percentage of mature mates from a population as possible will reduce inbreeding and increase the retention of alleles (Miller and Kapuscinski 2003; Page et al. 2005) because more adults will have the opportunity to contribute progeny and thus genes. Using the greatest number of mature adults will help to prevent loss of rare alleles (Miller and Kapuscinski 2003). Thus, to maintain the highest levels of genetic integrity meaning reduced inbreeding and reduced loss of alleles, a widely held expectation is that supplementation practices with longer time frames, a 1:1 sex ratio, equal family contributions, and using a large percentage of mature fish will result in progeny with relatively higher levels of genetic variability and lower levels of inbreeding.

Given the longevity of lake sturgeon and the difficulty in directly determining the effects of supplementation, I used a modeling approach to explore the consequences of management actions (Boyce 1992). My objective was to determine the number of individuals that should be stocked in order to achieve population abundance goals while maintaining the smallest genetic impact. This was accomplished through the use of an

individual based model of demographics and genetics. Long-term persistence of populations was determined by probability of extinction and mean population size. Genetic integrity was determined by both individual inbreeding coefficients and the percent of genes retained within the population.

Although general advice is available for supplemental stocking practices (Miller and Kapuscinski 2008; Fraser 2008) and specific recommendations have been made for lake sturgeon in the Great Lakes basin (Rob Elliot, personal communication) deviations from such advice is common in practice. Because of this, I explored the genetic and demographic consequences of varying time frame of supplementation, differences in the sex ratio of adults contributing to the stocked progeny, number of progeny per mating released, and percentage of mature adults used for mating. From this model, the numbers of individuals that needed to be stocked to achieve a target population size or to retain a target level of genetic integrity were determined. This exploration of supplementation options will help to determine which stocking strategies are best for the long-term persistence and genetic integrity of lake sturgeon populations.

## METHODS

### *Model Development*

An individual based model was developed that incorporated demographic and genetic processes. Lake sturgeon exhibit a polygamous mating system which was represented based on available data whereby female lake sturgeon mature at approximately 20 years of age and spawn approximately once every 3 years, and male lake sturgeon mature at approximately 15 years of age and spawn approximately every other year (Auer 1999; Bruch 1999; Billard and Lecointre 2001; DeHaan 2003; Nichols

et al. 2003). Once an individual reached the minimum age for maturity then the individual was assigned a random number distributed Uniform(0,1) each year. If that random number was less than the probability of mating, then that individual returned to the river to mate that year. Empirical data from Black Lake, Michigan, lake sturgeon suggest that reproductive success is not related to the length or weight of the adult sturgeon, therefore, the size of individual fish wasn't included in this individual-based model (DeHaan 2003). For each fish returning to spawn, the number of potential mates or batches of offspring, *B*, for each spawning male and female was based on empirical data from Black Lake, MI (Figure B.1; DeHaan 2003). Random numbers of batches were generated using a discrete form of the exponential distribution by:

$$B = 1 + \text{integer}(-2 * \ln(1 - U(0,1)).$$

This distribution represents the number of mates from empirical data (Figure B.1; DeHaan 2003). The batches for the males and females were randomly shuffled, and female batches were paired with male batches. This process allowed random matings between individuals, and allowed individuals to mate with multiple other individuals as has been observed in lake sturgeon. In this model, any batches produced by a male or female without a pair, or mate, were deleted. This distribution allows for a large number of mates as the uniform distribution approaches one; however, the number of mates is decreased based on how the batches are paired with mates. Thus, extremely large numbers of mates is unlikely. The number of progeny, *P*, created (at the end of the summer) from each mating pair, or batch, was generated using an exponential equation of the form:

$$P = \text{integer}(1 * (-\ln(1 - U(0,1))))$$

producing a distribution of numbers of offspring similar to that seen in Black Lake, MI (DeHaan 2003). This distribution was based on the empirical number of progeny per adults as reported by DeHaan (2003; Figure B.2). The empirical distribution was based on a parentage analysis whereby progeny in a sample were assigned to parents. Only about 25% of progeny were assigned to parents, however. Because of this, the empirical number of progeny per parent should be treated cautiously. Because the number of progeny was modified by varying the YOY mortality rate to match observed population sizes and trajectories, this distribution was judged to be appropriate.

The sex of offspring was randomly determined with an equal probability. Following birth, age-specific mortality rates were applied to each individual sturgeon. Mortality rates were set up in the model such that a random number between 0 and 1 was generated for each individual and if that random number was less than the specified level of mortality, then that individual suffered mortality. As such, demographic stochasticity was implicitly incorporated into the model because the death of each individual was randomly determined. The mortality rate from the end of the summer through the winter to the end of the first year is unknown. Therefore, this mortality rate was varied to produce population growth rates that mimic observed growth rates for existing populations. This technique has proven useful in previous studies and provides a means to develop management advice even though parameter values are uncertain (Vaughn and Saila 1976; Hayes and Taylor 1990; Heppell et al. 2000). All parameter values were developed from literature review and further review by local Great Lakes sturgeon experts. Mortality after the first year was set to 0.05 based on Baker (1980). Henceforth, young of the year mortality will be referred to as such, and mortality after the first year

will be referred to simply as "mortality." Young of the year and post young of the year mortality rates have been treated this way by past elasticity studies for other sturgeon species (Gross et al. 2002).

Individual inbreeding coefficients were determined using path analysis of the individual's pedigree implemented in the INBREED procedure available in SAS® (SAS Institute Inc., 2003). From a pedigree, the inbreeding coefficient ($f_x$) for an individual was determined by summing all of the unique paths ($P$) through a common ancestor ($A$) as

$$f_x = \sum_{i-1}^{P} \left[\frac{1}{2}\right]^n (1 + f_A)$$

where n was the number of ancestors in the path and $f_A$ was the inbreeding coefficient of ancestor A (Wright 1922). Lake sturgeon are polyploid with a ploidy level of eight (Blacklidge and Bidwell 1993). Polyploidy is thought to mask inbreeding depression; however this effect has not been shown for other polyploid species such as salmon species *Oncorhynchus sp.* (Wang et al. 2002). Therefore, I assumed polyploidy of lake sturgeon did not affect the accrual of inbreeding or inbreeding depression. This approach allowed for the tracking of overall individual inbreeding levels and accrual of inbreeding rather than specifying certain alleles as deleterious.

Gene retention from the founding population was tracked based on a one locus system whereby each individual at the start of the simulations had two unique, hypothetical alleles at one locus (MacCluer et al. 1986). The hypothetical locus was assumed to be inherited as a Mendelian trait. As mating occurred between individuals, some alleles were lost from the population before they could be passed on to offspring.

Random loss of unique alleles results in genetic differentiation among populations and determines the percentage of founders that have contributed genes to the population. The loss of unique alleles can be described through a technique called gene drop analysis (MacCluer et al. 1986; Hedrick and Miller 1992), which tracks all unique alleles that are retained or lost from the population through time (Haig et al. 1993). Thus, the percent of remaining alleles at the end of each simulation can then be expressed as the number of remaining alleles over the number of unique alleles at the beginning of the simulation which is two times the initial population size.

*Stocking scenarios*

For the baseline stocking scenarios, I ran simulations which represented the ideal situation for maintaining genetic diversity as described by the literature (Frankham 1995; Wang et al. 2002; Miller and Kapuscinski 2003; Page et al. 2005; Fraser 2008). All adult males and females entering the spawning stream were selected for mating and bred in a 1:1 sex ratio. Although this is an idealized situation, it does occur in practice in some situations. Equal numbers of offspring were produced from each mating, and the offspring were randomly assigned sex and one gene from each parent. From these potential progeny, a specific number were randomly supplemented. Although stocking of lake sturgeon in the Great Lakes generally occurs in the fall, my model represented those individuals that survive over winter. If supplementation occurs in the fall, then numbers need to be scaled to reflect overwinter survival. The survival rate from stocking to the following spring has been estimated as 40% for the population in Black Lake, MI (Crossman 2009).

I explored three situations representing different populations in need of supplementation. These scenarios reflect a range of population sizes representative of lake sturgeon in the Great Lakes basin and thus, are relevant to current management. Moreover, a major objective was to determine if different stocking strategies would be required for different starting conditions. In the first scenario, the population was less than the minimum viable population size (MVP, which was defined as a population with approximately a 5% extinction risk over 250 years Shaffer 1981; Boyce 1992). Many populations are below their MVP in the Great Lakes basin, and are in need of rehabilitation to offset their inherent decline (Hay-Chmielewski and Whelan 1997). Moreover, populations less than the MVP are likely at high risk of inbreeding because they are small populations (Hedrick and Kalinowski 2000; Brook et al. 2002; Keller and Waller 2002). The MVP for lake sturgeon in the Great Lakes basin was estimated to be approximately 80 individuals (Schueller and Hayes *in prep*; Chapter 2). Accordingly, I simulated a population size of 50 with a 3% decline in population size over time ($\lambda$=0.97). This scenario will be referred to as "less than MVP".

The second scenario represented populations slightly above MVP but stable. Although such populations have minimal risk of extinction in the short run, they have substantial risk of accruing excess inbreeding. Thus, many management plans have objectives to increase the abundance of lake sturgeon populations in this condition. For this scenario, I simulated populations of 100 individuals with a stable growth rate over time ($\lambda$=1.0). This scenario will be referred to as "brink of MVP".

In the final scenario, I considered larger, declining populations. Although large populations have a lower risk of extinction and accrual of inbreeding, supplementation is

a useful tool to offset declines and prevent the population from eventually reaching MVP. Thus, I simulated populations of 250 individuals with a declining population growth rate over time ($\lambda$=0.97). This scenario will be referred to as "large, declining".

I simulated stocking over two different time frames for each population scenario in order to test the influence of this aspect of supplementation on genetic integrity (Wang et al. 2002; Miller and Kapuscinski 2003; Page et al. 2005). First, stocking occurred over a relatively long time frame of 25 years, which is approximately one generation for lake sturgeon. I termed this strategy "trickle" because in general a relatively small number of young sturgeon would need to be stocked each year. Because the duration of supplementation was large relative to the spawning interval, both males and females would likely be available multiple times over the course of the supplementation program. In the second time frame, stocking occurred for 4 years, which is approximately the time needed to allow all mature individuals to be available for mating at least once. I termed this strategy "pulse" because stocking occurs in a very brief period at the beginning of the simulation. For each scenario, I determined the number of individuals that would need to be stocked to offset declines or increase the population abundance to target levels.

We explored several additional factors to determine their impact on genetic integrity in each supplementation scenario. These factors included: different sex ratios, unequal family sizes, and reduced numbers of adults sampled for breeding purposes (Wang et al. 2002; Miller and Kapuscinski 2003; Page et al. 2005; Fraser 2008). One level of stocking was chosen for each population size and time frame stocked (6 total), and each of the following scenarios was run against those six baseline scenarios to evaluate the impact on gene retention and inbreeding accrual. For each population size

and time frame stocked, the sex ratio was varied from 1:1 and was allowed to range up to 5:1 and 10:1 (males per female). Thus, for a sex ratio of 10:1, up to 10 males could create progeny with one female. The simulation represents a female's eggs being divided into 10 lots where one male fertilizes each lot. This is the recommended strategy when mating a female with more than one male (Miller and Kapuscinski 2003). Eggs from each female were broken into lots, and then males were randomly paired with lots, with any excess males not contributing to reproduction. This allowed for a sex ratio of up to 10 males per female. Because males spawn at a younger age and more frequently, in practice more males are often available for supplementation purposes. However, the number of males and females available each year were random in my simulation (and in nature). Thus, sex ratios were designed to be a constraint rather than an exact number, and in some years could be as low as 1:1 in practice.

For each population size and time frame stocked, unequal family contributions were tested by allowing up to a fivefold difference in the number of progeny per mating. For each mating, the number of progeny was randomly determined from a uniform distribution where the largest number of progeny that could be produced was five times the smallest number of progeny that could be produced. Thus, a range in progeny production up to a fivefold difference could occur. Finally, for each population size and time frame stocked, decreased numbers of adults contributing progeny was tested by only sampling 20% of the mature adult population for breeding purposes.

Lake sturgeon have been shown to reproduce naturally even if their gametes have been collected for supplementation purposes (Crossman 2008); therefore, all adults used

to create progeny for supplementation purposes were also allowed to reproduce naturally in the model.

*Simulations and outputs*

A simulation duration of 250 years was used as this allowed time for transient responses to dissipate. For each scenario, 250 simulations were run to provide precise estimates of the mean response and the variance across the factors explored. A yearly time step was used in all simulations. The percent of extinct populations, mean final abundance, average individual inbreeding coefficient in the final year, and percent of unique alleles retained were recorded for each simulation run of 250 years. The mean final abundance was the average abundance including zeroes for those populations that went extinct. The average individual inbreeding coefficient was the average inbreeding coefficient for progeny produced in the final year. No uncertainty estimates could be provided for the inbreeding coefficients because only the mean was an output for the model. The average percent of unique alleles retained was the average percent of genes retained including zeroes for those populations that went extinct. For the percent of extinct populations and the average percent of genes retained, confidence intervals were calculated as:

$$(\text{estimate} \pm 2*SE)*100$$

where the SE = (pq/n) ^ (1/2), p = (percent of extinct populations or genes retained/100), q = 1-p, and n=number of simulations. A confidence interval for the mean final abundance was given as the estimate ± 2*SE where the SE = ($\sigma$/n) ^ (1/2). The mean final abundance and the average percent of genes retained were used as opposed to the median because the mean and median were very similar in value, even with zeroes

included. Simulations were assumed to have current environmental and demographic conditions, which remained constant into the future. For all of the outputs, functions were fitted to smooth the relationship between the output and the total number stocked over the supplementation period. This was then used to estimate the number of individuals to stock in order to attain a specific benchmark (e.g., a population size of 250, inbreeding level below 0.01). The total number of individuals supplemented to reach a target was the number of years in the time frame multiplied by the number of individuals each year. This should be useful for lake sturgeon managers, who will be able to determine the approximate number of individuals that would need to be stocked in order to achieve a defined goal or objective.

## RESULTS

As intended in the baseline simulations without stocking, mean abundance for the less than MVP and large, declining scenarios declined from the starting population size over the 250 year time frame. Mean abundance in the brink of MVP scenario remained near the starting value of 100. In the two declining populations, a substantial proportion of the populations went extinct, while in the brink of MVP scenario, no populations went extinct (Table 3.1). The percent of genes retained was highest in the brink of MVP scenario, followed the less than MVP scenario, and finally by large, declining populations (Table 3.1). In all scenarios, the mean inbreeding coefficient increased over time, reaching approximately 0.13 to 0.14 in the two scenarios with declining populations, and 0.068 in the brink of MVP scenario.

