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Recovery Potential Modelling of Northern Madtom (*Noturus stigmosus*) in Canada

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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.

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ABSTRACT

The Committee on the Status of Endangered Wildlife in Canada (COSEWIC) has assessed Northern Madtom (*Noturus stigmosus*) 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 Northern Madtom was most sensitive to perturbations to juvenile 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 an adult and juvenile population size of ~97,000 (CI: 29,000 – 230,000) at a 99% probability of persistence over 100 years. Such a population would require ~1,700 hectares in the Detroit River, ~1,900 ha in the St. Clair River and ~1,600 ha in the Thames River.

INTRODUCTION

The Northern Madtom (*Noturus stigmosus*) is a small, benthic ictalurid catfish species historically found in Lake St. Clair and the Detroit, St. Clair, Sydenham and Thames rivers, although it is currently considered to be extirpated from the Sydenham river. It is a nocturnal, warmwater fish and can occupy a wide range of habitats from small streams to large rivers and lakes with slow to swift currents (COSEWIC 2012). It spawns in cavities in the substrate between July and August in Ontario when water temperature reaches 23-25°C (MacInnis 1998, Scheibly et al. 2008). Major threats to Northern Madtom include increased turbidity, siltation, toxins and aquatic invasive species (COSEWIC 2012).

This species was assessed as Endangered in November 2002 by the Committee on the Status of Endangered Wildlife in Canada (COSEWIC). It was re-assessed and the status confirmed in May 2012, and a Recovery Potential Assessment (RPA) was conducted by Fisheries and Oceans Canada (DFO) in March 2012 (DFO 2012). Results from a population model were incorporated in DFO (2012), but the model and the detailed results of its analysis were not published as a separate document. Another RPA was conducted in 2022 to incorporate new information, as well as new modelling and analysis techniques.

The *Species at Risk Act* (SARA) mandates the development of strategies for the protection and recovery of species that are at risk of extinction or extirpation from Canada. In response, DFO has developed the RPA (DFO 2007a, 2007b) as a means of providing information and scientific advice. Three components of the RPA will be addressed in this report: 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. (2009).

METHODS

Information on vital rates was compiled to build projection matrices that incorporated parameter uncertainty, 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). All analyses and simulations were conducted using the statistical program R 4.2.1 (R Core Team 2022). Parameter values incorporated into the population model are listed in Tables 1 and 2.

SOURCES

Life history estimates for the Northern Madtom were based on sampling data collected by DFO from 2009 to 2016 on the St. Clair, Detroit and Thames rivers and by the Michigan Department of Natural Resources (MDNR) between 2003 and 2021 on the Detroit and St. Clair rivers.

LIFE HISTORY

Age and Growth

Northern Madtom lives to a maximum of age 5 or 6 (Manny et al. 2014, Conard 2015) although Scheibly (2003) found the maximum age to be 3 in Kentucky, US. For the population model, the maximum age was assumed to be 5 based on available age-length data from MDNR. MDNR

provided age-length data along with the parameters for a von Bertalanffy growth function (VBGF) fitted to those data. Northern Madtom length-at-age, in mm, can be described as:

$$L_t = 137.8(1 - e^{-0.54(t-0.32)}) \quad (1)$$

Where t is the age of the fish.

Length-weight relationship for Northern Madtom was based on data collected from the Detroit, Thames and St. Clair rivers and modeled as:

$$W = 10^{-5.5269}L^{3.28} \quad (2)$$

Where L is total length in mm and W is weight in grams. Figure 1 depicts the data and relationships from equations 1 and 2.

Table 1. Parameter definitions and values used in the population model describing Northern Madtom.

