Fisheries and Oceans Canada
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Canadian Science Advisory Secretariat (CSAS)

Research Document 2023/011

Ontario and Prairie Region

Updated Recovery Potential Modelling of Lake Chubsucker (*Erimyzon sucetta*) in Canada

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February 2023

Foreword

This series documents the scientific basis for the evaluation of aquatic resources and ecosystems in Canada. As such, it addresses the issues of the day in the time frames required and the documents it contains are not intended as definitive statements on the subjects addressed but rather as progress reports on ongoing investigations.

Published by:

Fisheries and Oceans Canada
Canadian Science Advisory Secretariat
200 Kent Street
Ottawa ON K1A 0E6

http://www.dfo-mpo.gc.ca/csas-sccs/
csas-sccs@dfo-mpo.gc.ca

ISSN 1919-5044
ISBN 978-0-660-46983-6 Cat. No. Fs70-5/2023-011E-PDF

Correct citation for this publication:

Fung, S.R. and Koops, M.A. 2023. Updated Recovery Potential Modelling of Lake Chubsucker (*Erimyzon sucetta*) in Canada. DFO Can. Sci. Advis. Sec. Res. Doc. 2023/011. iv + 25 p.

Aussi disponible en français :

*Fung, S.R. et Koops, M.A. 2023. Mise à jour de l'évaluation du potentiel de rétablissement du sucet de lac (*Erimyzon sucetta*) au Canada. Secr. can. des avis sci. du MPO. Doc. de rech. 2023/011. iv + 27 p.*

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ABSTRACT

The Committee on the Status of Endangered Wildlife in Canada (COSEWIC) has assessed Lake Chubsucker (*Erimyzon sucetta*) in Canada as Endangered. Population modelling is presented to assess the impacts of harm and determine abundance and habitat recovery targets in support of a recovery potential assessment (RPA). This analysis demonstrated that Lake Chubsucker were most sensitive to perturbations to adult survival. Population viability analysis was used to identify potential recovery targets. Demographic sustainability (i.e., a self-sustaining population over the long term) can be achieved with population sizes of ~ 33,600 individuals of age-1 and older with a catastrophe frequency of 15% per generation and desired persistence probability of 99% over 100 years. Such a population would require 0.41 km^2 of lacustrine habitat or 0.12 km^2 of riverine habitat.

INTRODUCTION

The Lake Chubsucker (*Erimyzon sucetta*) is a small sucker species found in the Great Lakes basin. This warmwater fish grows up to a maximum total length of 280 mm in Ontario and prefers clear, shallow water with abundant aquatic plants. It spawns in marshes in the spring between April and June in Ontario. Lake Chubsucker is found in fragmented populations among the wetlands and tributaries of lakes Erie, Huron, and St. Clair. Only eleven extant populations remain, and three are in serious decline. Threats to Lake Chubsucker include increased turbidity, siltation, wetland drainage driven by increased agricultural, industrial, and urban development. Aquatic invasive species, most notably European common reed (*Phragmites australis australis*), also pose a severe threat to this species.

The Lake Chubsucker was designated as Endangered in 2008 and a Recovery Potential Assessment (RPA) was produced (DFO 2011). As support for the assessment process, a population model was created and analyzed in Young and Koops (2011). This species was reassessed in 2021. This report re-examines the data used in Young and Koops (2011), updates the model to incorporate density-dependence effects and applies new techniques to analyze the model.

The *Species at Risk Act* mandates the development of strategies for the protection and recovery of species that are at risk of extinction or extirpation from Canada. In response, Fisheries and Oceans Canada (DFO) has developed the recovery potential assessment (RPA; DFO 2007a,b) as a means of providing information and scientific advice. There are three components to each RPA: an assessment of species status, the scope for recovery, and scenarios for mitigation and alternatives to activities. This report contributes to the RPA through the use of population modelling to assess the impact of anthropogenic harm to populations and identify recovery targets for abundance and habitat with associated uncertainties. This work is based on a demographic approach developed by Vélez-Espino and Koops (2009, 2012) and Vélez-Espino et al. (2010).

METHODS

Information on vital rates was compiled to build projection matrices that incorporate environmental stochasticity and density-dependence. The impact of anthropogenic harm to populations was quantified with the use of elasticity and simulation analyses. Estimates of recovery targets for abundance and habitat were made with estimation of the minimum viable population (MVP) and the minimum area for population viability (MAPV).

SOURCES

Life history estimates for the Lake Chubsucker were based on sampling data from Canadian populations between 2002 and 2010. Locations included: Old Ausable Channel, Long Point Bay, Lyon’s Creek, Big Creek, L Lake, Turkey Point marshes, and St. Clair National Wildlife Area (NWA) (Bouvier and Mandrak 2011). Data used to estimate fecundity were obtained from Winter (1984).

All analyses and simulations were conducted using the statistical program R 3.6.3 (R Core Team 2020). Parameter values incorporated into the population model are listed in Tables 1 and 2.

LIFE HISTORY

Age and Growth

Following the data from Young and Koops (2011), Lake Chubsucker matures at age 2 and lives to age 8. A new von Bertalanffy growth function (VBGF) was fitted to their data (Figure 1, left panel) with the curve fixed to a hatch length of 6 mm (Scott and Crossman 1973), whereas Young and Koops (2011) had fixed the asymptotic length (L_∞) to 268 mm. Lake Chubsucker length-at-age, in mm, can be described as:

$$L_t = 209.3(1 - e^{-0.39(t+0.075)}) \tag{1}$$

Where t is the age of the fish.

Length-weight relationship for Lake Chubsucker was obtained from Schneider et al. (2000):

$$W = 10^{-5.24128} L^{3.19} \tag{2}$$

Where L is total length in mm and W is weight in grams.

Table 1. Parameter definitions and values used in the population model describing Lake Chubsucker.

	Symbol	Description	Parameter Value	Source
Age	t_{max}	Longevity	8	Young and Koops (2011)
	t_{mat}	Age-at-maturity	2	
	ζ	Generation time	4.18	Calculated
Growth	L_∞	Asymptotic length (mm)	209.3	Fitted
	k	von Bertalanffy growth coefficient	0.388	
	t_0	Age at 0 mm in length	-0.075	
Spawning	α_f	Fecundity allometric intercept	-4.14	Winter (1984)
	β_f	Fecundity allometric slope	2.617	
	φ	Proportion female at hatch	0.5	Assumed
	T	Spawning periodicity	1	
Weight	α_W	Length-weight allometric intercept	5.74×10^{-6}	Schneider et al. 2000
	β_W	Length-weight allometric exponent	3.19	
Mortality	$\sigma_{0,1}$	Egg to age-1 survival rate at λ = 1	0.00025	Calculated
	$\sigma_{0,max}$	Egg to age-1 survival rate at maximum λ	0.00128	
Density-dependence	β_d	Beverton-Holt density-dependence parameter	4.191	Calculated

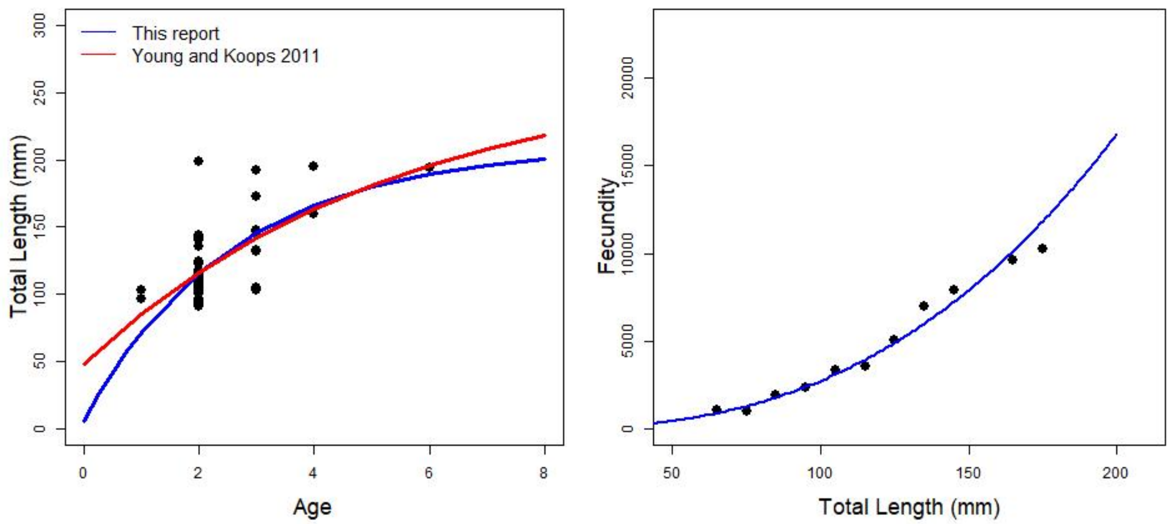

Figure 1. The left panel depicts the fitted von Bertalanffy growth curves for Lake Chubsucker based on data from Old Ausable Channel. The red curve is the one used in Young and Koops (2011) with a fixed asymptotic length and the blue curve is the curve with fixed hatch length used in this paper. The right panel depicts the length-fecundity relationship using data from Nebraska obtained from Winter (1984).