Stocking decreased the extinction risk to zero with only a few individuals stocked for all of the scenarios, thus no table was provided. Stocking increased the mean

abundance for all scenarios, with higher stocking rates producing higher mean ending populations (Table 3.2). Although the number of sturgeon that needed to be stocked per year was higher under the pulse stocking strategy than the trickle stocking strategy to achieve a specified mean ending population, the total number of sturgeon stocked over the course of the entire stocking program was similar (Table 3.2). For example, under the less than MVP scenario, to reach an abundance of 250 individuals, approximately 475 individuals would need to be stocked over the course of either the pulse or trickle strategies (Table 3.2). Stocking also increased the percent of genes retained (Table 3.3), and decreased the mean final inbreeding coefficient (Table 3.4). As with mean population abundance, the pulse stocking strategy required more individuals stocked per year than the trickle strategy, but the total number stocked was in most cases similar for the duration of the stocking program to achieve a specified target (Table 3.3; Table 3.4). Two exceptions to this were for large, declining populations, where the trickle strategy required somewhat fewer individuals stocked over the course of the entire stocking program when compared to the pulse scenario to retain an equivalent percentage of genes (Table 3.3), and for the mean inbreeding coefficient within the brink of MVP scenario where the trickle strategy required substantially more individuals stocked over the course of the entire stocking program (Table 3.4). For example, to maintain a population below an average inbreeding coefficient level of 0.03, 925 individuals would need to be stocked over the course of the time period for the trickle strategy while only 74 would need to be stocked for the pulse strategy (Table 3.4).

Skewing the sex ratio toward a greater males to female ratio did not substantially affect the demographic characteristics of the stocked population or the genetics of the

population for all of the scenarios when compared to a 1:1 sex ratio. All sex ratios explored resulted in increased population sizes, more genes retained, and reduced inbreeding when compared to no stocking. For all scenarios, skewing the sex ratio did not result in large differences in the percent of genes retained or the accrual of inbreeding for either the pulse or trickle time frames (Table 3.5).

Unequal family sizes, so that some families had more progeny than others, did not affect the demographic characteristics of the stocked population and did not significantly affect the genetics of the population for all of the scenarios when compared to equal family sizes. Unequal family sizes still resulted in increased population size, more genes retained, and reduced inbreeding when compared to no stocking. For all scenarios, unequal family sizes did not result in large differences in the percent of genes retained or the accrual of inbreeding for either the pulse or trickle time frames (Table 3.6).

Decreasing the percent of adults contributing progeny for stocking did not affect the demographic characteristics relative to stockings where all returning adults contributed gametes, but did require more individuals be produced from each mating to achieve abundance goals. When the percent of adults contributing progeny was reduced to 20% of the spawning run, stocking still resulted in increased population size, more genes retained, and reduced inbreeding when compared to no stocking. In the pulse stocking strategy, no discernable impact of using a lower percentage of the spawning run was evident for gene retention or final mean inbreeding (Table 3.7). Reducing the percent of adults contributing progeny for stocking purposes under the trickle strategy resulted in a decreased percent of genes retained and a coincident increase in the inbreeding coefficient (Table 3.7).

# DISCUSSION

Overall, stocking was beneficial under all scenarios explored in this analysis both demographically and genetically. Without stocking, lake sturgeon populations were at risk of extinction, had smaller population sizes, reduced gene retention, and increased inbreeding accrual. With stocking, the extinction risk was considerably decreased, with nearly all populations remaining extant even with small numbers of individuals being stocked. Stocking is generally suggested as a management tool in order to avoid extinction and increase abundance (Ryman and Laikre 1991). In these scenarios, stocking greatly decreased the risk of extinction and allowed for much larger population sizes when compared to scenarios with no stocking. However, stocking has been cautioned against because of the possibility of inbreeding, inbreeding depression, and reduced gene retention (Ryman and Laikre 1991; Tessier et al. 1997). For these scenarios with stocking, gene retention increased and inbreeding accrual decreased which is in contrast to expected results given much of the prevailing advice. In my simulations, I considered two situations where the population was experiencing a decline. As shown in my baseline simulations without stocking, declining populations had a rapid loss of genetic diversity and higher levels of inbreeding. As such, stocking was beneficial because losses of genetic integrity due simply to greatly reduced population size were offset. Thus, it is important to consider not just the final amount of inbreeding and loss of genes, but to determine how this relates to how these measures of genetic integrity would change without stocking (i.e., with continued population decline).

The most appropriate stocking strategy has been found to be dependent upon the population size and population trajectory (Duchesne and Bernatchez 2002). All of the

populations explored in my study were relatively small and declining, and all benefited both demographically and genetically from supplementation using the best genetic practices recommended (Wang et al. 2002; Miller and Kapuscinski 2003; Page et al. 2005; Fraser 2008). Improved supplementation practices can reduce genetic consequences of supplementation (Tessier et al. 1997). Eldridge and Killebrew (2008) found non-significant decreases in genetic integrity with the implementation and expansion of a supplementation program for Chinook salmon *Oncorhynchus tshawytscha* in the Stillaguamish River over several generations. All three plausible lake sturgeon population scenarios resulted in improved demographic and genetic outputs with stocking, which is most likely due to increased population sizes over time. Jager (2005) predicted higher gene retention with supplementation using a demographic and genetic individual based model for white sturgeon *Acipenser transmontanus*. Supplementing over multiple generations could lead to increased genetic integrity, if the population size is larger in the long-term (Wang and Ryman 2001; Jager 2005). Additionally, the life history strategy of the lake sturgeon could have contributed to the increased genetic integrity with supplementation. Given that the probability of survival to maturity is low for each individual, the probability that two related individuals would survive and mate to produce progeny is likely low. Also, males and females reach maturity at different ages and reproduce at different intervals (Hay-Chmielewski and Whelan 1997), which would reduce the probability that an individual would encounter a related individual on the spawning grounds. Thus, with larger population sizes in the long-term and without mating between related individuals due to life history characteristics, the accrual of

inbreeding would be lower and gene retention would be higher than in species with different life histories.

Supplementing over a 25-year time frame was not found to be better for avoiding extinction, attaining a target mean population size, retaining genes, or for reducing inbreeding than stocking over a 4-year time frame when using recommended genetic practices (Wang et al. 2002; Miller and Kapuscinski 2003; Page et al. 2005; Fraser 2008) for less than MVP and brink of MVP, but not for large, declining. If the total numbers of individuals stocked over the two time frames were approximately equal for the less than MVP and brink of MVP scenarios, the two strategies (pulse and trickle) were equally as effective. However, for the brink of MVP scenario, greater numbers of individuals needed to be stocked with the trickle scenario in order to be below a desired level of inbreeding. Thus, the genetic recommendation of stocking over a longer time frame (Wang et al. 2002; Miller and Kapuscinski 2003; Page et al. 2005) may not be necessary for smaller population sizes given the scenarios explored, especially given the financial constraints of most management agencies. Thus, the pulse strategy is recommended as a means to more rapidly achieve conservations goals, and would most likely cost less because of the shorter time frame needed for collection of gametes on rivers. For large, declining populations, supplementing using the trickle scenario resulted in a greater percent of genes retained over the long-term than supplementing using the pulse scenario. Also, for the large, declining populations, greater numbers of individuals needed to be stocked under the pulse scenario in total in order to achieve the desired mean final population size, percent of genes retained, and mean final inbreeding coefficient. Thus, the genetic recommendation of stocking over a longer time frame (Wang et al. 2002;

Miller and Kapuscinski 2003; Page et al. 2005) may be more important for larger populations in order to retain larger percentages of genes.

Skewing the sex ratio and unequal family sizes did not lead to an impact in either the inbreeding coefficient or the percent of genes retained for populations less than MVP, on the brink of MVP, or for large, declining populations under the conditions explored. This is not what was expected given the genetic guidelines set out for effective stocking practices (Wang et al. 2002; Miller and Kapuscinski 2003; Page et al. 2005; Fraser 2008). However, this may be simply due to much larger population sizes in the long-term given that supplementation could lead to increased genetic integrity, if the population size is larger in the long-term (Wang and Ryman 2001; Jager 2005). This is in contrast to findings by Oota and Matsuishi (2005) who found that skewing the sex ratio, from 1:1, of adults contributing progeny through stocking practices resulted in increased inbreeding coefficients using data for the Japanese flounder. However, this is not in contrast to findings by Jager (2005) who used an individual based model of demographics and genetics and who found that unequal family sizes did not affect the genetic integrity of white sturgeon populations. These findings may also be due to nearly all adults still having the opportunity to spawn and contribute progeny to the future during these simulations given that the percent of mature adults contributing progeny was held constant. Thus, even though the sex ratio was skewed or the family sizes were unequal, most adults were still able to contribute progeny and thus genes thereby reducing the impact of sex ratio and family size on the retention of genes and the accrual of inbreeding. Finally, these findings may also be due to low probabilities of surviving to adulthood and encountering a related individual to mate with. This may be especially

true for the two scenarios that were declining, and would result in higher gene retention and lower inbreeding accrual over time.

For the skewed sex ratios, gametes were mixed in a way that would not allow for sperm competition. Often, stocking for management purposes uses milt that has been mixed or milt is sequentially added to eggs (Campton 2004; Wedekind et al. 2007). Sperm competition is then possible whereby one male's sperm may fertilize a large proportion of the eggs available (Miller and Kapuscinski 2003). This dissertation does not address that issue, although, I concur with recommendations (Wedekind et al. 2007) to avoid mixing of gametes prior to fertilization to eliminate the possibility of sperm competition which could increase relatedness among progeny and result in gene loss over time.

The greater the percent of mature adults contributing progeny to the supplemented population, the less likely inbreeding will accrue and the greater the retention of genes for the trickle scenarios explored. This finding is what would be expected given the recommended genetic practices for supplementation (Wang et al. 2002; Miller and Kapuscinski 2003; Page et al. 2005). Duchesne and Bernatchez (2002) found that the size of the hatchery population was the most pivotal parameter controlling inbreeding. The greater the number of adults contributing progeny in a hatchery setting, the lower the risk of inbreeding accrual (Duchesne and Bernatchez 2002). Given these results, managers should collect as many mature adults as possible for mating purposes. This practice should help to reduce inbreeding accrual and help to retain genes in the population.

Based on the high levels of coancestry (probability that genes are identical by descent between two individuals; Bila et al. 1999; Perrin and Mazalov 1999; Wang and Ryman 2001) between progeny produced for supplementation purposes, the mean inbreeding coefficient was expected to be much higher with supplementation as compared to no supplementation. Coancestry increases the risk of inbreeding with mating in future generations (Bila et al. 1999; Perrin and Mazalov 1999). My results are counterintuitive, but are most likely a function of the initial population sizes that were explored and the life history of the lake sturgeon. Because the population sizes that were explored were small and declining, the chance of surviving to reproductive age and mating with a related individual who has also survived to reproductive age is low. Thus, inbreeding would not accrue even though the coancestry of individuals supplemented into the population may be relatively high. Male and female lake sturgeon also do not reach sexual maturity at the same age or mate at the same interval, therefore, the probability of encountering a related individual may be low because of the life history of the species. Again, this would lead to lower levels of inbreeding accrual than one would expect given coancestry levels.

Rearing individuals in captivity may result in unwanted consequences when the individuals are released into the wild. With captive rearing, individuals with specific traits may be inadvertently selected over others, and those traits may not be advantageous in the wild (e.g. large body size, run time; Lynch and O'Hely 2001). With captive rearing, selection may be decreased or changed to select for traits that are not advantageous in the wild, for instance in situations with reduced predation (Lynch and O'Hely 2001). However, this model did not explore the effects of domestication, and I

assume limited domestication selection on lake sturgeon while in captivity given the short time frame of rearing.

This model assumed that all supplemented progeny had the same demographic parameters as the naturally produced progeny in the future. All supplemented progeny had the same mortality rates and produced progeny at the same rate as progeny produced in the wild. Many studies show that mortality rates are higher for stocked fish and that stocked fish produce lower numbers of offspring than their wild counterparts (Miller and Kapuscinski 2003; Araki et al. 2007a; Araki et al. 2007b). However, the differences that result in survival and future reproductive success from supplemented versus stocking using broodstock are difficult to distinguish, and supplemented individuals may not experience the same mortality and reduced reproductive success of individuals stocked using broodstock (Miller and Kapuscinski 2003). For example, Araki et al. (2007b) found that supplemented fish didn't have lower reproductive success when compared to wild fish. Given that the lifetime performance of lake sturgeon produced by supplemental stocking is unknown relative to naturally produced individuals, experiments evaluating this possibility would be very valuable.

Overall, these results suggest that demographic stochasticity may be the more important factor with respect to retaining genes and populations. Lande (1988) advocated that demographic stochasticity was the more important force in extinction processes for small population sizes. Generally, these populations faced an extinction risk if they were not supplemented, and given that supplementation did not result in large decreases in gene retention or increases in inbreeding using the recommended genetic

practices, avoiding extinction resulting from demographic stochasticity seemed to be the more pressing issue.

## MANAGEMENT IMPLICATIONS

Depending upon the population size and trajectory, different numbers of individuals need to be stocked in order to move a population towards rehabilitation. For lake sturgeon populations less than MVP or on the brink of MVP, relatively few individuals need to be stocked in order to maintain both positive population trajectories and reduced genetic impacts. For larger, declining populations, more individuals need to be stocked if a short time frame is used. How many fish should be stocked is dependent upon the target, when you stock, and overwinter mortality rates. For example, the number that needs to be stocked in the fall each year is the recommended stocking number (which accounts for over winter mortality) divided by the actual over winter survival for the population. If you wanted to supplement a population below MVP under the pulse scenario, so that the population size in the long-term was on average 500 individuals, and if the over winter survival was 0.40% (Crossman et al. 2009), then you would need to stock (244/0.40=610) 610 individuals in the fall each year (Table 3.2). This strategy should be used when determining how many to stock to achieve specific population sizes, percent of genes retained, and mean final inbreeding coefficients.

Based on the scenarios explored, if all recommended genetic practices cannot be followed, some recommendations appear more important than others with respect to maintaining genes and reducing inbreeding. First, if supplementing a larger population, supplementing over a longer time frame is recommended for the retention of genes over the long term. Second, capturing the greatest number of adults from the population for

supplementation purposes seems to be the most crucial recommendation for retaining genes and reducing inbreeding accrual. Third, sex ratio and family size variation have smaller effects on the genetics of populations, thus, following these genetic guidelines is less crucial.

Many lake sturgeon populations are in need of rehabilitation, and supplementation is one potential management tool. My analyses show that supplementing populations can increase the retention of unique genes and decrease inbreeding, and achieve target population sizes with reduced risks of extinction when compared to not supplementing the population. However, other limitations, such as reduced spawning habitat availability, may influence the need to stock if the limitation can't be remedied. Thus, this study has provided advice on how many to stock and what genetic guidelines are important, but it is up to the managers to determine goals and objectives for populations of interest and then take actions to meet those goals and objectives.