	Symbol	Description	Parameter Value	Source
Age	t_{max}	Longevity	5	MDNR
	t_{mat}	Age-at-maturity	3	
	ζ	Generation time	3.6	Calculated
Growth	L_{∞}	Asymptotic length (mm)	137.8	MDNR
	k	von Bertalanffy growth coefficient	0.54	
	t_0	Age at 0 mm in length	0.32	
Spawning	f_{μ}	Mean fecundity	177.9	MDNR
	f_{sd}	Standard deviation for fecundity	61.4	
	φ	Proportion female at hatch	0.5	Assumed
	T	Spawning periodicity	1	
Weight	α_w	Length-weight allometric intercept	2.97×10^{-6}	Calculated
	β_w	Length-weight allometric exponent	3.28	
Mortality	$\sigma_{0,1}$	Egg to age-1 survival rate at population equilibrium (i.e., when $\lambda = 1$)	0.0444	Calculated
	$\sigma_{0,max}$	Maximum egg to age-1 survival rate	0.0625-0.3995	
Density-dependence	β_d	Beverton-Holt density-dependence parameter	0.41-7.99	Calculated

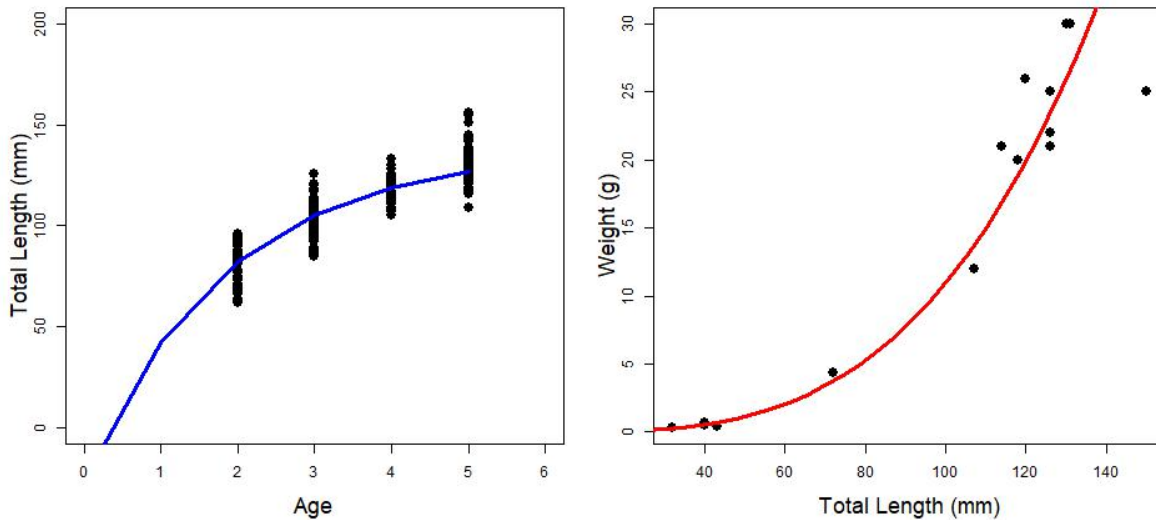


Figure 1. The left panel depicts the fitted von Bertalanffy growth curve for Northern Madtom based on data and parameter values from MDNR ($n=690$). The right panel depicts the length-weight relationship using data from MDNR and DFO ($n=15$).

Reproduction

Fecundity data on Northern Madtom were obtained from sampling conducted by MDNR in 2019 ($n=10$). Egg count ranged from 115 to 288 with a mean of 177.9 and standard deviation of 61.4. There was insufficient data to construct a length-fecundity relationship. Instead, the mean and standard deviation values for fecundity were used for all adult ages.

A 50% sex ratio and a spawning periodicity of 1 year were assumed. Northern Madtom matures at age 2 or 3 (Manny et al. 2014, Conard 2015). Based on the fecundity data from MDNR, which only had fecundity data for ages 3 and higher, age-at-maturity was assumed to be age 3 for this model.

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:

$$M_t = \frac{m_0}{L_t} \quad (3)$$

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 equation 4 below (van der Lee and Koops 2016):

$$\sigma_t = \left[\frac{L_t e^{-k}}{L_{t+1}} \right]^{m_0 / k L_\infty} \quad (4)$$

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 5:

$$\ln L_t + kt \quad (5)$$

The slope of this catch curve regression (τ) is m_0 divided by VBGF parameters as described in equation 6.

$$\tau = \frac{-m_0}{kL_\infty} \quad (6)$$

Un-aged fish from DFO and MDNR sampling ($n=450$) were 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 (τ) of -0.987. Annual survival rates were calculated based on this value and equations 4 and 6. Age-based annual survival rates ranged from 0.3 to 0.55.