Reproduction

Data on the length-fecundity relationship of Lake Chubsucker were taken from Winter (1984); the same data were used in Young and Koops (2011). A relationship between length and egg count was fitted as a log-transformed linear model (Figure 1, right panel) and follows the equation:

$$\log(f) = -4.14 + 2.617 * \log(TL) \tag{3}$$

A 50% sex ratio and a spawning periodicity of 1 year was assumed. Age at maturity was assumed to be age 2 based on Young and Koops (2011).

Mortality

Size-dependent mortality was estimated by combining a size-dependent mortality model (Lorenzen 2000) and a catch curve analysis of age-frequency data (Ogle 2016). Mortality was assumed to decline proportionally with increases in size (Lorenzen 2000) such that

$$M_t = \frac{m_0}{L_t} \tag{4}$$

Where M_t and L_t are mortality and length at time *t* and m_0 is the mortality when $L_t = 1$. If L_t is described by the VBGF, the mean survival rate between ages *t* to *t*+1 (σ_t) can be estimated from (van der Lee and Koops 2016):

$$\sigma_t = \left[\frac{L_t e^{-k}}{L_{t+1}}\right]^{m_0/kL_\infty} \tag{5}$$

Where *k* and L_∞ are VBGF parameters. The parameter m_0 can be estimated via a length-modified catch curve analysis where the logged frequencies are binned based on Equation 6.

$$\ln L_t + kt \tag{6}$$

The slope of this catch curve regression (β) is m_0 divided by VBGF parameters as described in Equation 7.

$$\beta = \frac{-m_0}{kL_\infty} \quad (7)$$

Un-aged fish (n = 203) were randomly assigned ages based on their lengths via the Isermann-Knight method (Ogle 2016) and using the fitted VBGF as an age-key. This was repeated 1000 times to obtain an average catch curve regression slope (β) of -1.04 with a SD of 0.17. Annual survival rates were calculated based on this value and Equations 5 and 7.

To obtain the survival rate from egg to age-1, a desired level of population growth rate (λ) was first determined and then solved for the survival rate which would provide that λ given the population matrix (shown below). YOY survival rates required for a stable population (λ = 1) and for a theoretical maximum population growth obtained from allometric relationships as presented in Randall and Minns (2000) were calculated. λ_{max} can be calculated from the maximum intrinsic rate of increase (r_{max}) where $\lambda_{max} = e^{r_{max}}$, and r_{max} can be estimated based on the productivity-weight relationship described in Randall and Minns (2000):

$$r_{max} = 2.64W_{mat}^{-0.35} \quad (8)$$

Where W_{mat} is the weight-at-maturity in grams. This gives λ_{max} = 1.59 for Lake Chubsucker.

THE MODEL

The Lake Chubsucker life cycle was modelled using a female only, density-dependent, birth-pulse, post-breeding, age-structured population matrix model with annual projection intervals (Caswell 2001, Figure 2).

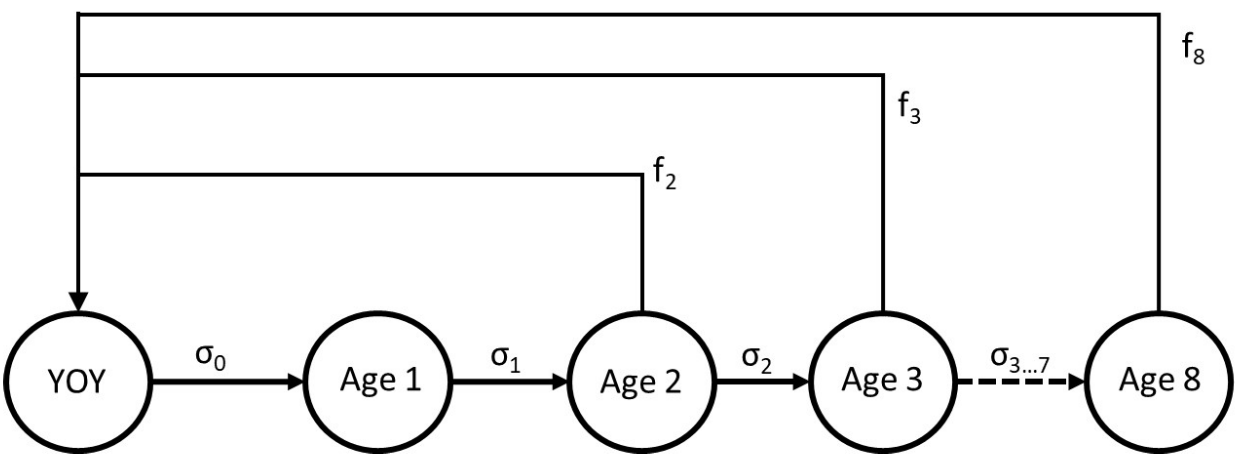

Figure 2. Generalized life cycle used to model the population dynamics of Lake Chubsucker. f_i represents stage-specific annual fecundity of an individual of age i and σ_i represents the survival from age i to i+1.

The matrix consisted of 9 stages (Figure 2) representing the YOY stage up to age 8. The fertility for the age-1 class (F_2) is positive since individuals counted as age-1 on a census in time *t* will mature to age-2 and produce offspring which would be counted at a census at *t*+1. The projection matrix **A** is the product of the transition matrix **B**, which contains the life-history parameters, and the density-dependence matrix **D** which represents the density-dependent effects.

$$
\boldsymbol{B} = \begin{bmatrix} 0 & F_2 & F_3 & \cdots & F_8 & 0 \\ \sigma_0 & 0 & 0 & \cdots & 0 & 0 \\ 0 & \sigma_1 & 0 & \cdots & 0 & 0 \\ 0 & 0 & \sigma_2 & \cdots & 0 & 0 \\ \vdots & \vdots & \vdots & \ddots & \vdots & \vdots \\ 0 & 0 & 0 & \cdots & \sigma_7 & 0 \end{bmatrix} \tag{9}
$$

and:

$$
\mathbf{A} = \mathbf{B} \circ \mathbf{D}, \tag{10}
$$

where the symbol ∘ represents the Hadamard product or the element by element multiplication of the matrices.

The age-based matrix model incorporated the fertility parameter F_i, and the annual survival rate σ_i, with the subscript *i* representing the age. Fertility, F_i, is the product of all reproductive parameters and as a post-breeding matrix also incorporates the probability of the female parent surviving from age *i*-1 to age *i* (σ_{i-1}):

$$
F_i = {f_i \varphi m_i \sigma_{i-1}}/{T} \tag{11}
$$

Where f_i represents age-specific fecundity at age *i*, φ represents the sex ratio, m_i represents the proportion of mature females of age *i*, σ_{i-1} represents the survival of a mature female from age *i*-1 to age *i*, and T represents spawning periodicity which was assumed to be 1 year.

Density-Dependence

Density dependence was assumed to only act on the first year of life. Density-dependence was incorporated using the Beverton-Holt (Equation 12) function. The function was adapted to the density-dependence matrix **D** which when multiplied by the equilibrium egg-to-age-1 survival rate $\sigma_{0,1}$ would produce the equilibrium rate when egg production is at carrying capacity and would approach the maximal survival rate $\sigma_{0,max}$ as egg production approaches 0 (Equation 13).

$$
R = \frac{\alpha N}{1+\beta N} \tag{12}
$$

$$
d_0 = \frac{{\sigma_{0,max}}/{\sigma_{0,1}}}{1+\beta_d \frac{N_e}{K_e}} \tag{13}
$$

Where $\sigma_{0,max}$ and $\sigma_{0,1}$ represent maximum and equilibrium egg-to-age-1 survival rates respectively. β_d is the density-dependence parameter scaled to a single individual and is equivalent to $\frac{\sigma_{0,max}}{\sigma_{0,1}} - 1$. N_e is the current annual egg production and K_e is egg production at carrying capacity.

The density-dependence matrix **D** was structured as shown below and is of the same size as the transition matrix **B**.

$$\mathbf{D} = \begin{bmatrix} 1 & 1 & 1 & 1 & \cdots & 1 \\ d_0 & 1 & 1 & 1 & \cdots & 1 \\ 1 & 1 & 1 & 1 & \cdots & 1 \\ 1 & 1 & 1 & 1 & \cdots & 1 \\ \vdots & \vdots & \vdots & \vdots & \ddots & \vdots \\ 1 & 1 & 1 & 1 & \cdots & 1 \end{bmatrix} \tag{14}$$

Stochasticity

Fertility and age-specific survival were varied annually to simulate environmental stochasticity in vital rates. The means and standard deviations of age-specific vital rates are listed in Table 2.

Age-specific survival was assumed to follow a lognormal distribution. Survival rate was varied as instantaneous mortality ($\sigma_i = e^{-M_i}$). *M* was assumed to vary following a normal distribution with a CV of 0.1 for the YOY stage. Variances for the survival rates of older ages was approximated by translating the standard error of the catch curve regression slope (β) into a standard error for m_0 and then applying the delta method (Oehlert 1992) to Equation 5 to estimate the variances. Stochasticity was then executed using the stretched-beta distribution to remove the extreme tails of the normal distribution but maintain the mean and standard deviation (Morris and Doak 2002). To account for similarities in mortality experienced by individuals of similar age, *M* was assumed to correlate between ages with an AR1 correlation structure (correlation diminishes as the difference between ages increases) with a correlation value of 0.5. YOY survival was assumed to vary independently of the older stages (correlation = 0).