Table 3.1. The percent of extinct populations (± 2 SE), percent of genes retained (± 2 SE), and mean final inbreeding coefficient for baseline conditions with no stocking at the end of 250 years.

| Scenario | Percent of extinct populations | Percent of genes retained | Mean final inbreeding coefficient |
|---|---|---|---|
| Less than MVP | 34.4 (30.1, 38.6) | 4.64 (2.76, 6.52) | 0.1388 |
| Brink of MVP | 0 (0, 0) | 10.05 (7.36, 12.74) | 0.0683 |
| Large, declining | 22.4 (18.7, 26.1) | 0.89 (0.05, 1.74) | 0.1303 |

Table 3.2. The number stocked per year under the trickle scenario, the total stocked under the trickle scenario, the number stocked per year under the pulse scenario, and the total stocked under the pulse scenario for each of the population types in order to achieve the desired mean final population size. Numbers stocked per year were obtained using interpolation using a linear equation, and total stocked was estimated as the number stocked per year before rounding times the number of years stocked. The first line under each scenario is the baseline with no stocking.

| Scenario | Mean final population size | Number stocked per year-Trickle | Trickle Total | Number stocked per year-Pulse | Pulse Total |
|---|---|---|---|---|---|
| Less than MVP-no stocking | 22 | 0 | 0 | 0 | 0 |
| Less than MVP | 50 | 2 | 60 | 18 | 70 |
| | 100 | 7 | 166 | 43 | 171 |
| | 150 | 11 | 273 | 68 | 272 |
| | 200 | 15 | 380 | 93 | 372 |
| | 250 | 19 | 487 | 118 | 473 |
| | 350 | 28 | 700 | 169 | 674 |
| | 500 | 41 | 1,020 | 244 | 977 |
| Brink of MVP-no stocking | 110 | 0 | 0 | 0 | 0 |
| Brink of MVP | 150 | 2 | 53 | 17 | 66 |
| | 200 | 6 | 141 | 38 | 152 |
| | 250 | 9 | 230 | 60 | 238 |
| | 350 | 16 | 406 | 102 | 410 |
| | 500 | 27 | 671 | 167 | 667 |
| Large, declining-no stocking | 6 | 0 | 0 | 0 | 0 |
| Large, declining | 50 | 47 | 1,183 | 365 | 1,461 |
| | 100 | 105 | 2,617 | 772 | 3,089 |
| | 150 | 162 | 4,051 | 1,179 | 4,717 |
| | 200 | 219 | 5,485 | 1,586 | 6,345 |
| | 250 | 277 | 6,919 | 1,993 | 7,973 |
| | 350 | 391 | 9,786 | 2,807 | 11,228 |
| | 500 | 564 | 14,088 | 4,028 | 16,112 |

Table 3.3. The number stocked per year under the trickle scenario, the total stocked under the trickle scenario, the number stocked per year under the pulse scenario, and the total stocked under the pulse scenario for each of the population types in order to achieve the desired percent of genes retained. Numbers stocked per year were obtained using interpolation using a power function, and total stocked was estimated as the number stocked per year before rounding times the number of years stocked. The first line under each scenario is the baseline with no stocking.

| Scenario | Percent of genes retained | Number stocked per year-Trickle | Trickle Total | Number stocked per year-Pulse | Pulse Total |
|---|---|---|---|---|---|
| Less than MVP-no stocking | 4.64% | 0 | 0 | 0 | 0 |
| Less than MVP | 5% | 0 | 6 | 1 | 4 |
| | 10% | 2 | 40 | 11 | 45 |
| | 25% | 11 | 265 | 68 | 272 |
| | 35% | 20 | 496 | 119 | 478 |
| | 50% | 38 | 944 | 212 | 847 |
| Brink of MVP-no stocking | 10.05% | 0 | 0 | 0 | 0 |
| Brink of MVP | 10% | 0 | 0 | 1 | 2 |
| | 25% | 16 | 406 | 100 | 400 |
| | 35% | 30 | 759 | 181 | 724 |
| | 50% | 54 | 1,352 | 313 | 1,253 |
| Large, declining-no stocking | 0.89% | 0 | 0 | 0 | 0 |
| Large, declining | 5% | 36 | 906 | 296 | 1,184 |
| | 10% | 96 | 2,394 | 736 | 2,944 |
| | 25% | 324 | 8,105 | 2,405 | 9,622 |
| | 35% | 503 | 12,570 | 3,705 | 14,820 |
| | 50% | 798 | 19,955 | 5,851 | 23,404 |

Table 3.4. The number stocked per year under the trickle scenario, the total stocked under the trickle scenario, the number stocked per year under the pulse scenario, and the total stocked under the pulse scenario for each of the population types in order to achieve the desired mean final inbreeding coefficient. Numbers stocked per year were obtained using interpolation using a Weibull function, and total stocked was estimated as the number stocked per year before rounding times the number of years stocked. The first line under each scenario is the baseline with no stocking.

| Scenario | Mean final inbreeding coefficient | Number stocked per year-Trickle | Trickle Total | Number stocked per year-Pulse | Pulse Total |
|---|---|---|---|---|---|
| Less than MVP-no stocking | 0.1388 | 0 | 0 | 0 | 0 |
| Less than MVP | 0.125 | 0 | 12 | 3 | 13 |
| | 0.100 | 3 | 68 | 17 | 69 |
| | 0.075 | 8 | 190 | 45 | 181 |
| | 0.050 | 18 | 450 | 100 | 401 |
| | 0.025 | 44 | 1,100 | 227 | 908 |
| Brink of MVP-no stocking | 0.0683 | 0 | 0 | 0 | 0 |
| Brink of MVP | 0.050 | 0 | 4 | 4 | 14 |
| | 0.040 | 3 | 83 | 9 | 36 |
| | 0.030 | 37 | 925 | 18 | 74 |
| | 0.025 | 111 | 2,778 | 26 | 104 |
| Large, declining-no stocking | 0.1303 | 0 | 0 | 0 | 0 |
| Large, declining | 0.125 | 0 | 0 | 4 | 17 |
| | 0.100 | 0 | 8 | 31 | 125 |
| | 0.075 | 3 | 74 | 102 | 409 |
| | 0.050 | 16 | 393 | 270 | 1,082 |
| | 0.025 | 82 | 2,038 | 739 | 2,954 |
| | 0.010 | 310 | 7,744 | 1,703 | 6,811 |

Table 3.5. The percent of genes retained (±2 SE) and mean final inbreeding coefficient for skewed sex ratios for each population size and stocking strategy. For each initial population size or scenario, baseline outputs are included for no stocking.

| Scenario | Stocking strategy | Sex ratio (Males:Females) | Percent of genes retained | Mean final inbreeding coefficient |
|---|---|---|---|---|
| Less than MVP | No Stocking | - | 4.64 (2.76, 6.52) | 0.1388 |
| | Pulse | 1:1 | 13.85 (9.47, 18.22) | 0.0975 |
| | | 5:1 | 13.63 (9.29,17.97) | 0.0943 |
| | | 10:1 | 14.25 (9.83,18.67) | 0.0893 |
| | Trickle | 1:1 | 15.62 (11.03, 20.21) | 0.0804 |
| | | 5:1 | 15.89 (11.26, 20.51) | 0.0881 |
| | | 10:1 | 15.64 (11.04, 20.23) | 0.0819 |
| Brink of MVP | No Stocking | - | 10.05 (7.36, 12.74) | 0.0683 |
| | Pulse | 1:1 | 13.51 (9.19, 17.83) | 0.0565 |
| | | 5:1 | 12.96 (8.72, 17.21) | 0.0565 |
| | | 10:1 | 13.84 (9.47, 18.21) | 0.0558 |
| | Trickle | 1:1 | 15.85 (11.23, 20.47) | 0.0482 |
| | | 5:1 | 14.98 (10.47, 19.50) | 0.0504 |
| | | 10:1 | 15.43 (10.86, 20.00) | 0.0486 |
| Large, declining | No Stocking | - | 0.89 (0.05, 1.74) | 0.1303 |
| | Pulse | 1:1 | 4.77 (2.08, 7.47) | 0.0425 |
| | | 5:1 | 4.99 (2.23, 7.74) | 0.0405 |
| | | 10:1 | 4.70 (2.03, 7.38) | 0.0503 |
| | Trickle | 1:1 | 17.27 (12.49, 22.06) | 0.013 |
| | | 5:1 | 17.11 (12.35, 21.88) | 0.0144 |
| | | 10:1 | 16.62 (11.91, 21.33) | 0.0154 |

Table 3.6. The percent of genes retained (±2 SE) and mean final inbreeding coefficient for unequal family sizes for each population size and stocking strategy. None indicates equal family size, and up to 5x indicates that family size could vary up to five times higher than the baseline family size. For each initial population size or scenario, baseline outputs are included for no stocking.

| Scenario | Stocking strategy | Variance in family size | Percent of genes retained | Mean final inbreeding coefficient |
|---|---|---|---|---|
| Less than MVP | No Stocking | - | 4.64 (2.76, 6.52) | 0.1388 |
| | Pulse | None | 13.85 (9.47, 18.22) | 0.0975 |
| | | Up to 5x | 12.90 (8.66, 17.14) | 0.0951 |
| | Trickle | None | 15.62 (11.03, 20.21) | 0.0804 |
| | | Up to 5x | 15.95 (11.32, 20.58) | 0.0845 |
| Brink of MVP | No Stocking | - | 10.05 (7.36, 12.74) | 0.0683 |
| | Pulse | None | 13.51 (9.19, 17.83) | 0.0565 |
| | | Up to 5x | 13.73 (9.38, 18.09) | 0.0531 |
| | Trickle | None | 15.85 (11.23, 20.47) | 0.0482 |
| | | Up to 5x | 14.75 (10.27, 19.24) | 0.0487 |
| Large, declining | No Stocking | - | 0.89 (0.05, 1.74) | 0.1303 |
| | Pulse | None | 4.77 (2.08, 7.47) | 0.0425 |
| | | Up to 5x | 5.04 (2.27, 7.81) | 0.0474 |
| | Trickle | None | 17.27 (12.49, 22.06) | 0.0130 |
| | | Up to 5x | 17.51 (12.71, 22.32) | 0.0119 |

Table 3.7. The percent of genes retained (±2 SE) and mean final inbreeding coefficient for reduced numbers of adults used for mating purposes for each population size and stocking strategy. One hundred percent indicates all adults contributing progeny for stocking purposes, and 20% indicates only 20% of mature adults contributing progeny for stocking purposes. For each initial population size or scenario, baseline outputs are included for no stocking.

| Scenario | Stocking Strategy | Percentage of adult contribution | Percent of genes retained | Mean final inbreeding coefficient |
|---|---|---|---|---|
| Less than MVP | No Stocking | - | 4.64 (2.76, 6.52) | 0.1388 |
| | Pulse | 100% | 13.85 (9.47, 18.22) | 0.0975 |
| | | 20% | 13.24 (8.96, 17.53) | 0.0921 |
| | Trickle | 100% | 15.62 (11.03, 20.21) | 0.0804 |
| | | 20% | 13.37 (9.07, 17.68) | 0.0886 |
| Brink of MVP | No Stocking | - | 10.05 (7.36, 12.74) | 0.0683 |
| | Pulse | 100% | 13.51 (9.19, 17.83) | 0.0565 |
| | | 20% | 13.57 (9.24, 17.90) | 0.0562 |
| | Trickle | 100% | 15.85 (11.23, 20.47) | 0.0482 |
| | | 20% | 14.92 (10.42, 19.43) | 0.0490 |
| Large, declining | No Stocking | - | 0.89 (0.05, 1.74) | 0.1303 |
| | Pulse | 100% | 4.77 (2.08, 7.47) | 0.0425 |
| | | 20% | 4.53 (1.90, 7.16) | 0.0465 |
| | Trickle | 100% | 17.27 (12.49, 22.06) | 0.0130 |
| | | 20% | 15.94 (11.31, 20.57) | 0.0156 |

# CONCLUSIONS

Overall, this dissertation explored which population parameters are important for long-term persistence and the likely fate of populations with and without management intervention. If managers focus on the population parameters that will have the most impact on lake sturgeon persistence and genetic integrity, then managers should focus on reducing post YOY mortality rates. The estimated MVP range (estimated both with and without inbreeding depression) of 80-150 individuals provides guidance for populations at high risk of extinction, but the sensitivity of population outputs to changes in the baseline parameters needs to be accounted for. Without some form of management, populations below this level are unlikely to persist. Simulations indicate that stocking even small numbers of fingerlings can offset population declines, leading to greater abundance and genetic integrity. For the scenarios explored, stocking is generally beneficial for both abundance and genetic integrity, especially for small and declining populations.

The sensitivity analysis of the individual based model demonstrated that lake sturgeon population persistence and genetic integrity was hypersensitive to changes in most of the population parameters including young of the year mortality, mortality, age at first maturation for females, and the probability of mating for females. Changes in these parameters were essentially driving population outputs. The post YOY mortality rate was the most sensitive of all of the population parameters for the outcomes of interest. Lake sturgeon persistence was relatively insensitive to both age at first maturation for males and the probability of mating for males. Changes in these parameters had relatively little impact on population outputs.

Sensitivity was not linear for any of the outputs across the range of plausible values explored. In many previous sensitivity analyses, all of the model parameters are held at a nominal value and one parameter at a time is changed by ±10% (or less) to determine which parameters most strongly influence model predictions (McCarthy et al. 1996; Essington 2003). However, in my sensitivity analyses, I varied model inputs across a broader range of values, which helped to delineate the shape of the sensitivity curve, depicting a richer picture of model sensitivity. This sensitivity analyses helped to determine which parameters were most sensitive and in what range those parameters have the greatest influence on model outcomes.

I found that the use of any sensitivity analysis information for species management and conservation is dependent upon the initial population sizes that are explored. The outputs for the model were found to have joint sensitivity meaning that the outputs were related to one another. The joint sensitivity between final mean inbreeding and percent of genes retained indicated that for a given level of inbreeding, the percent of genes retained for the initial population size of 200 was much less than for the initial population size of 50. The differences in the functions for the two initial population sizes may be because the initial population size of 50 was more prone to extinction than the initial population size of 200. Generally, the differences observed between the two population sizes indicated that sensitivities were dependent upon initial population size. Therefore, parameter perturbation (for example, reduced mortality rate) will have a different demographic and genetic effect depending upon the population size, which will be important for management.

For naturally reproducing populations, without management, the minimum viable population size for lake sturgeon with no inbreeding depression was estimated at approximately 80 individuals with a 5% chance of extinction over 250 years for the baseline parameters used. The MVP allows managers to estimate extinction risks and identify populations for conservation (Shaffer 1981), but should acknowledge how the results of the sensitivity analysis would affect the estimate of MVP. This work is unique because few MVP's have been determined for fish species; only 9 of 287 MVP's were for fish species in the original dataset compiled for a large meta-analysis by Traill et al. (2007) and only 1 of 102 for a meta-analysis by Reed et al. (2003b).