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). Young-of-year (YOY) survival rates were calculated for a stable population ($\lambda = 1$), for a minimally growing population ($\lambda = 1.1$), and for a theoretical maximum population growth ($\lambda = \lambda_{max}$) obtained from allometric relationships as presented in Randall and Minns (2000). 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):

$$r_{max} = 2.64W_{mat}^{-0.35} \quad (7)$$

Where W_{mat} is the weight-at-maturity in grams. This gives $\lambda_{max} = 1.89$ for Northern Madtom.

THE MODEL

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

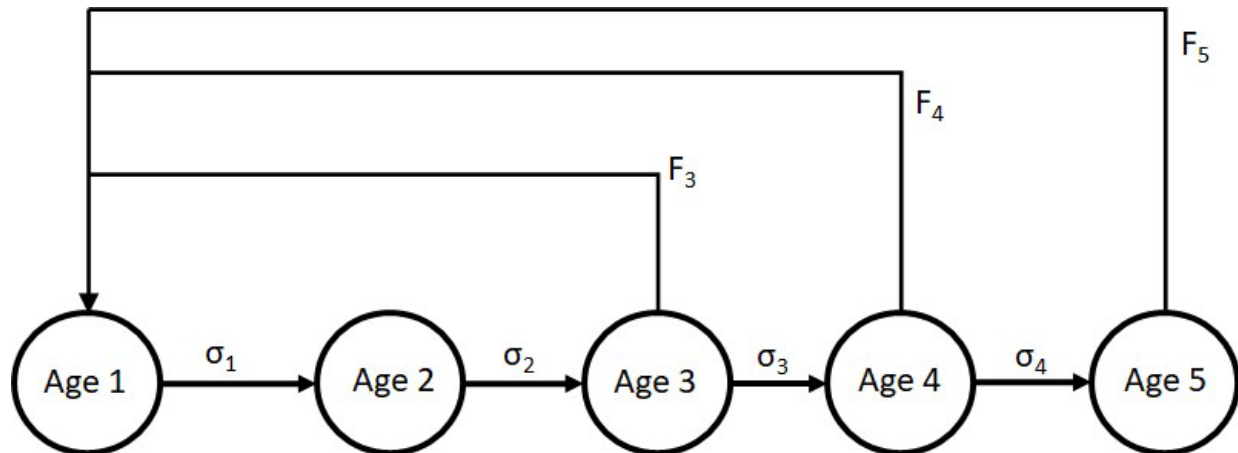


Figure 2. Generalized life cycle used to model the population dynamics of Northern Madtom. F_i represents stage-specific annual fertility of an individual of age i and σ_i represents the survival from age i to $i+1$.

The matrix consisted of 5 stages (Figure 2) representing ages 1 to 5. 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-dependence effects.

$$\mathbf{B} = \begin{bmatrix} 0 & 0 & F_3 & F_4 & F_5 \\ \sigma_1 & 0 & 0 & 0 & 0 \\ 0 & \sigma_2 & 0 & 0 & 0 \\ 0 & 0 & \sigma_3 & 0 & 0 \\ 0 & 0 & 0 & \sigma_4 & 0 \end{bmatrix} \quad (8)$$

and:

$$\mathbf{A} = \mathbf{B} \circ \mathbf{D}, \quad (9)$$

where the symbol \circ 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 pre-breeding matrix also incorporates the probability of surviving from the egg stage to age-1 (σ_0):

$$F_i = f_i \varphi m_i \sigma_0 / T \quad (10)$$

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_0 represents the survival from egg to age-1, and T represents spawning periodicity which was assumed to be 1 year.

Density-dependence

Density-dependence was assumed to act on the first year of life and was incorporated using the Beverton-Holt (Equation 11) function. The function was adapted to the density-dependence matrix \mathbf{D} which, when multiplied by the equilibrium YOY 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 12).

$$R = \frac{\alpha N}{1 + \beta N} \quad (11)$$

$$d_0 = \frac{\sigma_{0,max} / \sigma_{0,1}}{1 + \beta_d \frac{N_e}{K_e}} \quad (12)$$