Variances in fecundity were obtained via bootstrapping methods to estimate the 95% confidence intervals around the mean fecundity values at each age. Stochasticity was executed in a similar way to survival with the assumption that fecundity between age classes correlated with an AR1 structure with a correlation value of 0.5.

Table 2. Mean and standard deviations for Lake Chubsucker vital rates. Survival (σ_i) is the annual survival probability from age i to i+1. Fecundity (f_i) is the total number of eggs produced at age i.

Age	Length (mm)	Survival (σ_i) Mean	Survival (σ_i) SD	Fecundity (f_i) Mean	Fecundity (f_i) SD
1	71	0.432	0.063	0	NA
2	116	0.551	0.057	4012	144
3	146	0.606	0.053	7346	375
4	166	0.637	0.050	10351	719
5	180	0.655	0.048	12762	1066
6	190	0.666	0.047	14579	1345
7	196	0.674	0.046	15898	1562
8	200	0	NA	16833	1705

IMPACT OF HARM

The impact of anthropogenic harm to a Lake Chubsucker population was assessed with deterministic elasticity analyses of the projection matrix and stochastic simulations.

Elasticity analysis is a method to quantify the impact of changes to vital rates on a population. The elasticity of λ value represents the proportional change to the population growth rate (λ) from a proportional change in a vital rate. For example, an elasticity of λ value of 0.1 for fertility would indicate that the population growth rate would increase by 1% if fertility increased by 10%. The elasticity of N functions the same way except acting on stage-specific densities; for example, an elasticity of N value for adult density of 0.2 for perturbations to egg carrying capacity (K_e) would indicate that a 10% decrease in K_e would cause a 2% decrease in adult equilibrium density.

Elasticities are useful as they allow for assessment of how impactful changes to vital rates and other model parameters are to a population. Because they represent proportional changes their values are directly comparable, they are preferable to simulation analyses because of the speed with which they can be estimated allowing for many more perturbations to be examined than simulations. Elasticities are limited, however, as they represent permanent changes and assume all other model parameters remain unchanged. As a result, simulation analysis was used to examine the effects of transient or periodic harm to a population.

Elasticity of λ

Elasticities of λ (ε_λ) are calculated by taking the scaled partial derivatives of λ with respect to a vital rate (ν, Caswell 2001):

$$\varepsilon_\lambda = \frac{\nu}{\lambda}\sum_{i,j}\frac{\partial\lambda}{\partial a_{i,j}}\frac{\partial a_{i,j}}{\partial\nu}\,, \qquad (15)$$

where a_{ij} is the projection matrix element in row *i* and column *j*.

Elasticity of λ estimates are influenced by current conditions and elasticity analysis was performed for four states of population growth: declining, stable, growing and booming. A declining population was defined as one experiencing a 30% reduction in population size over 3 generations. This gives a λ_{min} = 0.972 for Lake Chubsucker. A stable population is defined as one with λ_1 = 1. A booming population was one with the population growth rate at the maximum value estimated using Equation 8, which was λ_{max} = 1.59. Finally, a growing population was defined as the geometric mean of λ_1 and λ_{max} and thus λ_{grow} is equal to 1.26.

Elasticity of N

Elasticities of N (ε_N) are calculated from the sensitivities of N ($\frac{d\widehat{\mathbf{N}}}{d\boldsymbol{v}^\intercal}$) where (Caswell 2019):

$$\frac{d\widehat{\mathbf{N}}}{d\boldsymbol{v}^\intercal} = \left(\mathbf{I}_i - \mathbf{A} - \left(\widehat{\mathbf{N}}^\intercal \otimes \mathbf{I}_i\right)\frac{\partial vec\mathbf{A}}{\partial\mathbf{N}^\intercal}\right)^{-1}\left(\widehat{\mathbf{N}}^\intercal \otimes \mathbf{I}_i\right)\frac{\partial vec\mathbf{A}}{\partial\boldsymbol{v}^\intercal}, \qquad (16)$$

and:

$$\varepsilon_{\mathrm{N}} = diag\left(\widehat{\mathbf{N}}\right)^{-1}\frac{dN}{d\boldsymbol{v}^\intercal}diag(\boldsymbol{v}). \qquad (17)$$

$\mathbf{A}$ is the projection matrix of dimension $i \times i$, $\mathbf{I}_i$ is an identity matrix of dimension $i \times i$, $\widehat{\mathbf{N}}$ is a vector of equilibrium densities, $\frac{\partial vec\mathbf{A}}{\partial\mathbf{N}^\intercal}$ is the partial derivatives of matrix $\mathbf{A}$ with respect to stage densities, $\frac{\partial vec\mathbf{A}}{\partial\boldsymbol{v}^\intercal}$ is the partial derivatives of matrix $\mathbf{A}$ with respect to the vital rates or the model parameters of interest, $\intercal$ is the transpose operator and $\otimes$ represents the Kronecker product.

$diag(\hat{\mathbf{N}})$ and $diag(\boldsymbol{v})$ represent diagonal matrices with the equilibrium densities and parameter values on the diagonal respectively and 0s on the off diagonal entries. See Caswell (2019) for more details.

Estimates of ε_N are provided with respect to perturbations of fecundity, life stage-specific survival rate, and density-dependence parameters for the Beverton-Holt model.

Simulation

Simulation analysis was used to investigate the impacts of stage-specific harm on adult population density. Stage-specific survival rates were reduced by some level of harm, ranging from 0 to 99%, in intervals of 10%. This harm was applied at different frequencies (once every 1, 2, 5 and 10 years) over a 100 year simulation period. A frequency of 1 indicates that harm is constant and applied every year, whereas a frequency of 10 indicates that harm is periodic and applied once every 10 years. To measure harm, the mean population size over the last 15 years of simulation was divided by the initial carrying capacity, resulting in a proportion of *K*. As a density-dependent model it is assumed for simulations where harm intervals are greater than one year that the population is able to recover in between applications of harm as conditions are returned to the initial state.

RECOVERY TARGETS

Abundance: Minimum Viable Population (MVP)

The concept of demographic sustainability was used to identify potential minimum recovery targets for Lake Chubsucker. Demographic sustainability is related to the concept of a minimum viable population (MVP, Shaffer 1981), and was defined as the minimum adult population size that results in a desired probability of persistence over 100 years, where ‘adult’ corresponds to mature females. MVP was estimated using simulation analysis which incorporated environmental stochasticity and density-dependence.

Important elements incorporated in population viability analysis include: the choice of time frame over which persistence is determined, the severity and frequency of catastrophic events, and the quasi-extinction threshold below which a population is deemed unviable. The choice of time frame is arbitrary and without biological rational; however, 100 years is likely reasonable for making management decisions.

The rate and severity of catastrophic events within Lake Chubsucker populations is not known. Based on a meta-analysis, Reed et al. (2003) determined that among vertebrate populations, catastrophic die-offs that resulted in a one-year decrease in population size > 50% occurred at a rate of 14% per generation on average. This result was used to guide the MVP simulations and six levels of catastrophe rate were used to allow for uncertainty and to examine the effects of varying catastrophe rates on the MVP. The rates chosen were 5%, 10%, 15%, 20%, 25% and 30% per generation. These rates correspond to annual catastrophe probabilities of 1.2%, 2.6%, 4.1%, 5.8%, 7.7% and 10% respectively.

The impact of catastrophes affect all life-stages simultaneously and was drawn randomly from a beta distribution scaled between 0.5 and 1 with shape parameters of 0.762 and 1.5 (based on Reed et al. 2003; Figure 3), representing the probability of a 50 to 100% decline in population size. Catastrophes represent any temporary and reversible large-scale disturbance to the population and may be from natural or anthropogenic causes.

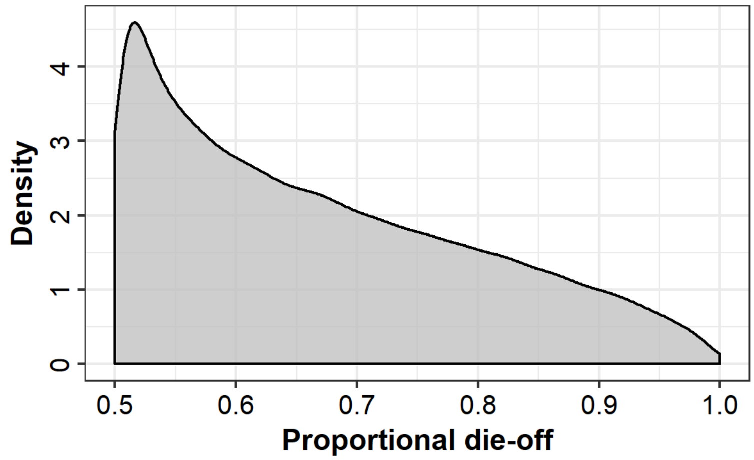

Figure 3. Beta distribution (scaled between 0.5 and 1) used in stochastic draws of catastrophic impacts. This represents the proportional decrease in population size following a catastrophic event. Shape parameters were 0.762 and 1.5 (based on Reed et al*. 2003).*

Quasi-extinction accounts for the compounding effects of Allee effects, demographic stochasticity and inbreeding depression (Lande 1988) leading a population to extinction once the threshold is crossed. The value of the quasi-extinction threshold cannot be empirically measured; therefore, 25 adult females was used as a reasonable approximation (Morris and Doak 2002).