Minimum viable population size was also estimated for several possible inbreeding depression scenarios. Some inbreeding depression scenarios explored in this analysis resulted in little or no change to the MVP required to maintain persistence when compared to the scenario without inbreeding depression. With inbreeding depression, the MVP was the same as the MVP with no inbreeding depression for post YOY viability for all thresholds. With gradual inbreeding depression for both YOY viability and progeny number, the MVP increased only slightly to 85. However, some inbreeding depression scenarios explored did result in changes to the predicted MVP required to maintain persistence. Inbreeding depression on progeny number resulted in an MVP of 150, nearly twice the MVP with no inbreeding depression. With threshold inbreeding on YOY viability, the MVP increased with decreasing thresholds. Thus, I have predicted that inbreeding depression can increase extinction risk, but the impact of inbreeding depended upon which life stage was influenced by inbreeding depression.

Much discussion has occurred over whether demographic stochasticity or genetic stochasticity is more important or has a greater influence on long-term persistence (Lande 1988; Young 1991; Frankham 1995a; Spielman et al. 2004). My study doesn't provide a clear picture of whether demographic or genetic stochasticity dominates extinction risk, because some estimated MVPs did change with the incorporation of inbreeding depression and some didn't. Based on the scenarios in my study, whether demographic or genetic stochasticity dominated the determination of MVP and extinction risk was dependent upon how inbreeding depression was expressed (threshold versus gradual) in the model and how fitness was reduced.

In many cases, management of lake sturgeon is likely to proceed using supplementation as the primary strategy because of impediments to habitat improvement. Recently, stocking has been cautioned against because of the possibility of inbreeding and inbreeding depression (Wang et al. 2002). However, for the scenarios explored, my results show that stocking reduced extinction risk, increased population size, increased gene retention, and decreased inbreeding accrual for all of the scenarios explored when compared to no stocking. While supplementation is expected to increase abundance and reduce extinction risk, supplementation is not expected to increase gene retention nor reduce inbreeding accrual. The genetic integrity of supplemented populations was thought to benefit because stocking reduced extinction risk and resulted in larger population sizes in the long-term. Some evidence suggests that this may be the case, if population sizes are larger in the future (Wang and Ryman 2001).

Supplementing over a 25-year time frame was not found to be better for avoiding extinction, attaining a target mean population size, retaining genes, or for reducing

inbreeding than stocking over a 4-year time frame when using recommended genetic practices (Wang et al. 2002; Miller and Kapuscinski 2003; Page et al. 2005) for population sizes less than MVP or on the brink of MVP. If the total numbers of individuals stocked over the two time frames were approximately equal for the less than MVP and brink of MVP scenarios, the two strategies were equally as effective for the scenarios explored. Thus, the genetic recommendation of stocking over a longer time frame (Wang et al. 2002; Page et al. 2005) may not be necessary for smaller population sizes, especially given the financial constraints of most management agencies. For larger, declining populations, supplementing using the 25-year time frame resulted in a greater percent of genes retained over the long-term than supplementing using the shorter time frame. Thus, the genetic recommendation of stocking over a longer time frame (Wang et al. 2002; Miller and Kapuscinski 2003; Page et al. 2005) may be more important for larger populations in order to retain larger percentages of genes.

Skewing the sex ratio and unequal family sizes did not lead to an impact in either the inbreeding coefficient or the percent of genes retained for populations less than MVP, on the brink of MVP, or for larger, declining populations given the conditions explored. This is not what was expected given the genetic guidelines set out for effective stocking practices (Wang et al. 2002; Miller and Kapuscinski 2003; Page et al. 2005; Fraser 2008). However, this may be simply due to much larger population sizes in the long-term given that supplementation could lead to increased genetic integrity, if the population size is larger in the long-term (Wang and Ryman 2001; Jager 2005). These findings may also be due to nearly all adults still having the opportunity to spawn and contribute progeny to the future during these simulations given that the percent of mature adults contributing

progeny was held constant. Thus, even though the sex ratio was skewed or the family sizes were unequal, most adults were still able to contribute progeny and thus genes thereby reducing the impact of sex ratio and family size on the retention of genes and the accrual of inbreeding. Finally, these findings may also be due to low probabilities of surviving to adulthood and encountering a related individual to mate with. This may be especially true for the two scenarios that were declining, and would result in higher gene retention and lower inbreeding accrual over time.

However, reduced numbers of adults contributing progeny did result in a decrease in genetic integrity when compared to using more adults for progeny production for the scenarios explored. The greater the percent of mature adults contributing progeny to the supplemented population, the less likely inbreeding will accrue and the greater the retention of genes for supplementation over a longer time frame. This finding is what would be expected given the recommended genetic practices for supplementation (Wang et al. 2002; Miller and Kapuscinski 2003; Page et al. 2005).

Overall, these results suggest that demographic stochasticity may be the more important factor with respect to retaining genes and populations. Lande (1988) advocated that demographic stochasticity was the more important force in extinction processes for small population sizes. Generally, these populations faced an extinction risk if they were not supplemented, and given that supplementation did not result in large decreases in gene retention or increases in inbreeding using the recommended genetic practices, avoiding extinction resulting from demographic stochasticity seemed to be the more pressing issue.

## MANAGEMENT IMPLICATIONS

The sensitivity analysis indicated that reducing the mortality or increasing survival of lake sturgeon will have the largest impact on population persistence. Reductions in mortality can be accomplished through reducing and regulating harvest, both legal and illegal (Beamesderfer and Farr 1997). Increases in YOY survival can be accomplished through stocking or supportive breeding via stream-side rearing. Each of these practices have been suggested in past lake sturgeon rehabilitation strategies (Beamesderfer and Farr 1997; Hay-Chmielewski and Whelan 1997). Second, maintaining lake sturgeon persistence and genetic integrity is dependent upon maintaining populations which are above the minimum viable population size. Thus, I recommend that populations should be maintained above 80 to 150 individuals. These recommendations should help to foster the protection of sustainable lake sturgeon populations for the future by minimizing extinction risks due to both demographic stochasticity and inbreeding depression. Also, estimation of MVP should help lake sturgeon managers prioritize populations for future rehabilitation efforts, given extinction risks. For populations below the MVP level, management efforts such as some form of supplementation may be necessary to overcome demographic stochasticity and maintain persistence.

Supplementing populations using appropriate genetic guidelines was shown to increase the retention of unique genes and decrease inbreeding, and achieve target population sizes with reduced risks of extinction when compared to not supplementing the population for the scenarios explored. Thus, I recommend supplementing those populations at high risk of extinction or populations showing sustained decline. Depending upon the population size and trajectory, different numbers of individuals need

to be stocked in order to move a population towards rehabilitation. For lake sturgeon populations less than MVP or on the brink of MVP, relatively few individuals need to be stocked in order to maintain both positive population trajectories and reduced genetic impacts. For larger, declining populations, more individuals need to be stocked if a short management time horizon is used. The number that needs to be stocked in the fall each year is the recommended stocking number (which accounts for over winter mortality) divided by the actual over winter survival for the population. For example, if you wanted to supplement a population below MVP under the pulse scenario, so that the population size in the long-term was on average 500 individuals, and if the over winter survival was 0.40% (Crossman et al. 2009), then you would need to stock (244/0.40=610) 610 individuals in the fall each year. This strategy should be used when determining how many to stock to achieve specific population sizes, percent of genes retained, and mean final inbreeding coefficients. This study provides specific advice on how many to stock and what genetic guidelines are important, but it is up to the managers to determine goals and objectives for populations of interest and then take action to meet those goals and objectives.

If all recommended genetic practices cannot be followed, some recommendations appear more important than others with respect to maintaining genes and reducing inbreeding for the scenarios explored. First, if supplementing a larger population, supplementing over a longer time frame is recommended for the retention of genes over the long term. Second, capturing the greatest number of adults from the population for supplementation purposes seems to be the most crucial recommendation for retaining genes and reducing inbreeding accrual. Third, sex ratio and family size variation have

smaller effects on the genetics of populations, thus, following these genetic guidelines is less crucial.

## FUTURE RESEARCH

Many research tracks would be useful for enhancing the conservation of lake sturgeon in the Great Lakes basin. The impacts of dams and value of dam removal, or the potential impact of food web changes on the diet of lake sturgeon are just a couple of examples of areas of inquiry that would be valuable. Focusing on topics that emerge directly from my research, I feel two areas should take priority. For empirical research, researchers should try to measure inbreeding depression in lake sturgeon, most likely focusing on YOY mortality or progeny numbers produced. This research would be important because it will help to estimate the effects of inbreeding depression on long-term population persistence for lake sturgeon. Given the longevity of lake sturgeon and model results, measuring inbreeding depression in YOY mortality and progeny numbers would be most feasible because these measurements occur over a relatively short time period. Also, this research will add greatly to the literature on inbreeding depression in wild populations for fish species because few studies have addressed inbreeding depression in wild populations of fish species, especially long-lived species.

Lastly, based on the stocking strategies chapter and using the individual based model developed, future work could explore outbreeding depression, caused by stocking individuals from another population. Outbreeding depression is a reduction in fitness due to the loss of locally adapted gene complexes (Edmands 2007). This research is important because it will address an important issue with direct management implications. If outbreeding depression is found to be important, then only fish from the

same spawning location or closely related locations should be used for supplementation purposes. However, if outbreeding depression is not found to be important, then individuals for supplementation purposes could be obtained from any population of lake sturgeon. Thus, understanding how outbreeding depression may influence the long-term dynamics of lake sturgeon populations is important for population persistence, as well as, determining which populations should provide progeny for supplementation purposes.

# APPENDIX A

Table A.1. Sensitivity, S, of percent of extinct populations for each of the parameters for an initial population size of 50 where $R_a$ is the model response for the altered parameter, $R_n$ is the model response for the nominal parameter, $P_a$ is the altered parameter, and $P_n$ is the nominal parameter.

| Parameter | Pn | Pa | Rn | Ra | S |
|---|---|---|---|---|---|
| Young of the year mortality rate | 0.47 | 0.32 | 34.4 | 1.2 | 3.02 |
| | 0.47 | 0.35 | 34.4 | 3.8 | 3.48 |
| | 0.47 | 0.38 | 34.4 | 10.0 | 3.70 |
| | 0.47 | 0.41 | 34.4 | 12.8 | 4.92 |
| | 0.47 | 0.44 | 34.4 | 19.2 | 6.92 |
| | 0.47 | 0.50 | 34.4 | 56.2 | 9.93 |
| | 0.47 | 0.53 | 34.4 | 61.6 | 6.19 |
| | 0.47 | 0.56 | 34.4 | 74.2 | 6.04 |
| | 0.47 | 0.59 | 34.4 | 78.4 | 5.01 |
| | 0.47 | 0.62 | 34.4 | 91.4 | 5.19 |
| Mortality rate | 0.05 | 0.035 | 34.4 | 0.0 | 3.33 |
| | 0.05 | 0.04 | 34.4 | 0.0 | 5.00 |
| | 0.05 | 0.045 | 34.4 | 4.2 | 8.78 |
| | 0.05 | 0.055 | 34.4 | 84.8 | 14.65 |
| | 0.05 | 0.06 | 34.4 | 98.2 | 9.27 |
| | 0.05 | 0.065 | 34.4 | 99.2 | 6.28 |
| Age at first maturation for females | 20 | 14 | 34.4 | 3.0 | 3.04 |
| | 20 | 16 | 34.4 | 6.8 | 4.01 |
| | 20 | 18 | 34.4 | 19.8 | 4.24 |
| | 20 | 22 | 34.4 | 49.6 | 4.42 |
| | 20 | 24 | 34.4 | 67.2 | 4.77 |
| | 20 | 26 | 34.4 | 74.0 | 3.84 |
| Probability of mating for females | 0.33 | 0.231 | 34.4 | 91.8 | -5.56 |
| | 0.33 | 0.264 | 34.4 | 65.8 | -4.56 |
| | 0.33 | 0.297 | 34.4 | 57.2 | -6.63 |
| | 0.33 | 0.363 | 34.4 | 20.4 | -4.07 |
| | 0.33 | 0.396 | 34.4 | 6.8 | -4.01 |
| | 0.33 | 0.429 | 34.4 | 2.8 | -3.06 |
| Age at first maturation for males | 15 | 11 | 34.4 | 20.0 | 1.57 |
| | 15 | 12 | 34.4 | 26.4 | 1.16 |
| | 15 | 13 | 34.4 | 29.4 | 1.09 |
| | 15 | 14 | 34.4 | 32.4 | 0.87 |
| | 15 | 16 | 34.4 | 31.4 | -1.31 |
| | 15 | 17 | 34.4 | 42.4 | 1.74 |
| | 15 | 18 | 34.4 | 47.0 | 1.83 |
| | 15 | 19 | 34.4 | 52.0 | 1.92 |

Table A.1 (cont'd).

| | | | | | |
|---|---|---|---|---|---|
| Probability of mating for males | 0.5 | 0.35 | 34.4 | 77.8 | -4.21 |
| | 0.5 | 0.4 | 34.4 | 59.8 | -3.69 |
| | 0.5 | 0.45 | 34.4 | 41.0 | -1.92 |
| | 0.5 | 0.55 | 34.4 | 29.4 | -1.45 |
| | 0.5 | 0.6 | 34.4 | 25.8 | -1.25 |
| | 0.5 | 0.65 | 34.4 | 20.0 | -1.40 |

Table A.2. Sensitivity, S, of average percent of genes retained for each of the parameters for an initial population size of 200 where $R_a$ is the model response for the altered parameter, $R_n$ is the model response for the nominal parameter, $P_a$ is the altered parameter, and $P_n$ is the nominal parameter. NR represents no response because of computing limitations.

| Parameter | Pn | Pa | Rn | Ra | S |
|---|---|---|---|---|---|
| Young of the year mortality rate | 0.47 | 0.33 | 9.487 | 19.289 | -3.47 |
| | 0.47 | 0.36 | 9.487 | 17.055 | -3.41 |
| | 0.47 | 0.39 | 9.487 | 15.087 | -3.47 |
| | 0.47 | 0.42 | 9.487 | 12.752 | -3.24 |
| | 0.47 | 0.45 | 9.487 | 10.801 | -3.25 |
| | 0.47 | 0.48 | 9.487 | 8.831 | -3.25 |
| | 0.47 | 0.51 | 9.487 | 6.996 | -3.09 |
| | 0.47 | 0.54 | 9.487 | 5.451 | -2.86 |
| | 0.47 | 0.57 | 9.487 | 4.019 | -2.71 |
| | 0.47 | 0.60 | 9.487 | 2.621 | -2.62 |
| | 0.47 | 0.63 | 9.487 | 1.819 | -2.37 |
| Mortality rate | 0.05 | 0.035 | 9.487 | NR | |
| | 0.05 | 0.04 | 9.487 | 29.412 | -10.50 |
| | 0.05 | 0.045 | 9.487 | 18.580 | -9.58 |
| | 0.05 | 0.055 | 9.487 | 3.527 | -6.28 |
| | 0.05 | 0.06 | 9.487 | 1.075 | -4.43 |
| | 0.05 | 0.065 | 9.487 | 0.560 | -3.14 |
| Age at first maturation for females | 20 | 14 | 9.487 | 22.481 | -4.57 |
| | 20 | 16 | 9.487 | 17.292 | -4.11 |
| | 20 | 18 | 9.487 | 13.071 | -3.78 |
| | 20 | 22 | 9.487 | 6.998 | -2.62 |
| | 20 | 24 | 9.487 | 5.012 | -2.36 |
| | 20 | 26 | 9.487 | 3.598 | -2.07 |
| Probability of mating for females | 0.33 | 0.231 | 9.487 | 2.135 | 2.58 |
| | 0.33 | 0.264 | 9.487 | 3.816 | 2.99 |
| | 0.33 | 0.297 | 9.487 | 6.355 | 3.30 |
| | 0.33 | 0.363 | 9.487 | 12.961 | 3.66 |
| | 0.33 | 0.396 | 9.487 | 16.753 | 3.83 |
| | 0.33 | 0.429 | 9.487 | 20.487 | 3.86 |