Where $\sigma_{0,max}$ and $\sigma_{0,1}$ represent YOY survival rates at maximum population growth and at population equilibrium, respectively. The maximum population growth rate (λ'_{max}) is unknown and is included as a stochastic parameter drawn from a uniform distribution between 1.1 (minimally growing population) and 1.89 (theoretical maximum growing population, λ_{max}). The value of $\sigma_{0,max}$ is then calculated based on the selected λ'_{max} . 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 \mathbf{D} was structured as shown below and is of the same size as the transition matrix \mathbf{B} .

$$\mathbf{D} = \begin{bmatrix} 1 & d_0 & d_0 & d_0 & d_0 \\ 1 & 1 & 1 & 1 & 1 \\ 1 & 1 & 1 & 1 & 1 \\ 1 & 1 & 1 & 1 & 1 \\ 1 & 1 & 1 & 1 & 1 \end{bmatrix} \quad (13)$$

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 on 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 coefficient of variation (CV) of 0.05 for YOY and 0.15 for juveniles and adults. These CVs were chosen to avoid overly large swings in population between years. 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 age with an AR1 correlation structure (correlation diminishes as difference between ages increases) with a correlation value of 0.5. YOY survival was assumed to vary independently of the older stages (correlation = 0).

Stochasticity for fecundity uses the mean and standard deviation calculated from MDNR data and was executed using the stretched-beta distribution in a similar manner as survival stochasticity.

Table 2. Mean and standard deviations for Northern Madtom 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)		Fecundity (f_i)	
		Mean	SD	Mean	SD
1	42	0.305	0.011	0	NA
2	82	0.459	0.012	0	NA
3	105	0.521	0.011	177.9	61.4
4	119	0.551	0.011	177.9	61.4
5	127	0	NA	177.9	61.4

IMPACT OF HARM

The impact of anthropogenic harm to a Northern Madtom 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 adult survival (σ_a) would indicate that a 10% decrease in σ_a would cause a 2% decrease in adult equilibrium density.

Elasticities are useful as they allow for assessment of how impactful any changes to vital rates and other model parameters may be 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, accurately represent only small perturbations 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 (v , Caswell 2001):

$$\varepsilon_\lambda = \frac{v}{\lambda} \sum_{i,j} \frac{\partial \lambda}{\partial a_{i,j}} \frac{\partial a_{i,j}}{\partial v}, \quad (14)$$

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

Elasticity of λ estimates are influenced by the current population growth rate and, in order to capture the range of possible conditions, 5000 population growth rates were randomly chosen from a uniform distribution between a minimum and maximum λ . For the minimum λ , a growth rate leading to a 30% reduction in population size over 3 generations was chosen, giving a $\lambda_{min} = 0.968$. For the maximum λ , the theoretical maximum population growth estimated by Equation 7 was used, giving a $\lambda_{max} = 1.89$.

Elasticity of N

Elasticities of N (ε_N) are calculated from the sensitivities of N ($\frac{d\hat{N}}{dv^T}$) where (Caswell 2019):

$$\frac{d\hat{N}}{dv^T} = \left(\mathbf{I}_i - \mathbf{A} - (\hat{\mathbf{N}}^T \otimes \mathbf{I}_i) \frac{\partial \text{vec} \mathbf{A}}{\partial \mathbf{N}^T} \right)^{-1} (\hat{\mathbf{N}}^T \otimes \mathbf{I}_i) \frac{\partial \text{vec} \mathbf{A}}{\partial v^T}, \quad (15)$$

and:

$$\varepsilon_N = \text{diag}(\hat{\mathbf{N}})^{-1} \frac{dN}{dv^T} \text{diag}(v). \quad (16)$$

\mathbf{A} is the projection matrix of dimension $i \times i$, \mathbf{I}_i is an identity matrix of dimension $i \times i$, $\hat{\mathbf{N}}$ is a vector of equilibrium densities, $\frac{\partial \text{vec} \mathbf{A}}{\partial \mathbf{N}^T}$ is the partial derivatives of matrix \mathbf{A} with respect to stage densities, $\frac{\partial \text{vec} \mathbf{A}}{\partial v^T}$ is the partial derivatives of matrix \mathbf{A} with respect to the vital rates or the model parameters of interest, \top is the transpose operator and \otimes represents the Kronecker product. $\text{diag}(\hat{\mathbf{N}})$ and $\text{diag}(v)$ 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 the maximum population growth rate (λ'_{max}) which influences the density-dependence parameters for the Beverton-Holt model.