Density-dependent, stochastic simulations were conducted for populations of various initial densities (initial density represented adult female carrying capacity, K_a, where λ = 1). Simulations were run for 100 years. Independent simulations incorporated six rates of catastrophes. Each simulation was replicated 5,000 times and the number of quasi-extinctions were counted. The probability of extinction (*P[ext.]*) was modelled as a logistic regression, such that:

$$P[ext.] = \frac{1}{1+e^{-(b_{MVP} log_{10}(N_a)+a_{MVP})}}, \qquad (18)$$

where a_{MVP} and b_{MVP} represent the fitted intercept and slope from the logistic regression. Equation 18 can be rearranged to estimate the adult population size required to give a desired level of population persistence (MVP):

$$MVP = 10^{-\frac{\log\left(1/_{P[ext.]}-1\right)+a_{MVP}}{b_{MVP}}}. \qquad (19)$$

MVP estimates are presented for quasi-extinction probabilities of 5% and 1%.

Habitat: Minimum Area for Population Viability (MAPV)

Minimum area for population viability (MAPV) is defined as the quantity of habitat required to support a population of MVP size (Velez-Espino et al. 2010). MAPV is estimated simply as MVP divided by mean population density. Some Lake Chubsucker population density estimates were available from field sampling and previous studies. Depletion surveys were undertaken in 2010 at Lyons Creek and L Lake. Mean population density was estimated to be 0.0105 (± 0.0156) individuals/m^2 at Lyons Creek and 0.0861 (± 0.1385) and 0.0119 (± 0.0181) individuals/m^2 at L Lake in June and August respectively (Ministry of Northern Development, Mines, Natural Resources and Forestry (NDMNRF) unpublished data). A 2021 study of the St. Clair National Wildlife Area (NWA) East cell estimated a population abundance of 1375 individuals in an area of 60.93 hectares (DFO 2021). Fifty-nine percent of that population were estimated to be YOY, 21% to be age-1 and 18% to be adults. Considering only individuals of age-1 or older, the population density is estimated to be 9.252 individuals/ha.

Allometric relationships were also used to provide a population density estimate. Equations describing the relationship between the density and mean weight of a community could be found on Table 2 of Randall et al. (1995):

$$\log_{10} D = 4.48 - 1.01 * \log_{10} W \quad (20)$$

$$\log_{10} D = 4.90 - 0.94 * \log_{10} W \quad (21)$$

Where D is the number of individuals per hectare and W is the mean weight of the fish in grams. Equation 20 describes the population density for communities in lacustrine habitats while Equation 21 describes the density for riverine habitats.

To obtain the MAPV, the MVP number of adult females was first converted to a total population size of both sexes based on assumptions of a stable age structure, the maturity schedule and the sex ratio. The total population is then divided into age classes based on a stable age structure and the average length for each age class was calculated based on the geometric mean of the lengths at the endpoints of each class. Average weight for each age class was calculated from the average lengths based on allometric length-weight relationships and the density for each age class was calculated based on Equation 20 or 21. The MAPV for each age class was obtained by dividing the number of individuals by the density and the sum of MAPV across all age classes is the total MAPV.

RECOVERY TIMES

Time to recovery was estimated using simulation analysis similar to MVP simulations. Since current Lake Chubsucker population abundance is unknown, simulations began with initial population sizes set to 10% of MVP. Simulations incorporated: stochasticity, density-dependence, and catastrophes in the same manner as MVP simulations. The population was deemed recovered when MVP was reached (MVP was also used as carrying capacity). Simulations were repeated 5,000 times. Setting carrying capacity at MVP can be viewed as the minimum population size necessary for population persistence. This assumption would result in the longest times for recovery for a viable population. If carrying capacity were greater than MVP, recovery times would be shorter.

RESULTS

IMPACT OF HARM

The impact of harm to Lake Chubsucker populations was analyzed with deterministic elasticity analysis on the population growth rate (Figures 4 and 5) and on life-stage densities (Figure 6), and via the use of population simulations (Figure 7).

Elasticity of λ

The elasticity of λ to perturbations of vital rates gives an indication of how the population may respond to changes in vital rates; positive values indicate that population growth rate will increase if the vital rate is increased.

Figure 4 presents elasticity estimates for fertility (F) and survival rates (σ) broken down by age classes. Based on this breakdown, the growth rate is most sensitive to changes in early life (e.g., σ_0 and σ_1) and sensitivity decreases as age increase. However, because impacts to vital rates will rarely be constrained to only a single age class, a breakdown of elasticity values by life-stages is presented on Figure 5 which shows the combined elasticity estimates for fertility and survival rates for the YOY (age 0), juvenile (age 1), and adult (age 2-8) life-stages. Because the adult life-stage includes more age classes than the YOY and juvenile stages, the combined elasticity estimate for the adult stage becomes greater than those of the earlier life-stages.

In addition, sensitivity to changes in vital rates is also dependent on the population's current growth rate. For the vital rates of early life age classes, sensitivity increases as growth rate increases while the reverse is true for older ages. The result is that adult survival has the strongest impact on λ when the population growth rate is stable or declining while YOY and juvenile rates increase in importance when the population is growing or booming. Elasticity values for fertility, YOY and juvenile survival rate increase from ~ 0.23 to ~ 0.33 as λ increases while the elasticity for adult survival decreases from ~ 0.53 to ~ 0.35. These results indicate that a population of Lake Chubsucker would be most sensitive to changes in adult survival. For example, if adult survival is reduced by 5% while the population is stable (λ = 1, elasticity of $\sigma_{a,stable}$ = 0.52), the population will experience a 2.6% annual decline (1 – 0.05 x 0.52).

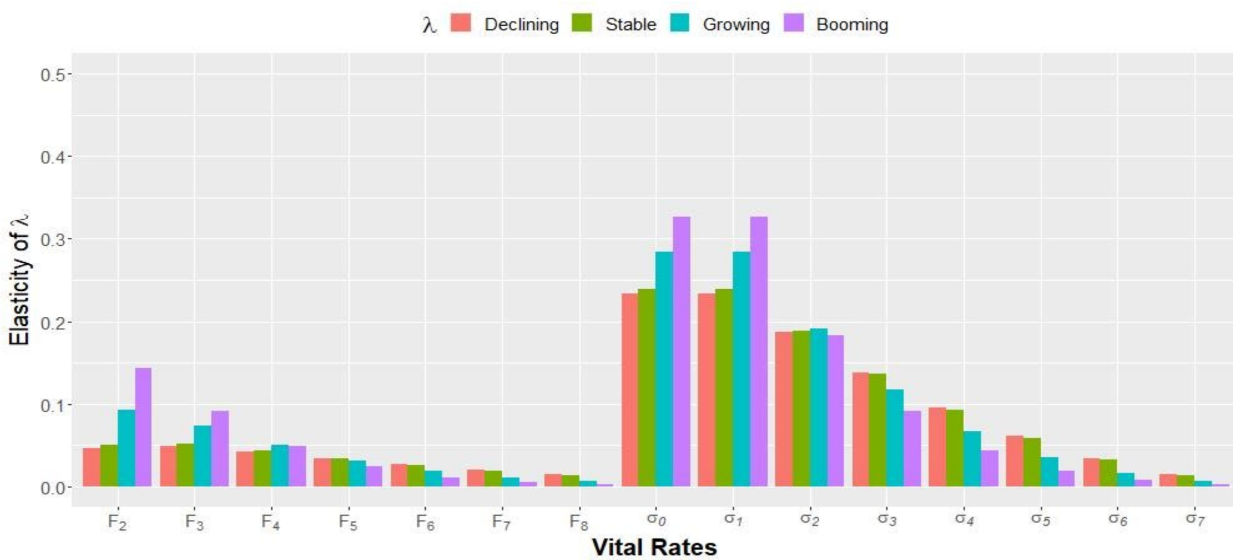

Figure 4. Elasticity of λ analysis broken down into all age classes under 4 population growth states: declining, stable, growing and booming. F represents fertility indicating the effects of independent perturbations to all parameters that contribute to fertility (Equation 11) and σ represents survival.