Table A.2 (cont'd).

| | | | | | |
|---|---|---|---|---|---|
| Age at first maturation for males | 15 | 11 | 9.487 | 9.858 | -0.15 |
| | 15 | 12 | 9.487 | 9.739 | -0.13 |
| | 15 | 13 | 9.487 | 9.660 | -0.14 |
| | 15 | 14 | 9.487 | 9.713 | -0.36 |
| | 15 | 16 | 9.487 | 9.811 | 0.51 |
| | 15 | 17 | 9.487 | 9.286 | -0.16 |
| | 15 | 18 | 9.487 | 9.135 | -0.19 |
| | 15 | 19 | 9.487 | 8.8155 | -0.27 |
| Probability of mating for males | 0.5 | 0.35 | 9.487 | 7.147 | 0.82 |
| | 0.5 | 0.4 | 9.487 | 8.405 | 0.57 |
| | 0.5 | 0.45 | 9.487 | 9.134 | 0.37 |
| | 0.5 | 0.55 | 9.487 | 9.842 | 0.37 |
| | 0.5 | 0.6 | 9.487 | 9.635 | 0.08 |
| | 0.5 | 0.65 | 9.487 | 9.767 | 0.10 |

Table A.3. Sensitivity, S, of the percent of increasing populations for each of the parameters for an initial population size of 200 where $R_a$ is the model response for the altered parameter, $R_n$ is the model response for the nominal parameter, $P_a$ is the altered parameter, and $P_n$ is the nominal parameter. NR represents no response because of computing limitations.

| Parameter | Pn | Pa | Rn | Ra | S |
|---|---|---|---|---|---|
| Young of the year mortality rate | 0.47 | 0.33 | 46.2 | 99.8 | -3.89 |
| | 0.47 | 0.36 | 46.2 | 100 | -4.98 |
| | 0.47 | 0.39 | 46.2 | 99.2 | -6.74 |
| | 0.47 | 0.42 | 46.2 | 93.8 | -9.68 |
| | 0.47 | 0.45 | 46.2 | 67.8 | -10.99 |
| | 0.47 | 0.48 | 46.2 | 30.8 | -15.67 |
| | 0.47 | 0.51 | 46.2 | 8.8 | -9.51 |
| | 0.47 | 0.54 | 46.2 | 0.8 | -6.60 |
| | 0.47 | 0.57 | 46.2 | 0 | -4.70 |
| | 0.47 | 0.60 | 46.2 | 0 | -3.62 |
| | 0.47 | 0.63 | 46.2 | 0 | -2.94 |
| Mortality rate | 0.05 | 0.035 | 46.2 | NA | |
| | 0.05 | 0.04 | 46.2 | 100 | -5.82 |
| | 0.05 | 0.045 | 46.2 | 100 | -11.65 |
| | 0.05 | 0.055 | 46.2 | 0 | -10.00 |
| | 0.05 | 0.06 | 46.2 | 0 | -5.00 |
| | 0.05 | 0.065 | 46.2 | 0 | -3.33 |
| Age at first maturation for females | 20 | 14 | 46.2 | 100 | -3.88 |
| | 20 | 16 | 46.2 | 99.8 | -5.80 |
| | 20 | 18 | 46.2 | 95 | -10.56 |
| | 20 | 22 | 46.2 | 5 | -8.92 |
| | 20 | 24 | 46.2 | 0.2 | -4.98 |
| | 20 | 26 | 46.2 | 0 | -3.33 |
| Probability of mating for females | 0.33 | 0.231 | 46.2 | 0 | 3.33 |
| | 0.33 | 0.264 | 46.2 | 0 | 5.00 |
| | 0.33 | 0.297 | 46.2 | 2.2 | 9.52 |
| | 0.33 | 0.363 | 46.2 | 94.8 | 10.52 |
| | 0.33 | 0.396 | 46.2 | 99.8 | 5.80 |
| | 0.33 | 0.429 | 46.2 | 100 | 3.88 |
| Age at first maturation for males | 15 | 11 | 46.2 | 50.6 | -0.36 |
| | 15 | 12 | 46.2 | 51.4 | -0.56 |
| | 15 | 13 | 46.2 | 52 | -0.94 |
| | 15 | 14 | 46.2 | 48.4 | -0.71 |
| | 15 | 16 | 46.2 | 47.4 | 0.39 |
| | 15 | 17 | 46.2 | 38.4 | -1.27 |
| | 15 | 18 | 46.2 | 34.8 | -1.23 |
| | 15 | 19 | 46.2 | 28.2 | -1.46 |

Table A.3 (cont'd).

| | | | | | |
|---|---|---|---|---|---|
| Probability of mating for males | 0.5 | 0.35 | 46.2 | 7.4 | 2.80 |
| | 0.5 | 0.4 | 46.2 | 23.6 | 2.45 |
| | 0.5 | 0.45 | 46.2 | 35.8 | 2.25 |
| | 0.5 | 0.55 | 46.2 | 50.8 | 1.00 |
| | 0.5 | 0.6 | 46.2 | 47.4 | 0.13 |
| | 0.5 | 0.65 | 46.2 | 51 | 0.35 |

Table A.4. Sensitivity, S, of the final mean inbreeding for each of the parameters for an initial population size of 200 where $R_a$ is the model response for the altered parameter, $R_n$ is the model response for the nominal parameter, $P_a$ is the altered parameter, and $P_n$ is the nominal parameter. NR represents no response because of computing limitations.

| Parameter | Pn | Pa | Rn | Ra | S |
|---|---|---|---|---|---|
| Young of the year mortality rate | 0.47 | 0.33 | 0.0413 | 0.0220 | 1.57 |
| | 0.47 | 0.36 | 0.0413 | 0.0241 | 1.78 |
| | 0.47 | 0.39 | 0.0413 | 0.0262 | 2.15 |
| | 0.47 | 0.42 | 0.0413 | 0.0309 | 2.37 |
| | 0.47 | 0.45 | 0.0413 | 0.0359 | 3.07 |
| | 0.47 | 0.48 | 0.0413 | 0.0407 | -0.68 |
| | 0.47 | 0.51 | 0.0413 | 0.0490 | 2.19 |
| | 0.47 | 0.54 | 0.0413 | 0.0570 | 2.55 |
| | 0.47 | 0.57 | 0.0413 | 0.0683 | 3.07 |
| | 0.47 | 0.60 | 0.0413 | 0.0816 | 3.53 |
| | 0.47 | 0.63 | 0.0413 | 0.0939 | 3.74 |
| Mortality rate | 0.05 | 0.035 | 0.0413 | NR | |
| | 0.05 | 0.04 | 0.0413 | 0.0147 | 3.22 |
| | 0.05 | 0.045 | 0.0413 | 0.0223 | 4.60 |
| | 0.05 | 0.055 | 0.0413 | 0.0724 | 7.53 |
| | 0.05 | 0.06 | 0.0413 | 0.1670 | 15.22 |
| | 0.05 | 0.065 | 0.0413 | NR | |
| Age at first maturation for females | 20 | 14 | 0.0413 | 0.0196 | 1.75 |
| | 20 | 16 | 0.0413 | 0.0247 | 2.01 |
| | 20 | 18 | 0.0413 | 0.0312 | 2.45 |
| | 20 | 22 | 0.0413 | 0.0476 | 1.53 |
| | 20 | 24 | 0.0413 | 0.0594 | 2.19 |
| | 20 | 26 | 0.0413 | 0.0664 | 2.03 |
| Probability of mating for females | 0.33 | 0.231 | 0.0413 | 0.0942 | -4.27 |
| | 0.33 | 0.264 | 0.0413 | 0.0722 | -3.74 |
| | 0.33 | 0.297 | 0.0413 | 0.0505 | -2.23 |
| | 0.33 | 0.363 | 0.0413 | 0.0302 | -2.69 |
| | 0.33 | 0.396 | 0.0413 | 0.0246 | -2.02 |
| | 0.33 | 0.429 | 0.0413 | 0.0208 | -1.65 |
| Age at first maturation for males | 15 | 11 | 0.0413 | 0.0392 | 0.19 |
| | 15 | 12 | 0.0413 | 0.0395 | 0.22 |
| | 15 | 13 | 0.0413 | 0.0389 | 0.44 |
| | 15 | 14 | 0.0413 | 0.0382 | 1.13 |
| | 15 | 16 | 0.0413 | 0.0387 | -0.94 |
| | 15 | 17 | 0.0413 | 0.0397 | -0.29 |
| | 15 | 18 | 0.0413 | 0.0394 | -0.23 |
| | 15 | 19 | 0.0413 | 0.0405 | -0.07 |

Table A.4 (cont'd).

| | | | | | |
|---|---|---|---|---|---|
| Probability of mating for males | 0.5 | 0.35 | 0.0413 | 0.0491 | -0.63 |
| | 0.5 | 0.4 | 0.0413 | 0.0409 | 0.05 |
| | 0.5 | 0.45 | 0.0413 | 0.0395 | 0.44 |
| | 0.5 | 0.55 | 0.0413 | 0.0385 | -0.68 |
| | 0.5 | 0.6 | 0.0413 | 0.0389 | -0.29 |
| | 0.5 | 0.65 | 0.0413 | 0.0383 | -0.24 |

Table A.5. Sensitivity, S, of average percent of genes retained for each of the parameters for an initial population size of 50 where $R_a$ is the model response for the altered parameter, $R_n$ is the model response for the nominal parameter, $P_a$ is the altered parameter, and $P_n$ is the nominal parameter.

| Parameter | Pn | Pa | Rn | Ra | S |
|---|---|---|---|---|---|
| Juvenile mortality rate | 0.47 | 0.32 | 4.638 | 17.052 | -8.39 |
| | 0.47 | 0.35 | 4.638 | 13.626 | -7.59 |
| | 0.47 | 0.38 | 4.638 | 10.964 | -7.12 |
| | 0.47 | 0.41 | 4.638 | 8.824 | -7.07 |
| | 0.47 | 0.44 | 4.638 | 6.860 | -7.51 |
| | 0.47 | 0.50 | 4.638 | 2.182 | -8.30 |
| | 0.47 | 0.53 | 4.638 | 1.810 | -4.78 |
| | 0.47 | 0.56 | 4.638 | 0.734 | -4.40 |
| | 0.47 | 0.59 | 4.638 | 0.726 | -3.30 |
| | 0.47 | 0.62 | 4.638 | 0.190 | -3.00 |
| Adult mortality rate | 0.05 | 0.035 | 4.638 | 40.152 | -25.52 |
| | 0.05 | 0.04 | 4.638 | 28.088 | -25.28 |
| | 0.05 | 0.045 | 4.638 | 14.974 | -22.29 |
| | 0.05 | 0.055 | 4.638 | 0.532 | -8.85 |
| | 0.05 | 0.06 | 4.638 | 0.036 | -4.96 |
| | 0.05 | 0.065 | 4.638 | 0.016 | -3.32 |
| Age at first maturation for females | 20 | 14 | 4.638 | 16.20 | -8.31 |
| | 20 | 16 | 4.638 | 12.036 | -7.98 |
| | 20 | 18 | 4.638 | 7.364 | -5.88 |
| | 20 | 22 | 4.638 | 2.822 | -3.92 |
| | 20 | 24 | 4.638 | 1.324 | -3.57 |
| | 20 | 26 | 4.638 | 0.834 | -2.73 |
| Probability of mating for females | 0.33 | 0.231 | 4.638 | 0.228 | 3.17 |
| | 0.33 | 0.264 | 4.638 | 1.254 | 3.65 |
| | 0.33 | 0.297 | 4.638 | 2.120 | 5.43 |
| | 0.33 | 0.363 | 4.638 | 7.516 | 6.21 |
| | 0.33 | 0.396 | 4.638 | 11.506 | 7.40 |
| | 0.33 | 0.429 | 4.638 | 15.228 | 7.61 |
| Age at first maturation for males | 15 | 11 | 4.638 | 6.490 | -1.50 |
| | 15 | 12 | 4.638 | 6.162 | -1.64 |
| | 15 | 13 | 4.638 | 5.686 | -1.69 |
| | 15 | 14 | 4.638 | 5.080 | -1.43 |
| | 15 | 16 | 4.638 | 4.520 | -0.38 |
| | 15 | 17 | 4.638 | 3.628 | -1.63 |
| | 15 | 18 | 4.638 | 3.172 | -1.58 |
| | 15 | 19 | 4.638 | 2.140 | -2.02 |

Table A.5 (cont'd).

| | | | | | |
|---|---|---|---|---|---|
| Probability of mating for males | 0.5 | 0.35 | 4.638 | 0.660 | 2.86 |
| | 0.5 | 0.4 | 4.638 | 1.746 | 3.12 |
| | 0.5 | 0.45 | 4.638 | 3.168 | 3.17 |
| | 0.5 | 0.55 | 4.638 | 5.196 | 1.20 |
| | 0.5 | 0.6 | 4.638 | 6.248 | 1.74 |
| | 0.5 | 0.65 | 4.638 | 7.342 | 1.94 |

Table A.6. Sensitivity, S, of the percent of increasing populations for each of the parameters for an initial population size of 50 where $R_a$ is the model response for the altered parameter, $R_n$ is the model response for the nominal parameter, $P_a$ is the altered parameter, and $P_n$ is the nominal parameter.