One thousand λ'_{max} values were randomly chosen between 1.1 and 1.89 for this elasticity analysis.

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%. 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. 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. One thousand replicates were simulated for each combination of harm frequency, harm level and targeted life-stage. To measure the impact of 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 .

RECOVERY TARGETS

Abundance: MVP

The concept of demographic sustainability was used to identify potential minimum recovery targets for Northern Madtom. Demographic sustainability is related to the concept of a 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 should be sufficient to represent long-term population viability; 100 years is commonly used and is likely reasonable for making management decisions.

The rate and severity of catastrophic events within Northern Madtom 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 the catastrophe rate was included as a stochastic parameter bound between 5% and 20% per generation. These rates correspond to an annual catastrophe probability of 1.4% and 6.6%, 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.

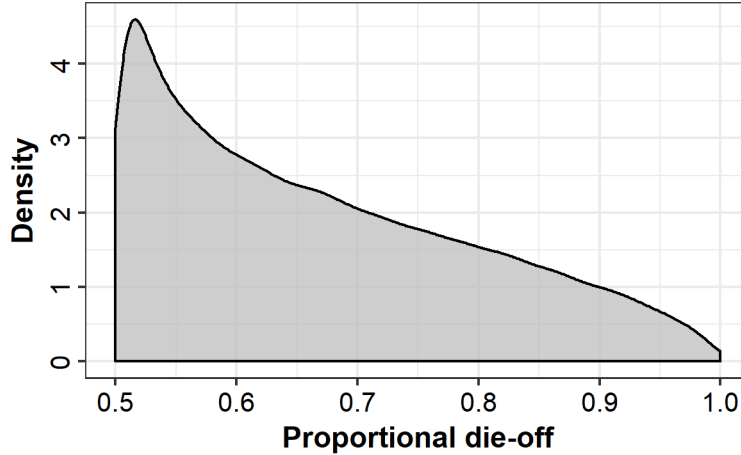


Figure 3. Beta distribution (scaled between 0.5 and 1) used in stochastic draws of catastrophic impacts. This represents the proportional decrease in population size following a catastrophic event. Shape parameters were 0.762 and 1.5 (based on Reed et al. 2003).

Quasi-extinction accounts for the compounding nature 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, a value of 25 adult females was used as a reasonable approximation (Morris and Doak 2002).

Density-dependent stochastic simulations were conducted for populations with various initial female abundances ranging from 100 to 10,000 (initial density represented adult female carrying capacity, K_a , where $\lambda = 1$). Simulations were run for 100 years. Independent simulations incorporated annual catastrophe rates drawn from a uniform distribution between 1.4% and 6.6%.

Each simulation was replicated 10,000 times and quasi-extinctions were tracked across all the simulations. The probability of extinction (P_{ext}) was modelled as a logistic regression that was a function of \log_{10} transformed initial female density ($\log_{10}(K_a)$), catastrophe rate per generation (P_{cat}), and maximum population growth rate (λ'_{max}) where:

$$P_{ext} = \frac{1}{1+e^{-(X\beta)}}, \quad (17)$$

X is a matrix of all covariates and β a vector of coefficients including the intercept. MVP estimates are presented for quasi-extinction probabilities of 5% and 1%.

Habitat: MAPV

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. Northern Madtom population density estimates were available for the Detroit, St. Clair, and Thames rivers based on DFO data from Smyth and Drake (2021). Density was estimated to be 0.57 (± 0.3), 0.51 (± 0.29) and 0.6 (± 0.29) individuals per 100 m² for the three rivers respectively. These densities are not age-specific and are assumed to apply equally to individuals of all age classes.

Theoretical density estimates were also available from equations in Table 2 of Randall et al. (1995):

$$\log_{10} D = 4.48 - 1.01 * \log_{10} W \quad (18)$$

$$\log_{10} D = 4.90 - 0.94 * \log_{10} W \quad (19)$$

Where D is the number of individuals per hectare and W is the mean weight of the fish in grams. Equation 18 describes the population density for communities in lacustrine habitats while equation 19 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 was then divided into age classes based on a stable age structure. The weight for each age class was calculated based on allometric length-weight relationships and the density for each age class was calculated based on equation 18 or 19. 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. The density values obtained using this method ranged from 4.65 and 11.87 individuals per m^2 for lacustrine and riverine habitats for age-1 fish to 0.12 and 0.4 individuals per m^2 for age-5 fish for the two habitats.