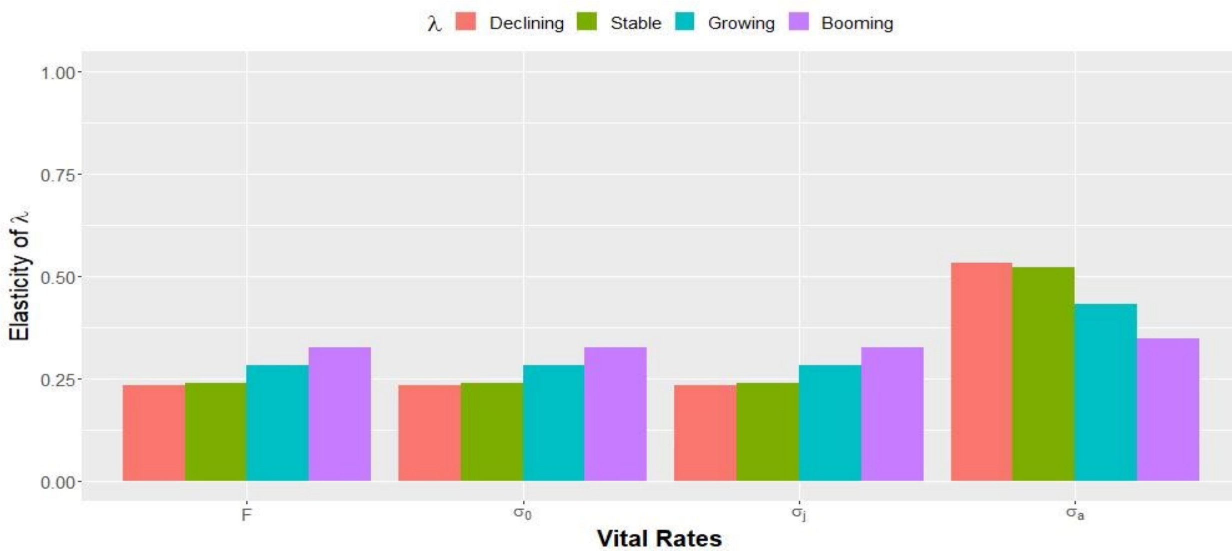

Figure 5. Elasticity of λ analysis with elasticities summed up by life-stages under 4 population states: declining, stable, growing and booming. F represents the total fertility across all stages and σ represents survival for the YOY (0), juvenile (j) and adult (a) stages.

Elasticity of N

The above analysis of elasticities of λ assumes density-independence, but if density-dependence acts on the populations the results may not hold. Therefore an analysis of the elasticity of life-stage-specific density (N_s) to changes in vital rates was performed to investigate the effects of density-dependence acting on the YOY life-stage. Positive elasticity values indicate that population density will increase in response to an increase in that vital rate.

For Lake Chubsucker, perturbations to density-dependence parameters have similar impacts on density across all life-stages. Increase in carrying capacity (K_e), equilibrium YOY survival ($\sigma_{0,1}$) and maximum YOY survival ($\sigma_{0,max}$) causes increases in density.

Perturbations to fertility (F) also have a similar positive impact on density across all life-stages while perturbations to survival rates exhibit some variation. Both adult (σ_a) and juvenile (σ_j) survival rates have positive elasticity values but densities are more sensitive to adult survival rates compared to juvenile rates. Adult densities are also more sensitive than juvenile densities to survival rate perturbations. These results are consistent with the results from the elasticity of λ analysis.

As an example, the elasticity values from changes in adult survival were 1.88 for adult density and 0.52 for juvenile density. Therefore a 10% increase in adult survival would lead to a 18.8% increase in the number of adults and a 5.2% increase in the number of juveniles in the population.

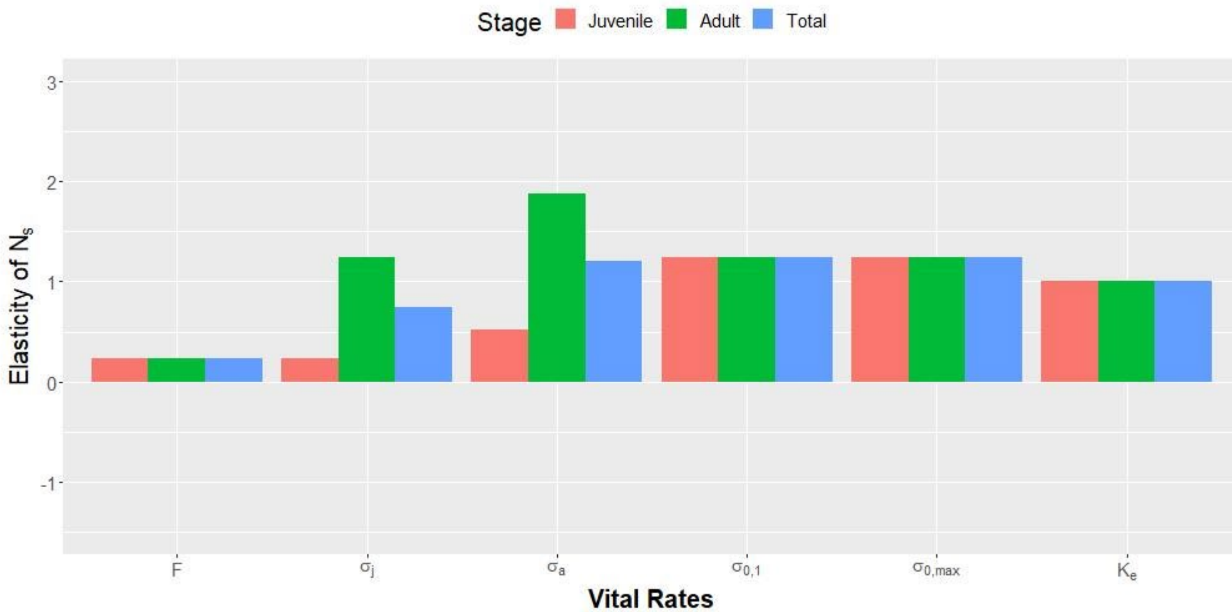

Figure 6. Elasticity of N_s analysis results for Lake Chubsucker. The x-axis represents the model parameter that is perturbed; the y-axis represents the resultant proportional change to life-stage-specific density. F represents total fertility, and σ_s represents life-stage specific survival and K_e represents egg carrying capacity.

Simulation

The above elasticity analyses assume that any change to a vital rate is permanent. Therefore, simulation analysis was used to investigate how adult population size may respond to periodic perturbations occurring annually (for comparison to elasticity analysis), every second year, fifth year, and tenth year. Harm was applied to either the YOY stage, the juvenile stage, the adult stage or to all stages.

Figure 7 depicts the impact of harm to a Lake Chubsucker population and the results are consistent with the elasticity analyses where the adult stage is most sensitive to perturbation. When harm is applied to adults, the population trajectories exhibit greater negative slopes and reach a lower population level than when harm is applied to YOY or juvenile stages.