| Parameter | Pn | Pa | Rn | Ra | S |
|---|---|---|---|---|---|
| Young of the year mortality rate | 0.47 | 0.32 | 9.2 | 87 | -26.50 |
| | 0.47 | 0.35 | 9.2 | 71 | -26.31 |
| | 0.47 | 0.38 | 9.2 | 59.2 | -28.38 |
| | 0.47 | 0.41 | 9.2 | 40.8 | -26.91 |
| | 0.47 | 0.44 | 9.2 | 22.2 | -22.14 |
| | 0.47 | 0.50 | 9.2 | 2.2 | -11.92 |
| | 0.47 | 0.53 | 9.2 | 1.2 | -6.81 |
| | 0.47 | 0.56 | 9.2 | 0 | -5.22 |
| | 0.47 | 0.59 | 9.2 | 0 | -3.92 |
| | 0.47 | 0.62 | 9.2 | 0 | -3.13 |
| Mortality rate | 0.05 | 0.035 | 9.2 | 100 | -32.90 |
| | 0.05 | 0.04 | 9.2 | 99.2 | -48.91 |
| | 0.05 | 0.045 | 9.2 | 76.2 | -72.83 |
| | 0.05 | 0.055 | 9.2 | 0 | -10.00 |
| | 0.05 | 0.06 | 9.2 | 0 | -5.00 |
| | 0.05 | 0.065 | 9.2 | 0 | -3.33 |
| Age at first maturation for females | 20 | 14 | 9.2 | 86.2 | -27.90 |
| | 20 | 16 | 9.2 | 66.0 | -30.87 |
| | 20 | 18 | 9.2 | 29.4 | -21.96 |
| | 20 | 22 | 9.2 | 2.2 | -7.61 |
| | 20 | 24 | 9.2 | 0.4 | -4.78 |
| | 20 | 26 | 9.2 | 0 | -3.33 |
| Probability of mating for females | 0.33 | 0.231 | 9.2 | 0.0 | 3.33 |
| | 0.33 | 0.264 | 9.2 | 0.4 | 4.78 |
| | 0.33 | 0.297 | 9.2 | 2.0 | 7.83 |
| | 0.33 | 0.363 | 9.2 | 29.0 | 21.52 |
| | 0.33 | 0.396 | 9.2 | 57.6 | 26.30 |
| | 0.33 | 0.429 | 9.2 | 79.4 | 25.43 |
| Age at first maturation for males | 15 | 11 | 9.2 | 21.8 | -5.14 |
| | 15 | 12 | 9.2 | 19.2 | -5.43 |
| | 15 | 13 | 9.2 | 18.6 | -7.66 |
| | 15 | 14 | 9.2 | 13.4 | -6.85 |
| | 15 | 16 | 9.2 | 8.0 | -1.96 |
| | 15 | 17 | 9.2 | 4.4 | -3.91 |
| | 15 | 18 | 9.2 | 3.6 | -3.04 |
| | 15 | 19 | 9.2 | 1.6 | -3.10 |

Table A.6 (cont'd).

| | | | | | |
|---|---|---|---|---|---|
| Probability of mating for males | 0.5 | 0.35 | 9.2 | 0 | 3.33 |
| | 0.5 | 0.4 | 9.2 | 1.4 | 4.24 |
| | 0.5 | 0.45 | 9.2 | 4.4 | 5.22 |
| | 0.5 | 0.55 | 9.2 | 12.4 | 3.48 |
| | 0.5 | 0.6 | 9.2 | 20.0 | 5.87 |
| | 0.5 | 0.65 | 9.2 | 26 | 6.09 |

Table A.7. Sensitivity, S, of the final mean inbreeding for each of the parameters for an initial population size of 50 where $R_a$ is the model response for the altered parameter, $R_n$ is the model response for the nominal parameter, $P_a$ is the altered parameter, and $P_n$ is the nominal parameter. NR indicates no response because none of the populations persisted long enough to determine a final mean inbreeding.

| Parameter | Pn | Pa | Rn | Ra | S |
|---|---|---|---|---|---|
| Young of the year mortality rate | 0.47 | 0.32 | 0.1388 | 0.0845 | 1.23 |
| | 0.47 | 0.35 | 0.1388 | 0.0960 | 1.21 |
| | 0.47 | 0.38 | 0.1388 | 0.1072 | 1.19 |
| | 0.47 | 0.41 | 0.1388 | 0.1124 | 1.49 |
| | 0.47 | 0.44 | 0.1388 | 0.1277 | 1.25 |
| | 0.47 | 0.50 | 0.1388 | 0.1547 | 1.79 |
| | 0.47 | 0.53 | 0.1388 | 0.1707 | 1.80 |
| | 0.47 | 0.56 | 0.1388 | 0.1236 | -0.57 |
| | 0.47 | 0.59 | 0.1388 | 0.2038 | 1.83 |
| | 0.47 | 0.62 | 0.1388 | 0.1643 | 0.58 |
| Mortality rate | 0.05 | 0.035 | 0.1388 | 0.0427 | 2.31 |
| | 0.05 | 0.04 | 0.1388 | 0.0586 | 2.89 |
| | 0.05 | 0.045 | 0.1388 | 0.0921 | 3.36 |
| | 0.05 | 0.055 | 0.1388 | 0.1996 | 4.38 |
| | 0.05 | 0.06 | 0.1388 | 0.7083 | 20.52 |
| | 0.05 | 0.065 | 0.1388 | NR | |
| Age at first maturation for females | 20 | 14 | 0.1388 | 0.0868 | 1.25 |
| | 20 | 16 | 0.1388 | 0.1018 | 1.33 |
| | 20 | 18 | 0.1388 | 0.1181 | 1.49 |
| | 20 | 22 | 0.1388 | 0.1825 | 3.15 |
| | 20 | 24 | 0.1388 | 0.1906 | 1.87 |
| | 20 | 26 | 0.1388 | 0.1619 | 0.55 |
| Probability of mating for females | 0.33 | 0.231 | 0.1388 | 0.167 | -0.68 |
| | 0.33 | 0.264 | 0.1388 | 0.2023 | -2.29 |
| | 0.33 | 0.297 | 0.1388 | 0.1667 | -2.01 |
| | 0.33 | 0.363 | 0.1388 | 0.1094 | -2.12 |
| | 0.33 | 0.396 | 0.1388 | 0.1008 | -1.37 |
| | 0.33 | 0.429 | 0.1388 | 0.0896 | -1.18 |

Table A.7 (cont'd).

| | | | | | |
|---|---|---|---|---|---|
| Age at first maturation for males | 15 | 11 | 0.1388 | 0.1362 | 0.07 |
| | 15 | 12 | 0.1388 | 0.1398 | -0.04 |
| | 15 | 13 | 0.1388 | 0.1331 | 0.31 |
| | 15 | 14 | 0.1388 | 0.1466 | -0.84 |
| | 15 | 16 | 0.1388 | 0.1458 | 0.76 |
| | 15 | 17 | 0.1388 | 0.1279 | -0.59 |
| | 15 | 18 | 0.1388 | 0.1377 | -0.04 |
| | 15 | 19 | 0.1388 | 0.1535 | 0.40 |
| Probability of mating for males | 0.5 | 0.35 | 0.1388 | 0.1770 | -0.92 |
| | 0.5 | 0.4 | 0.1388 | 0.1597 | -0.75 |
| | 0.5 | 0.45 | 0.1388 | 0.1341 | 0.34 |
| | 0.5 | 0.55 | 0.1388 | 0.1378 | -0.07 |
| | 0.5 | 0.6 | 0.1388 | 0.1269 | -0.43 |
| | 0.5 | 0.65 | 0.1388 | 0.1226 | -0.39 |

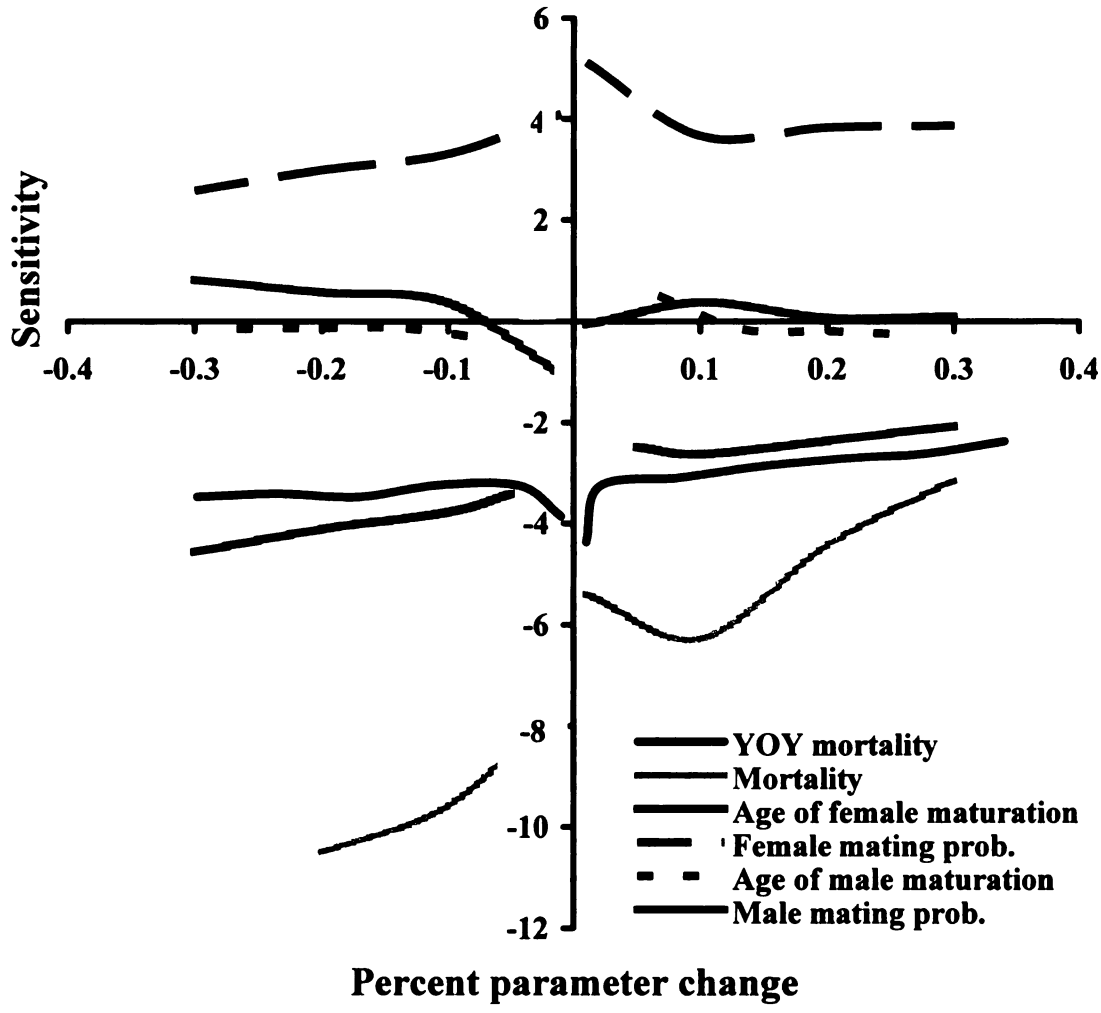


Figure A.1. Percent change in parameter versus sensitivity, *S*, for average percent of genes retained for lake sturgeon with an initial population size of 200.

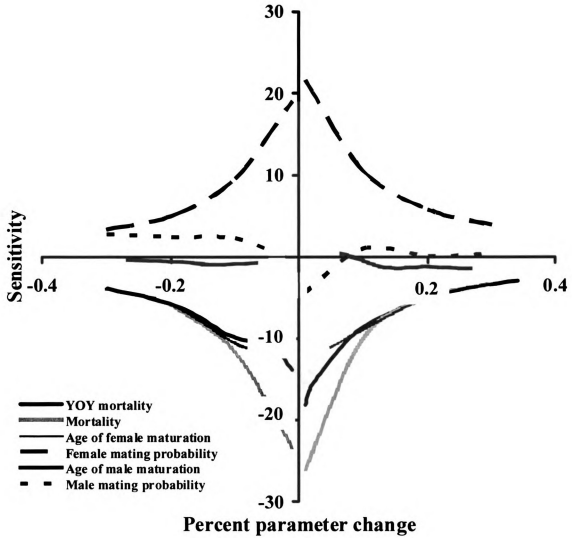


Figure A.2. Percent change in parameter versus sensitivity, *S*, for percent of increasing populations for lake sturgeon with an initial population size of 200.

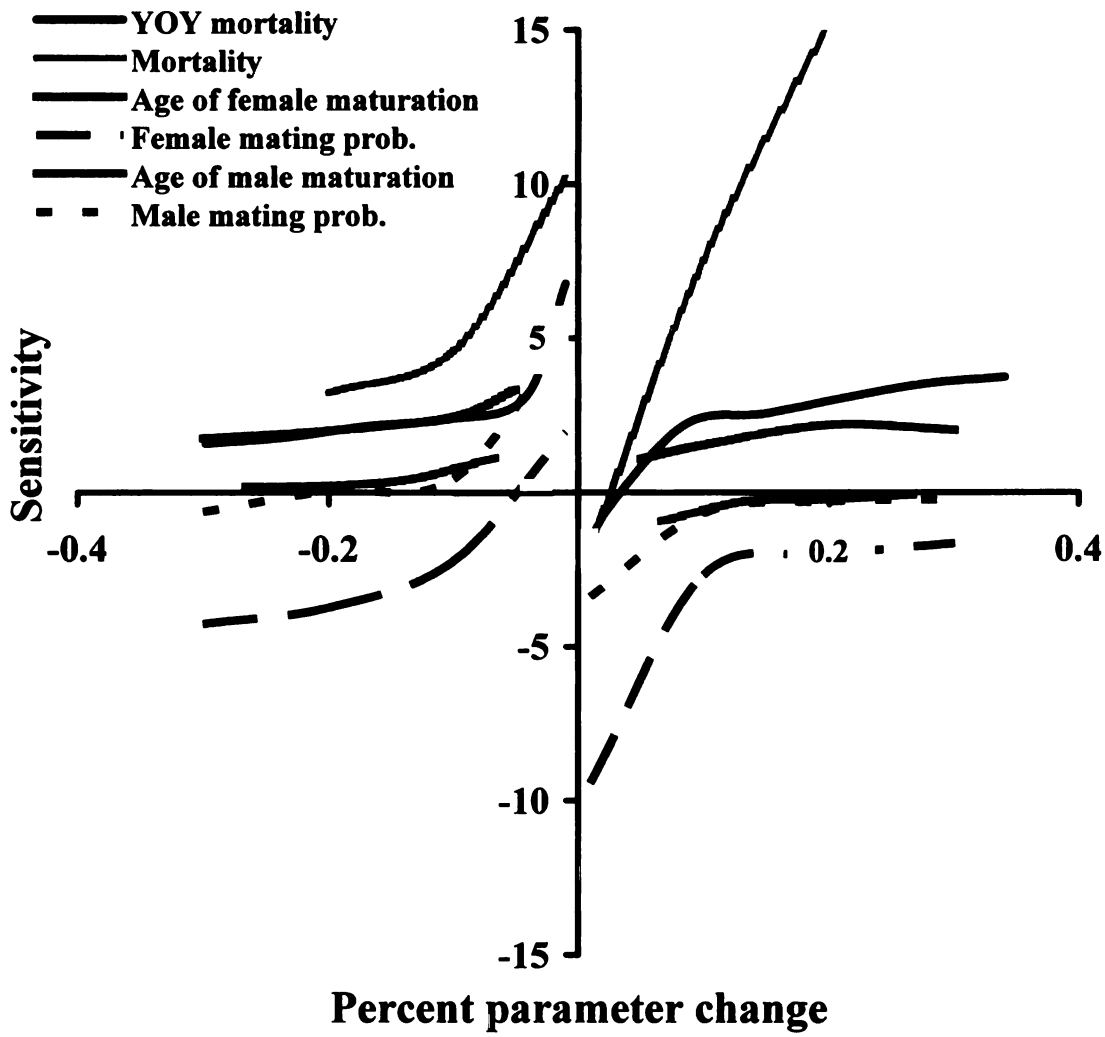


Figure A.3. Percent change in parameter versus sensitivity, *S*, for final mean inbreeding for lake sturgeon with an initial population size of 200.