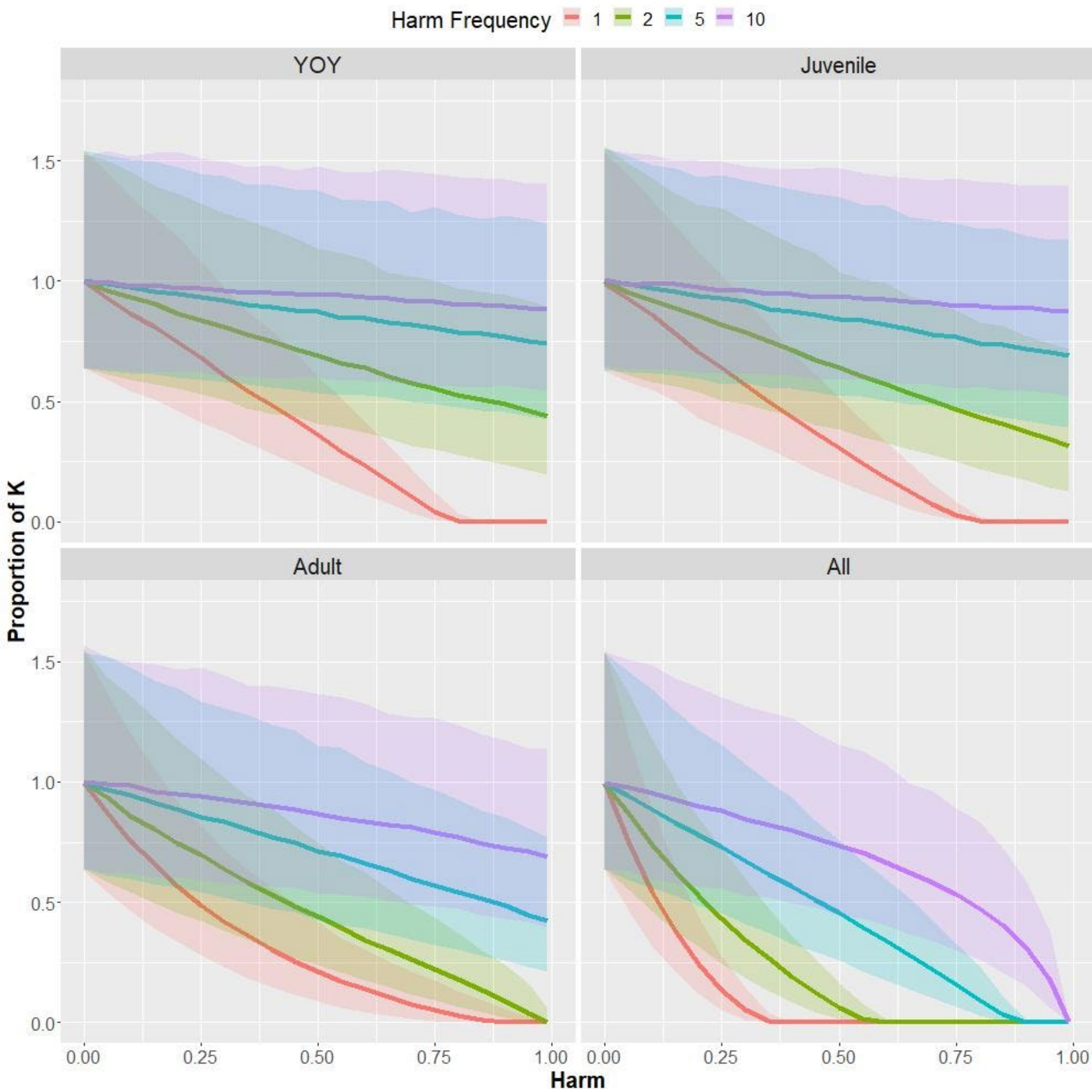

Figure 7. Results from harm simulation analysis where harm is applied at different frequencies to one or more life-stages for Lake Chubsucker. The x-axis represent the proportional harm (e.g., annual mortality) applied to the life-stage and the y-axis represents the proportional decrease in adult abundance in the final 15 years of a 100 year simulation. The solid lines represent the median impact and the surrounding polygons represent 95% confidence intervals.

RECOVERY TARGETS

Abundance: Minimum Viable Population (MVP)

Demographic sustainability was assessed using stochastic, density-dependent population simulations. Simulation outputs (the proportion of simulations reaching the threshold for quasi-extinctions) were fitted using a logistic regression (equation 18; Table 3; Figure 8).

Recovery target abundances that provide a 5% and 1% probability of quasi-extinction over 100 years are presented (Table 4). Simulation outputs applied solely to adult females in the population and should be doubled to obtain whole adult (male and female) population estimates.

Table 3. Parameter values from logistic regression of extinction probability and adult female population size (equation 18) for Lake Chubsucker population.

Regression Parameters	**Catastrophe Rates per Generation**					
	5%	**10%**	**15%**	**20%**	**25%**	**30%**
$\mathbf{a_{MVP}}$	6.431	6.867	6.930	7.151	6.686	6.473
$\mathbf{b_{MVP}}$	-3.378	-3.181	-2.932	-2.777	-2.421	-2.152

The number of adult female Lake Chubsucker required for a 99% persistence probability over 100 years is ~ 1,800 for a 5% generational catastrophe rate, ~ 4,000 for a 10% rate and ~ 8,500 for the 15% rate.

The MVP number for adults could be obtained by doubling the female numbers. Assuming a stable age structure and based on the maturity schedule, the number of adult females can also be converted to a population size comprised of both sexes and all individuals age-1 and older. Under a 99% chance of persistence, Lake Chubsucker adult and juvenile MVP is ~ 7,200 for a 5% generational catastrophe rate, ~ 15,800 for a 10% rate and ~ 33,600 for a 15% rate. All MVP values can be found on Table 4.

The frequency of catastrophes has a strong impact on the required population size for sustainability. The MVP required for a 99% persistence probability over 100 years increases exponentially according to the equation:

$$MVP = 4257 * e^{48.42 * P_{cat,a}} \tag{22}$$

Where $P_{cat,a}$ is the annual catastrophe rate. This relationship is depicted on Figure 9.

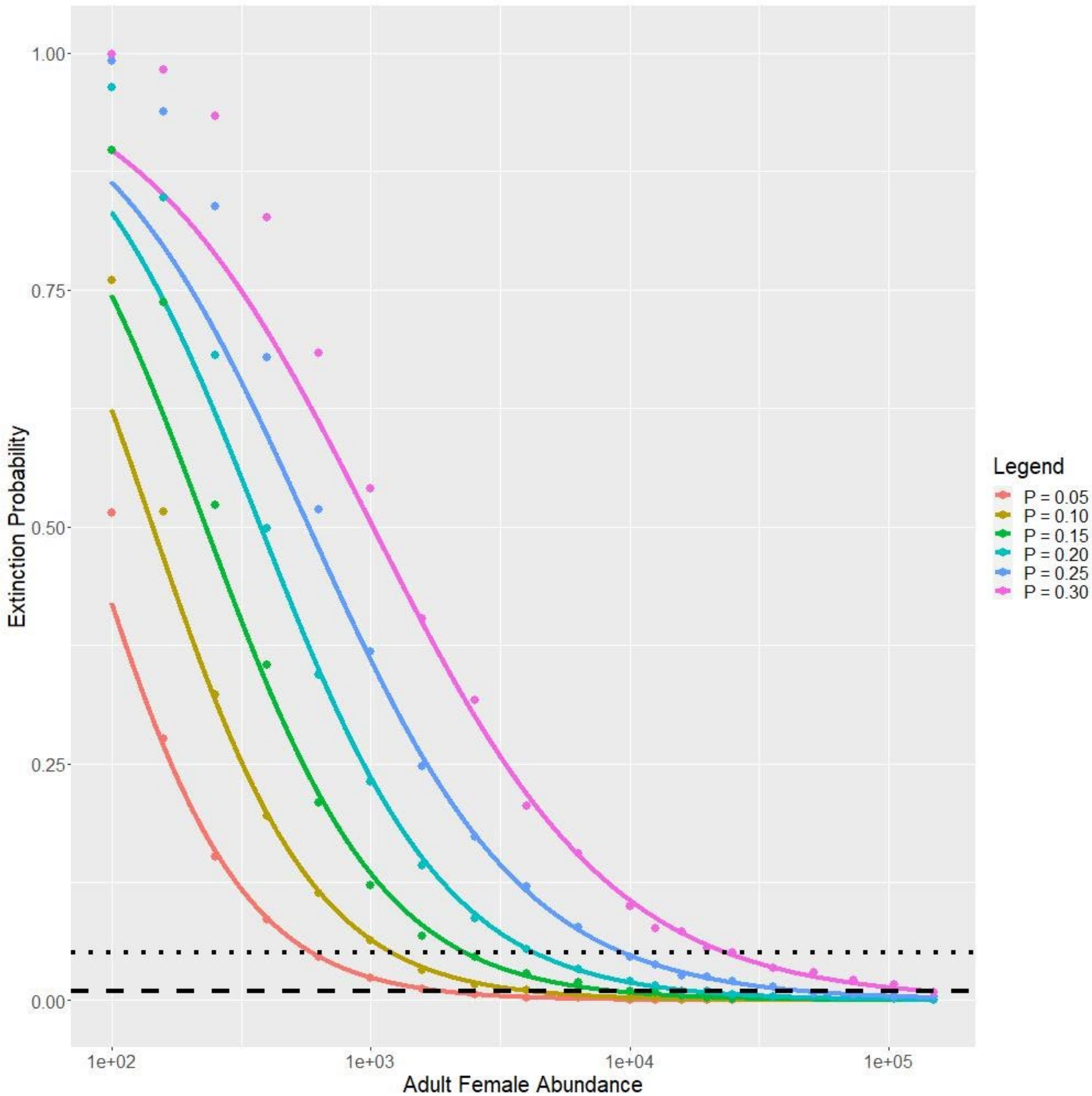

Figure 8. The probability of quasi-extinction at various adult female abundances ranging from 5% to 30% per generation catastrophe rate in 5% intervals. The points represent mean simulation values and the lines represent fitted logistic regressions. The horizontal dotted and dashed lines represents the 5% and 1% threshold for quasi-extinction respectively. Curves generated using a logistic regression (equation 18) with parameter values as per Table 3.

Table 4. The minimum viable population (MVP) and minimum area for population viability (MAPV) under six catastrophe rates and for two probabilities of quasi-extinction.

Risk of Extinction	Catastrophe Rate per Generation	MVP			MAPV (ha)	
		Adult Females	All Adults	Age-1 and Older	Lacustrine	Riverine
5%	5%	597	1,194	2,349	2.9	0.8
	10%	1,214	2,428	4,777	5.9	1.7
	15%	2,334	4,668	9,184	11	3.2
	20%	4,324	8,648	17,015	21	6
	25%	9,505	19,010	37,402	46	13
	30%	23,817	47,634	93,720	115	33
1%	5%	1,837	3,674	7,229	8.9	2.6
	10%	4,009	8,018	15,775	19	5.6
	15%	8,532	17,064	33,573	41	12
	20%	16,995	33,990	66,875	82	24
	25%	45,681	91,362	179,755	221	64
	30%	139,329	278,658	548,260	674	194

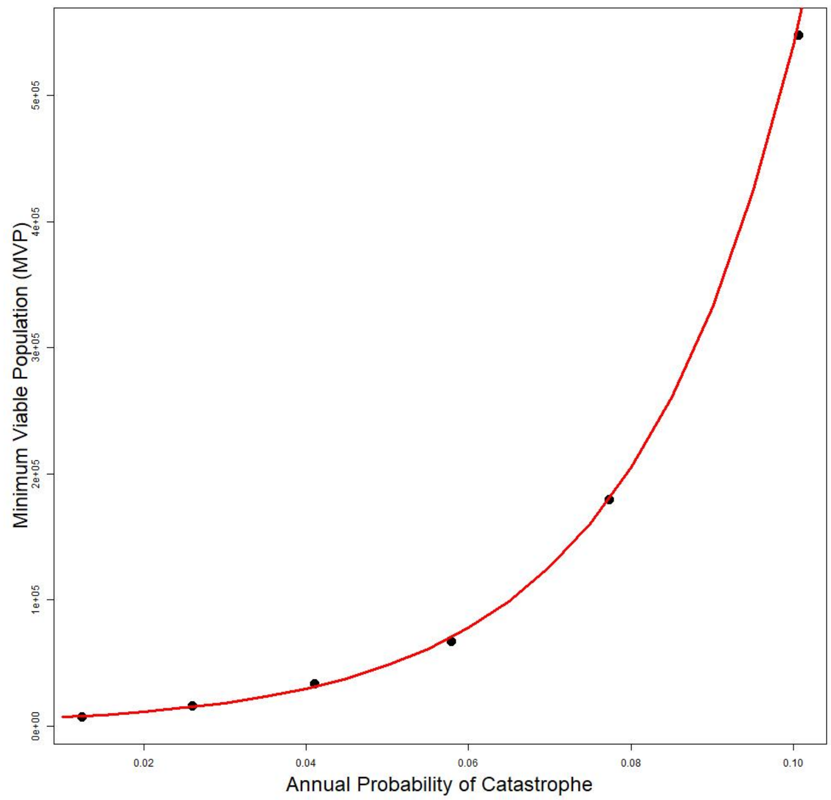

Figure 9. The minimum viable population (MVP) as an exponential function of the annual probability of catastrophe. The points represents the MVP values for generational catastrophe rates ranging from 5% to 30% at 5% intervals, expressed as annual probabilities.

Habitat: Minimum Area for Population Viability (MAPV)

The stable age distribution for Lake Chubsucker is 99.95% YOY, 0.025% juveniles (age 1) and 0.025% adults (age 2–8). With a 15% generational catastrophe rate and 1% extinction risk, the target MVP is ~ 33,600 age-1 and older individuals.

MAPV calculated using NDMNRF density estimates of 0.0861, 0.0119, and 0.0105 individuals/m^2 results in MAPV estimates of 0.39, 2.82 and 3.2 km^2 respectively. With the density estimate of 0.0009252 individuals/m^2 from the St. Clair NWA (East cell), the MAPV is estimated to be 36.3 km^2. MAPV values are sensitive to the density estimates used in their calculations. The density estimate from St. Clair NWA is much lower than densities from the other locations and might be reflective of a depleted population living in a degraded habitat and not representative of Lake Chubsucker natural density. The use of this density estimate to calculate MAPV might lead to an unreasonably high estimate.

When population density is estimated using allometric Equations 20 and 21, the required MAPV for this population is ~ 0.41 km^2 for lacustrine habitats and ~ 0.12 km^2 for riverine habitats. MAPV values for other MVP targets can be found on Table 4. A comparison of the MAPV with the amount of habitat available to various Lake Chubsucker populations is listed in Table 5. Habitat sizes were coarsely estimated in Staton et al. (2010) following an area of occupancy approach, modified where additional data permitted; these estimates have been updated to reflect how areas are currently differentiated and have been expanded to include recent detections (i.e., since 2010). These approximations are based on suitable habitat at a coarse scale, and do not necessarily include all of the habitat that contributes to life-history processes. Additionally, population-specific habitat requirements are poorly understood, and therefore, not accounted for in these estimates. A habitat size estimate for Lake St. Clair is not possible at this time as records from this area have been sporadic, and some localities within this area have only one record making it difficult to assign boundaries. A number of the habitats identified as lacustrine on Table 5 could also be identified as wetland habitat. These habitats would be expected to have a higher fish density, and hence a lower MAPV, compared to open water lacustrine habitats. However, because allometric relationships for wetlands are not available, the lacustrine MAPV estimate could be instead used as a conservative target for those wetlands.

Table 5. The amount of available habitat (km^2) for each Lake Chubsucker population and whether it meets the demand for the minimum area for population viability (MAPV).

Population	Available Habitat (km^2)	Habitat Type	MAPV Achieved (Y/N)?
Old Ausable Channel	0.61	Lacustrine	Yes
L Lake	0.136	Lacustrine	No
Lake St. Clair	NA	Lacustrine	-
Walpole Island dyked marshes	NA	Lacustrine	-
St. Clair NWA (East and West cells)	3.52	Lacustrine	Yes
Point Pelee National Park (Redhead, Girardin, Lake ponds)	1.44	Lacustrine	Yes
Rondeau Bay	9.43	Lacustrine	Yes
Long Point Bay	59.62	Lacustrine	Yes
Long Point NWA	81.34	Lacustrine	Yes
Big Creek NWA	0.53	Lacustrine	Yes
Lyons Creek	0.418	Riverine	Yes

RECOVERY TIMES

Since Lake Chubsucker abundance was unknown, simulations were used to estimate a time-to-recovery assuming a low current abundance. MVP was set as the carrying capacity and was used as the recovery target. Initial population was set at 10% of MVP. These simulations reflect a situation where there is sufficiently available habitat or a removal of threats or competitors such that vital rates return to a state that permits population size increase towards carrying capacity.

Recovery simulations result in a distribution of recovery times as shown on Figure 10. The median time to recovery is 15 years and 95% percent of populations reached recovery in 39 years or less.

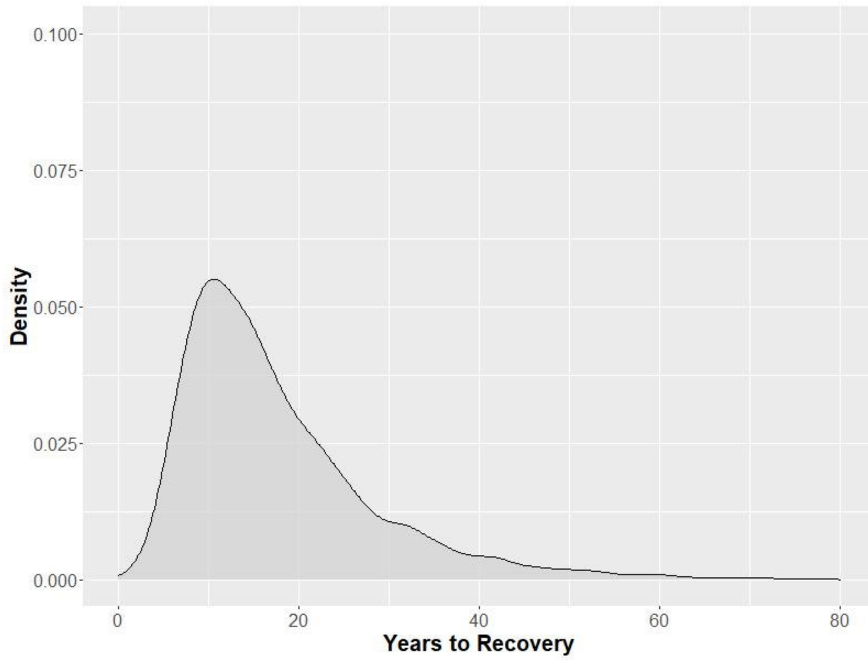

Figure 10. Distribution of recovery time-frames for all simulations of Lake Chubsucker given a recovery target of MVP and initial population of 10% of MVP.

DISCUSSION

A population model for Lake Chubsucker from Young and Koops (2011) was updated to make new predictions on how the population may respond to anthropogenic harm and estimate recovery targets for abundance and habitat. Limited information on Lake Chubsucker life-history characteristics has been published. The available information was compiled and additional parameters estimated using DFO and NDMNRF survey data.

There are a number of differences between the findings of this report and those of Young and Koops (2011). These differences are mainly due to the inclusion of density-dependence in the current model, the allowance of catastrophes to reduce a population by greater than 50%, the usage of a different von Bertalanffy growth curve to estimate vital rates, and the choice of using a larger number of individuals as the extinction threshold.

Multiple methods were used to assess the impacts of harm to Lake Chubsucker populations. All methods show that Lake Chubsucker are most sensitive to changes in adult survival. This result holds true for all population growth rates (λ), but as λ increases, the other vital rates increase in importance until they are almost equal under maximum λ. This contradicts the conclusion from Young and Koops (2011) which suggested that juvenile and early life vital rates were most important. Their finding was based on an elasticity analysis with a breakdown by age class similar to Figure 4 of this report. However, it seems unlikely that a perturbation would only affect a single age class, hence an analysis with a breakdown by life-stage (Figure 5) would be more appropriate. When analyzed this way, it becomes clear that the adult stage is more sensitive to impacts due to containing more age classes than the early life-stages.

Elasticity analysis of N (Figure 6) demonstrates the impact of changes to vital rates on stage-specific population densities incorporating the effects of density-dependence. Reduction in the adult survival rate by ~ 13% would cause the adult population to decline by 25% from its initial carrying capacity. This is similar to results from the annual harm simulations (Figure 7) where harm of ~ 12% to adult survival leads to a 25% decline in adult abundance. Adult abundance is less sensitive to YOY and juvenile survival where a ~ 20% in either rate would lead to a 25% decline.