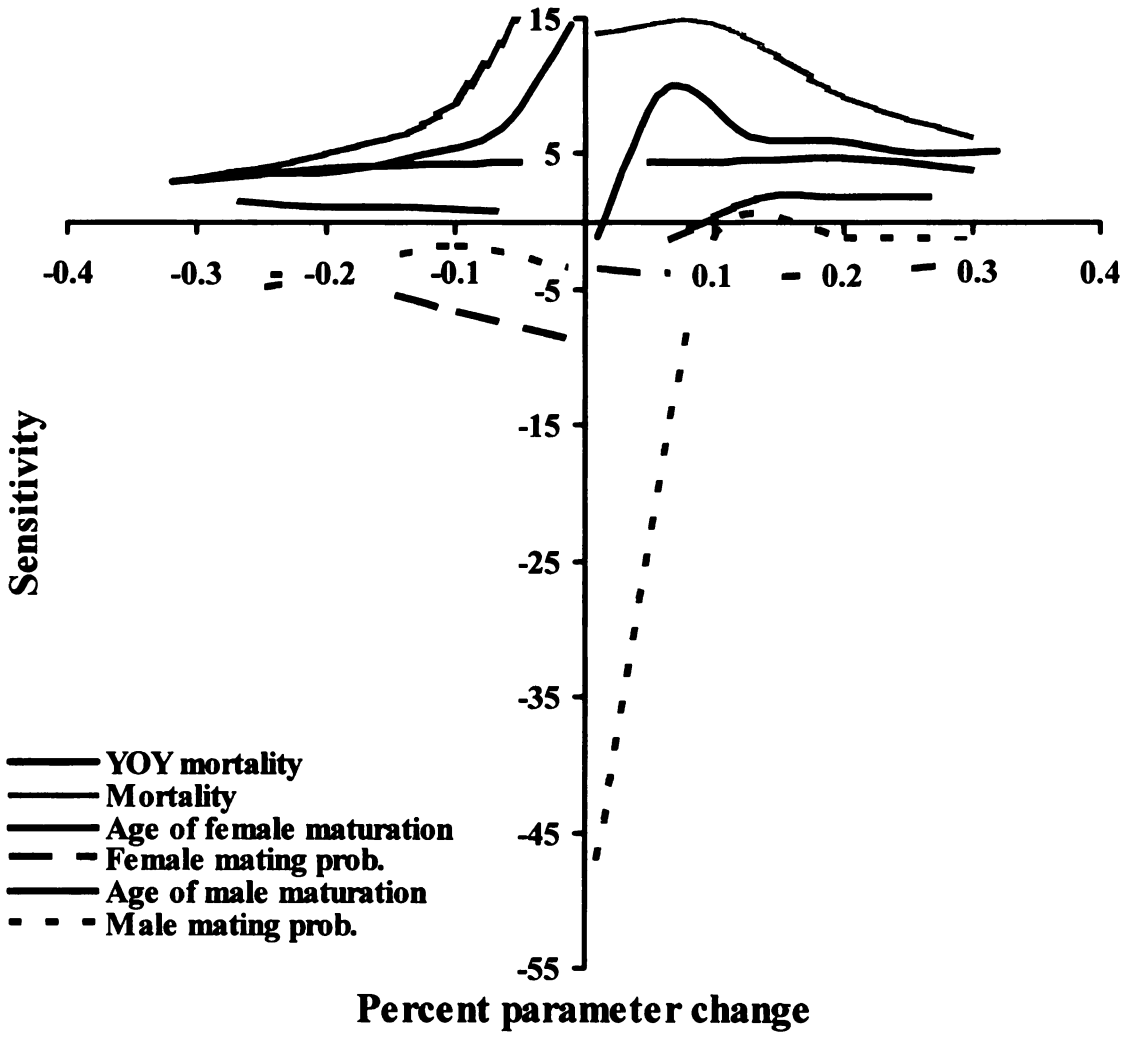


Figure A.4. Percent change in parameter versus sensitivity, *S*, for percent of extinct populations for lake sturgeon with an initial population size of 50.

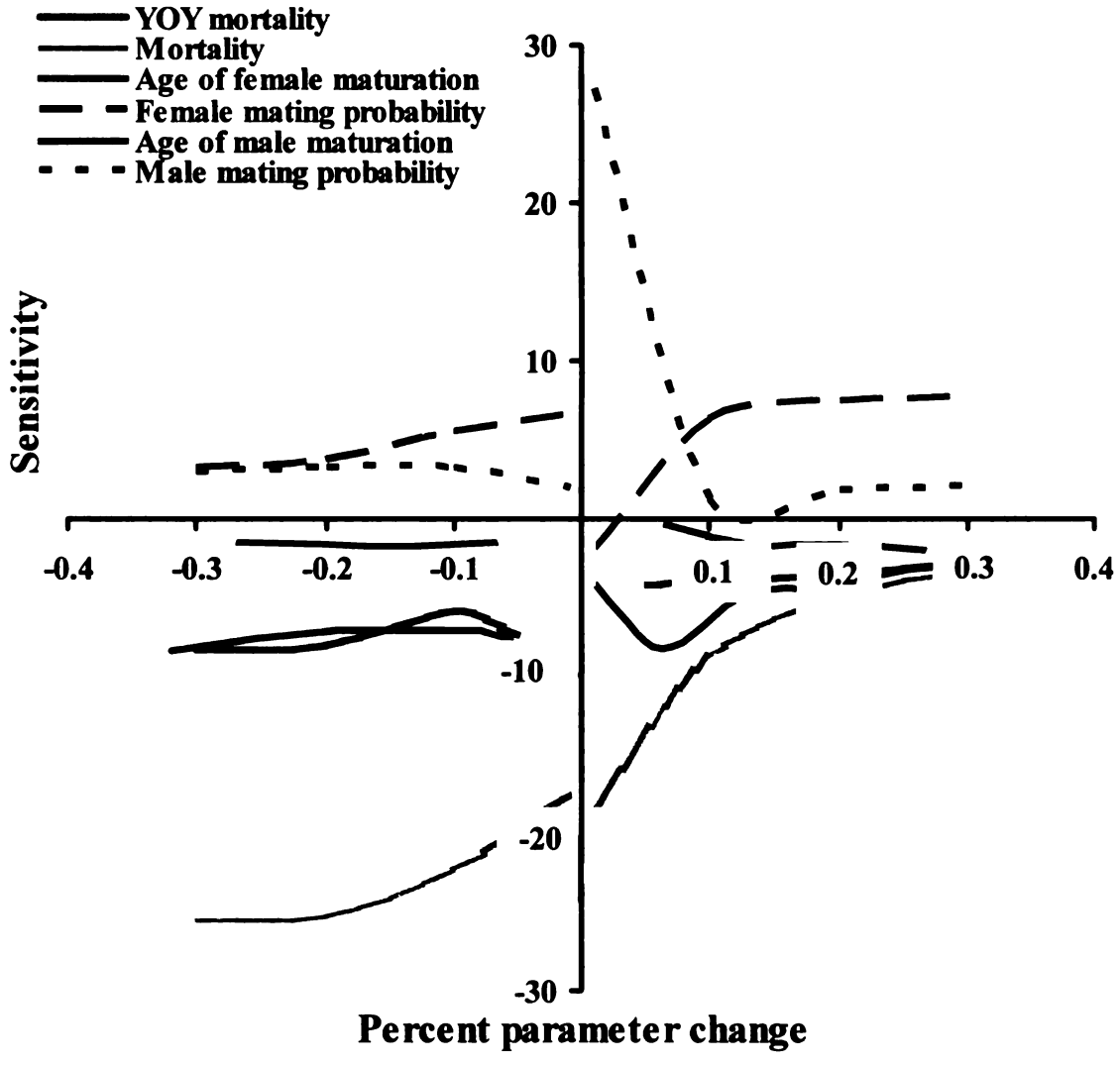


Figure A.5. Percent change in parameter versus sensitivity, *S*, for average percent of genes retained for lake sturgeon with an initial population size of 50.

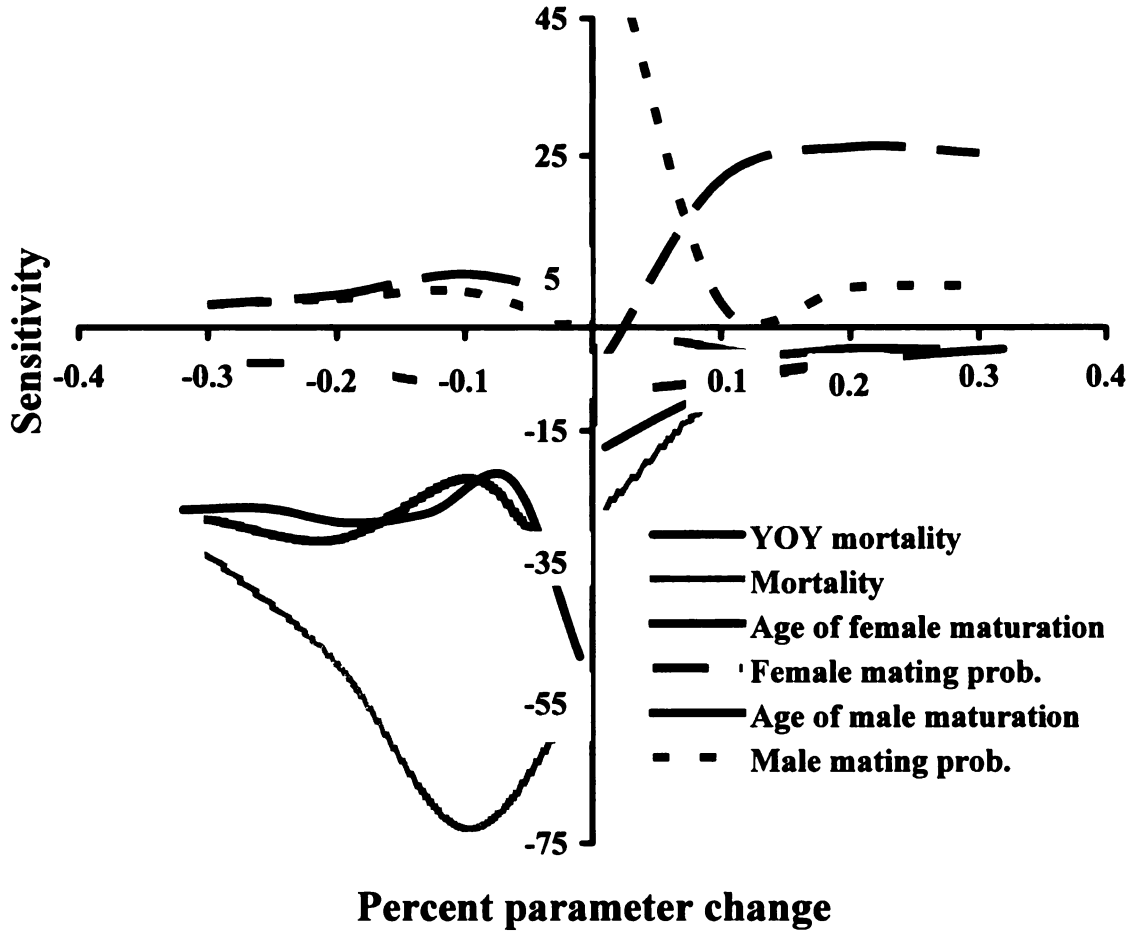


Figure A.6. Percent change in parameter versus sensitivity, *S*, for percent of increasing populations for lake sturgeon with an initial population size of 50.

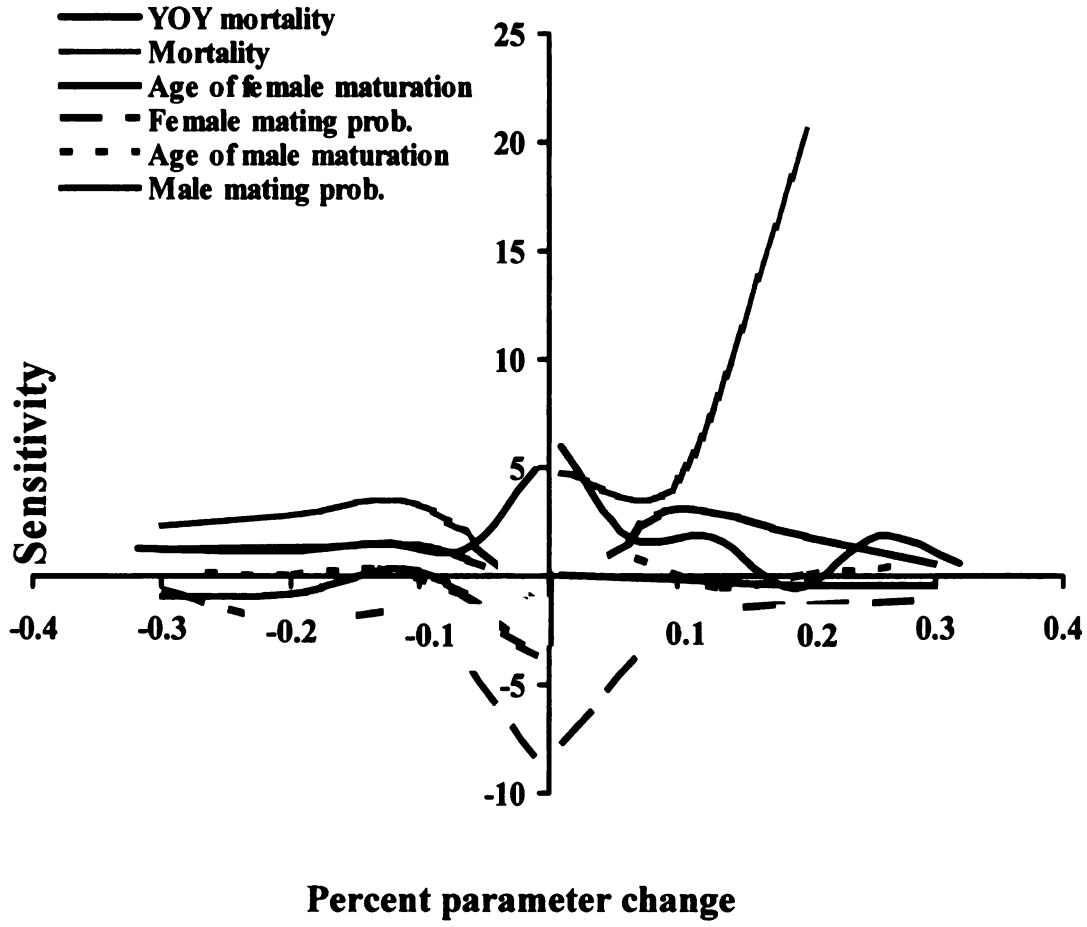


Figure A.7. Percent change in parameter versus sensitivity, *S*, for final mean inbreeding for lake sturgeon with an initial population size of 50.

# APPENDIX B

Table B.1. Baseline population parameter values for each of the three plausible scenarios explored. All under scenario means that the parameter value was used for all three scenarios.

| Parameter | Scenario | Value |
|---|---|---|
| Age at first reproduction (male) | All | 15 |
| Age at first reproduction (female) | All | 20 |
| Post YOY mortality | All | 0.05 |
| Probability of spawning each year (male) | All | 0.5 |
| Probability of spawning each year (female) | All | 0.33 |
| YOY mortality | Less than MVP | 0.47 |
| | Brink of MVP | 0.45 |
| | Large, declining | 0.67 |

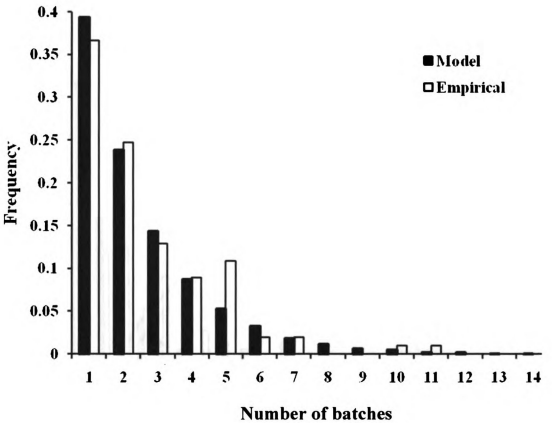


Figure B.1. The frequency of the number of batches, $B$, randomly assigned to males and females in the model using a random uniform distribution and the equation $B = 1 + \text{integer}(-2 * \ln(1 - U(0,1))$. The frequency of number of mates per individual from empirical data from DeHaan (2003).

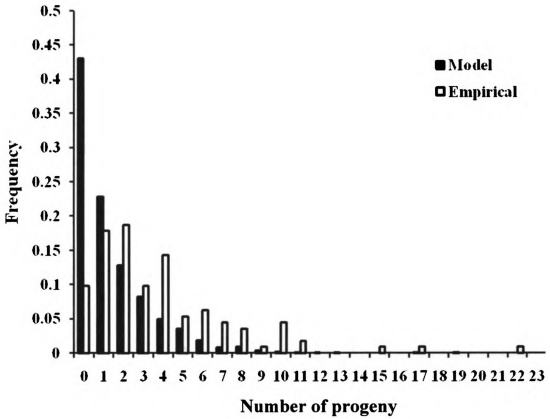


Figure B.2. The frequency of the number of progeny for an individual male or female from the model and from empirical data (DeHaan 2003).

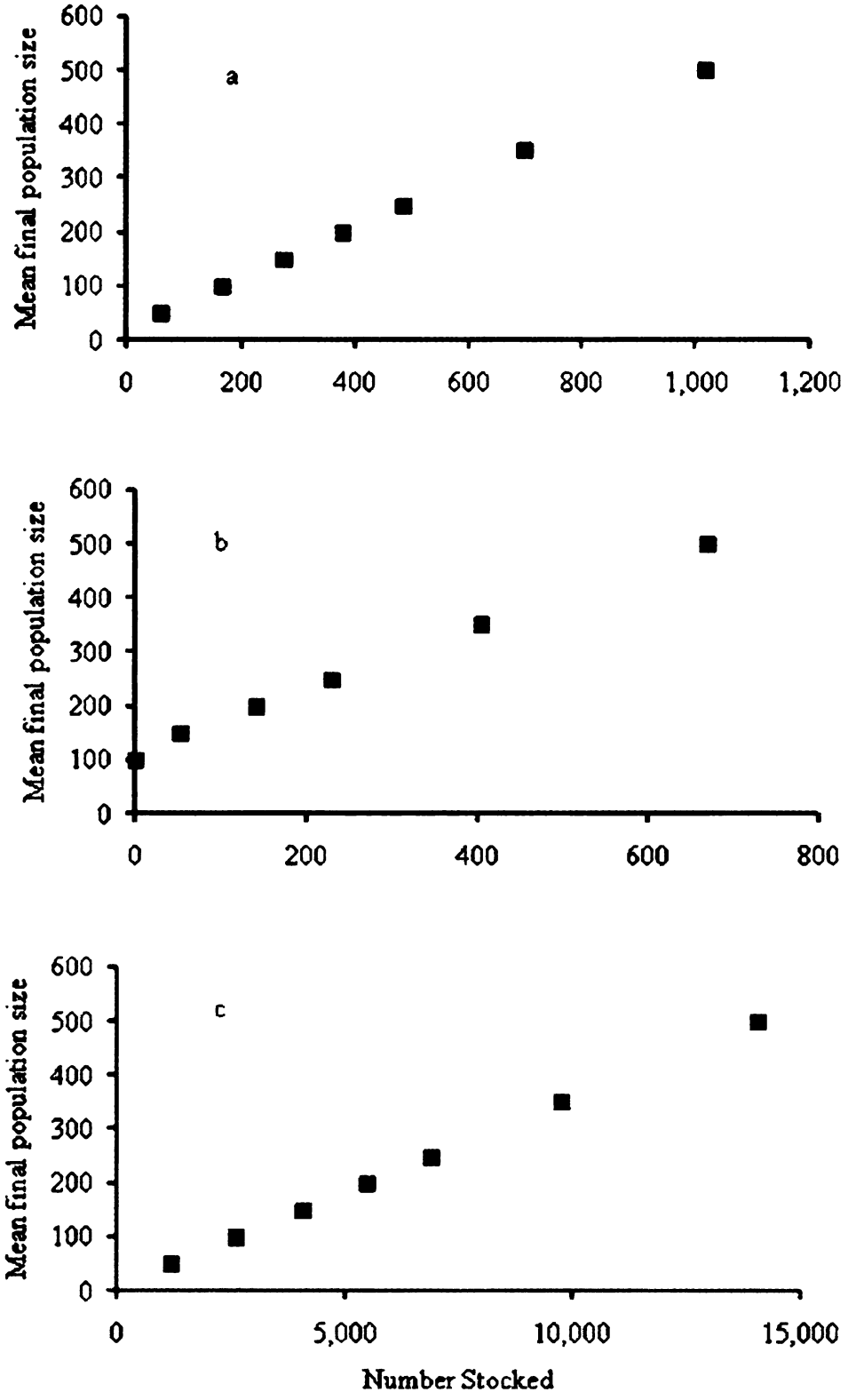


Figure B.3. The number of individuals that need to be stocked using the trickle strategy in order to attain a mean final population size for each scenario as determined by interpolation using a linear function where a) less than MVP, b) brink of MVP, and c) large, declining.

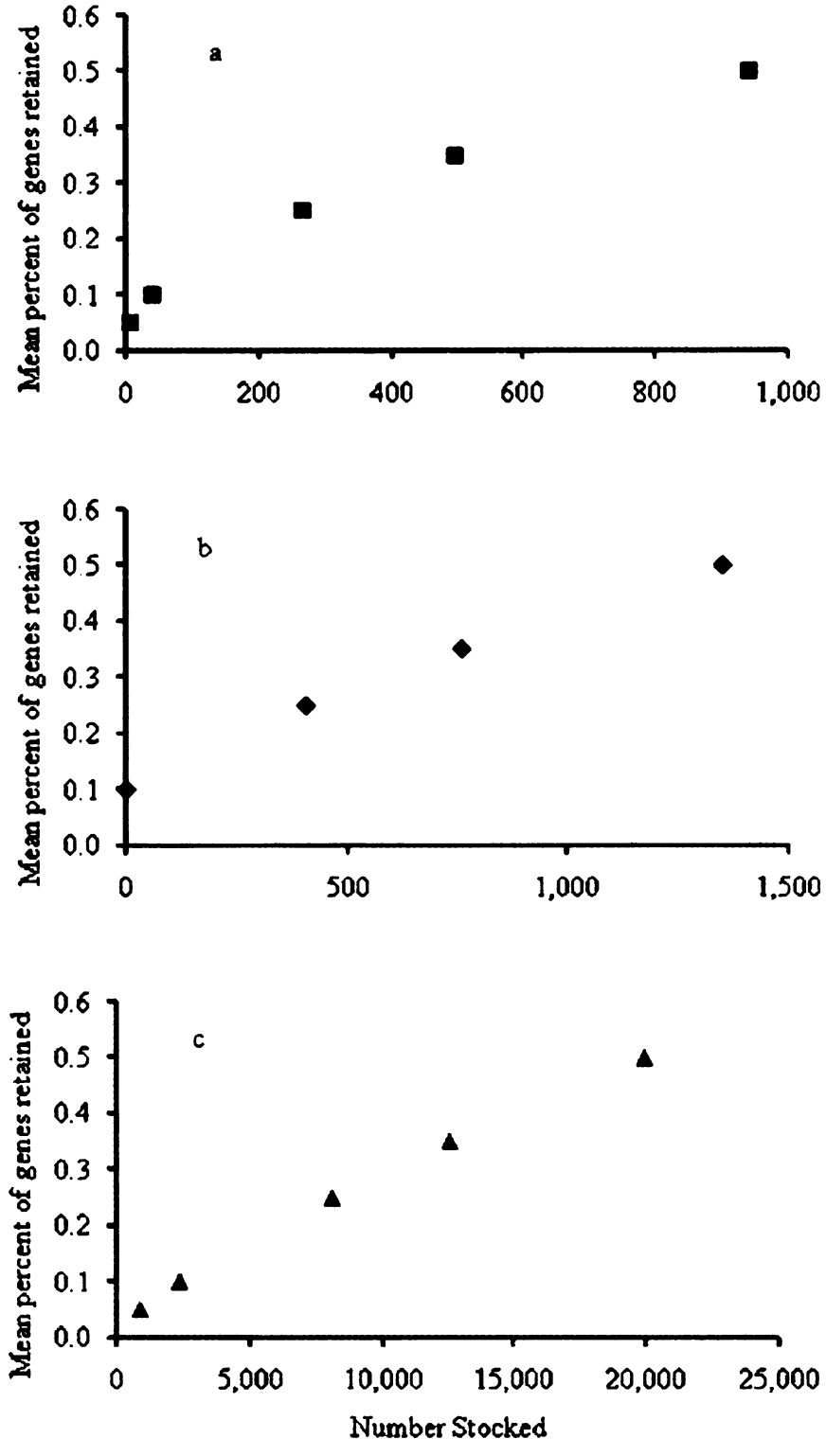


Figure B.4. The number of individuals that need to be stocked using the trickle strategy in order to attain a mean percent of genes retained for each scenario as determined by interpolation using a power function where a) less than MVP, b) brink of MVP, and c) large, declining.

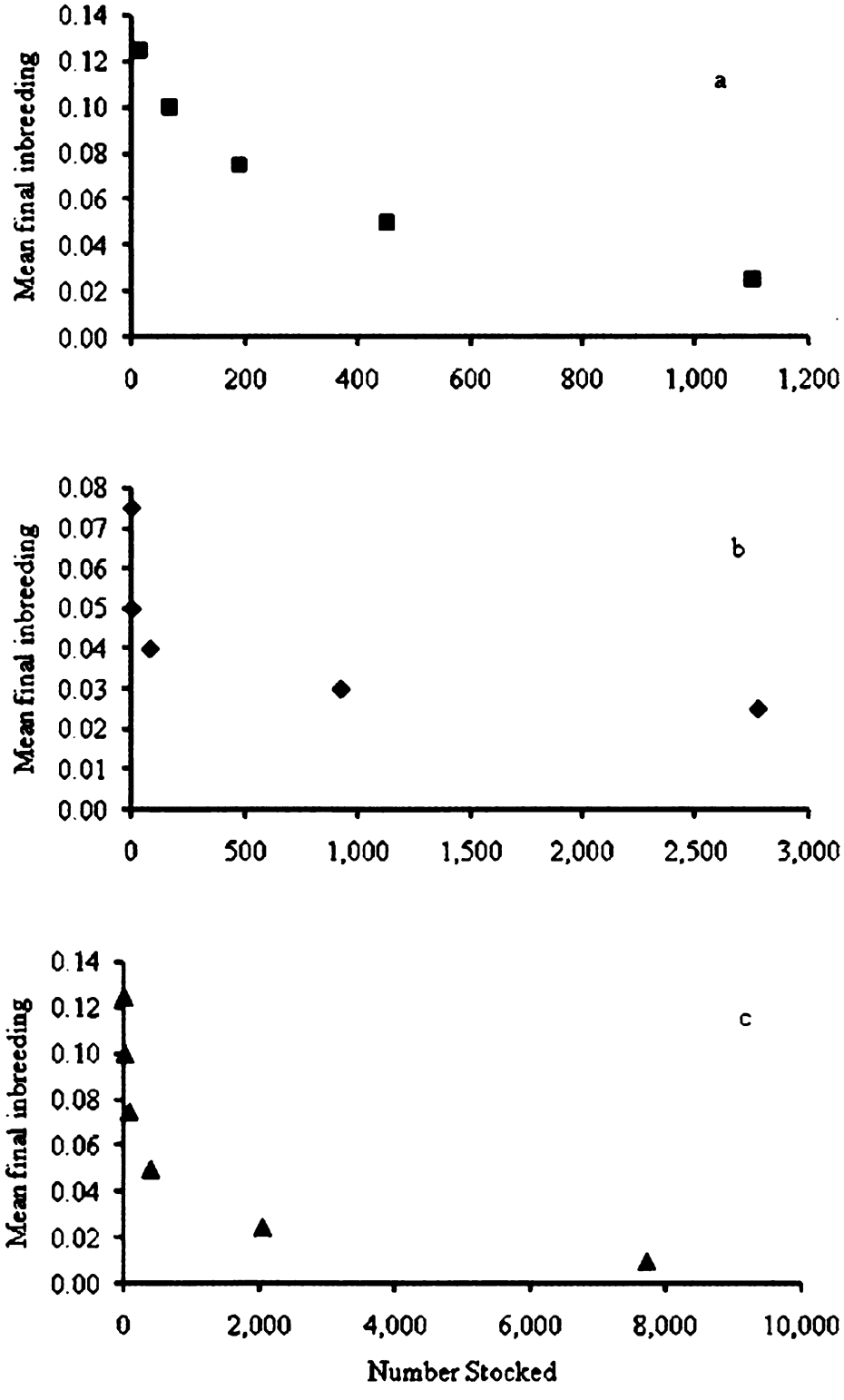


Figure B.5. The number of individuals that need to be stocked using the trickle strategy in order to attain a mean final inbreeding level for each scenario as determined by interpolation using a Weibull function where a) less than MVP, b) brink of MVP, and c) large, declining.

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