Estimates of recovery targets for abundance were made based on simulation analysis to determine the population sizes required for demographic stability through estimates of minimum viable population size (MVP). The results depend on persistence probability and rate of catastrophe. Under a 15% per generation catastrophe rate and a 99% persistence probability, Lake Chubsucker require ~ 8,500 female adults, which translate to ~ 17,000 adults of both sexes or ~ 33,600 age-1 and older individuals.

MVP targets for other catastrophe rates were also estimated and were fitted to an exponential function of the annual catastrophe probability. A 15% per generation catastrophe rate was considered most likely and the MVP target associated with that rate was used for further analyses. Other MVP targets could be used if new information about catastrophe rates becomes available.

This MVP target is much higher than the ~ 2,700 adults MVP target initially recommended in Young and Koops (2011). The main reason for this difference is that the previous report used 1 adult female as the extinction threshold whereas a quasi-extinction threshold of 25 adult females was used in this report. Their report's MVP estimate of ~ 45,000 adults under a quasi-extinction threshold of 50 adult (i.e., 25 male and 25 female adults) would be a more in-kind comparison. The inclusion of density-dependence effects in the new model is the likely reason why the new MVP estimate of ~ 17,000 adults is less than half of this previous estimate.

Estimates of MVP were converted to habitat requirements by dividing the MVP by mean estimates of density. Based on density estimates from NDMNRF field sampling, the MAPV for ~ 17,000 adults (or ~ 33,600 age-1 and older) is 0.39, 2.82 or 3.2 km^2. Based on the St. Clair NWA density estimate, the MAPV is 36.3 km^2. Based on body-size and population density relationships found in Randall et al. (1995), the MAPV is 0.41 km^2 for lacustrine habitats and 0.12 km^2 for riverine habitats. The two MAPV estimates from the allometric equations are comparable to the smallest MAPV estimated from the field sampling densities and smaller than all the others. Both estimates are also smaller than the recommended MAPV of 1 km^2 based on ~ 2,700 adults found in Young and Koops (2011).

UNCERTAINTIES

The life-history characteristics of Lake Chubsucker were not well-described in the literature. As a result, there is uncertainty in the parameterization of the population model. Somatic growth was fitted to a small data set (n = 66) with limited timespan. Maximum population growth was calculated using general allometric relationships. There is also uncertainty as to whether the age-of-maturity is at age-2 or age-3.

The data used to estimate life-history parameters were gathered decades ago and may not reflect current Lake Chubsucker population dynamics. Threats that have been acting on the population during this time could have shifted life history parameters. Fecundity data were obtained from an experimental stocking study conducted in Nebraska and might not accurately reflect the fecundity of wild Canadian populations.

Much of the data used to estimate mortality was originally un-aged. An age-key derived from von Bertalanffy growth curve was used to estimate fish age, adding potential error to mortality estimates. The fish data were also not individually sized but rather recorded as the number of fish caught at a certain location and time with the largest and smallest fish being of a particular length. Due to the uncertainty about the distribution of lengths within that interval, only the largest and smallest fish were used for further analysis. This could potentially introduce bias to the mortality estimate.

The density of Lake Chubsucker is poorly known. Density estimates used to calculate MAPV were derived from isolated, short-term field sampling studies or from general allometric relationships. When allometric relationships were used, the area-per-individual (API) estimated by Young and Koops (2011) is higher than the one estimated for this report, even though both originated from Randall et al. (1995). The equation for API (Equation 10 in Young and Koops 2011) could not be re-derived for this report. The large range of MAPV values derived from the various density estimates is a major source of uncertainty. The allometric relationship for wetland densities is unknown and lacustrine estimates were used as a substitute.

Finally, the frequency of catastrophic events for Lake Chubsucker was unknown and had significant impacts on estimates of MVP. Results are presented for various rates of catastrophes, however, which is most appropriate is not clear. Best practices may be to use 15% per generation as the estimate as this is close to the cross taxa average for vertebrates (Reed et al. 2003).

Elements

Element 3: Estimate the current or recent life-history parameters for Lake Chubsucker.

The best available data were assembled to provide life-history parameters for Lake Chubsucker. The value for each life-history parameter used in the modelling is presented in Tables 1 and 2.

Element 12: Propose candidate abundance and distribution target(s) for recovery

Abundance targets were estimated using population viability analysis and estimates of minimum viable population (MVP). Simulations incorporated density-dependence, environmental stochasticity, and random catastrophes. Targets varied depending on the model used, desired persistence probability and catastrophe rate (Table 4). Under a 15% generational catastrophe rate with 99% probability of persistence, the MVP target is 33,600 age-1 and older individuals of both sexes. These simulation abundance targets relate to single isolated populations. Since there are 11 extant populations in Canada, persistence of the species as a whole would be higher.

Element 13: Project expected population trajectories over a scientifically reasonable time frame (minimum 10 years), and trajectories over to the potential recovery target(s), given current Lake Chubsucker population dynamics parameters.

Population estimates of Lake Chubsucker are very limited. The only available estimate was from St. Clair NWA which estimated a very low abundance of 1375 individuals. No population trajectories were available.

Element 14: Provide advice on the degree to which supply of suitable habitat meets the demands of the species both at present and when the species reaches the potential recovery target(s) identified in element 12.

The quantity of habitat required to support an MVP-size population of Lake Chubsucker with a 1% extinction probability and a catastrophe frequency of 15% per generation was estimated to be ~ 0.41 km^2 of lacustrine habitat or ~ 0.12 km^2 of riverine habitat. The habitat supply available to various Lake Chubsucker populations and whether those area meets the demand for MAPV is listed on Table 5. Some of the habitats listed on Table 5 could be identified as wetlands instead of lacustrine, but due to the lack of knowledge about wetland fish community densities, lacustrine MAPV value was used to provide a conservative estimate. The habitat supply values also assume that the entire area is suitable and available for use by Lake Chubsucker. This is unlikely to be true and actual habitat supply would be lower than those listed on the table.

Element 15: Assess the probability that the potential recovery target(s) can be achieved under the current rates of population dynamics, and how that probability would vary with different mortality (especially lower) and productivity (especially higher) parameters.

Elasticity analyses could be used to inform how best to change vital rates to achieve a population growth rate leading to recovery targets. However, the lack of current information on population dynamics prevents this further analysis. Limited Lake Chubsucker population density estimates are available from sites such as the St. Clair NWA but lack population trajectories.

Element 19: Estimate the reduction in mortality rate expected by each of the mitigation measures or alternatives in element 16 and the increase in productivity or survivorship associated with each measure in element 17.

No clear links have been identified between mitigation measures and Lake Chubsucker mortality rates or productivity. Therefore, it is difficult to provide guidance about the effect of mitigation measures on mortality rates or productivity.

Element 20: Project expected population trajectory (and uncertainties) over a scientifically reasonable time frame and to the time of reaching recovery targets, given mortality rates and productivities associated with the specific measures identified for exploration in element 19. Include those that provide as high a probability of survivorship and recovery as possible for biologically realistic parameter values.

Without a direct link between mitigation measures and Lake Chubsucker mortality rates or productivity, this information cannot be provided under mitigation scenarios. Under ideal conditions, Lake Chubsucker can reach MVP 95% of the time in 39 years or less.

Element 21: Recommend parameter values for population productivity and starting mortality rates and, where necessary, specialized features of population models that would be required to allow exploration of additional scenarios as part of the assessment of economic, social, and cultural impacts in support of the listing process.

The parameter values presented in Tables 1 and 2 are based on the best available data for these populations and should be used for future population modelling. However, caution should be applied when using these parameters values because of the age of the data and threats that have been acting on populations that could have shifted life history parameters. Fecundity data were obtained from a US population held in experimental ponds and might not accurately reflect the status of wild Canadian populations.

Element 22: Evaluate maximum human-induced mortality and habitat destruction that the species can sustain without jeopardizing its survival or recovery.

The impact of harm to populations of Lake Chubsucker was evaluated through estimates of the elasticity of λ (Figure 4 and 5), elasticity of N (Figure 6) and simulations (Figure 7). Across each analysis perturbations to the adult stage had the greatest impact to a population.

Estimates of maximum human-induced harm can be estimated from the analysis but depend on the initial condition of the population and what the final state of the population is considered allowable. Maximum harm, which is defined here as an additional mortality or proportional reduction in habitat, can be estimated as:

$$Maximum\ Harm = \frac{final\ state - initial\ state}{initial\ state} \times \frac{1}{\varepsilon \times frequency} \quad (23)$$

Where ε, is the estimate of elasticity for the vital rate being perturbed, frequency is the number of times per year harm is applied (e.g., 0.2 represents a 5 year periodic cycle), and state is the population parameter being measured (λ or N). If the initial state is currently less than the acceptable final state, there is no scope for harm. For example, the elasticity of N_a for adult survival (σ_a) was ~ 1.88, if initial adult population size was 5,000 and one wishes to remain above 4,500 then the adult survival rate could be reduced by no more than ~ 5.3%.

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