RECOVERY TIMES

Time to recovery was estimated using simulation analysis similar to MVP simulations and incorporated stochasticity, density-dependence, and catastrophes in the same manner. Simulations were repeated 5,000 times. Since current Northern Madtom population abundance is unknown, simulations began with initial population sizes set to 10% of MVP. The population was deemed recovered when MVP (also used as the carrying capacity) was reached. 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 Northern Madtom 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 small (< 30%) changes in vital rates. The results of this elasticity analysis may not hold for large vital rate changes. Positive elasticity values indicate that population growth rate will increase if the vital rate is increased, and negative values indicate the opposite.

Figure 4 presents elasticity estimates for fertility (F) and survival rates for YOY (σ_o), juveniles (σ_j) and adults (σ_a). Elasticity values for fertility and YOY survival ranges from ~0.276 to ~0.301 with a median of ~0.291. Elasticity for juvenile survival ranges from ~0.552 to ~0.602 with a median of ~0.583. Finally, the elasticity for adult survival ranges from ~0.097 to ~0.172 with a median of ~0.126. Based on these results, changes in juvenile survival had the strongest impact on population growth, followed by fertility and YOY survival; changes in adult survival had the least impact. For example, comparing the median elasticity value for fertility (0.291) with the median value for adult survival (0.126), the population growth rate is ~2.3 times more sensitive to changes to fertility than adult survival. A 5% change in fertility would have the same impact on λ as a 11.5% change in adult survival.

The elasticity values for the vital rates are also dependent on the population's current growth rate; however, the ranking of which vital rate is most impactful remains unchanged. Figure 5 shows the change in elasticity of the four vital rates as a result of changes in λ . Elasticity for fertility, YOY and juvenile survival increases as λ increases, while the elasticity for adult survival decreases as λ increases. Based on this information, it is possible to predict a new population growth rate given the current growth rate and the amount of change a vital rate will undergo. For example, if juvenile survival is reduced by 5% while the population is stable ($\lambda = 1$, elasticity of $\sigma_{j,stable} = \sim 0.555$), the new population growth rate will be ~ 0.972 ($1 - 0.05 \times 0.555$), leading to an annual decline of 2.8%.

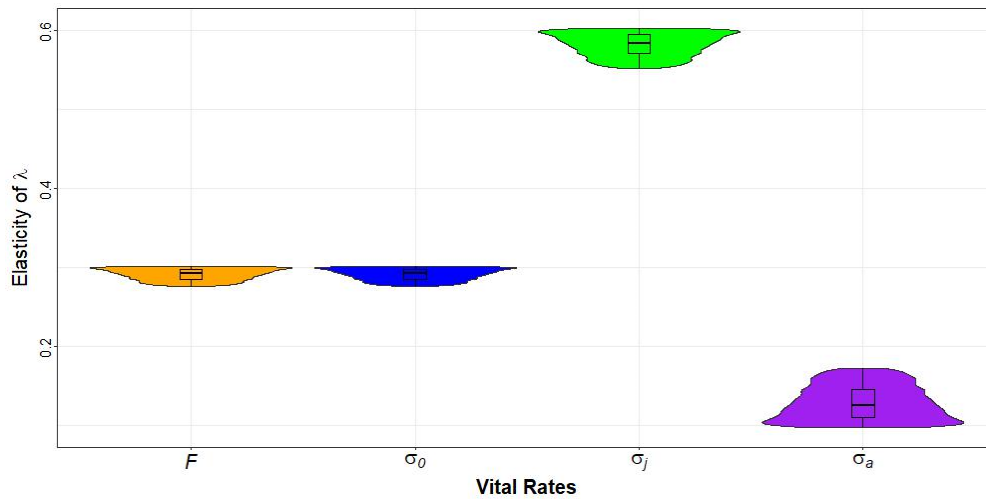


Figure 4. Elasticity of λ analysis results for Northern Madtom population represented using violin and box plots. Results reflect different values of population growth rate. F represents total fertility across all stages and σ represents survival for the YOY (o), juvenile (j) and adult (a) stages.

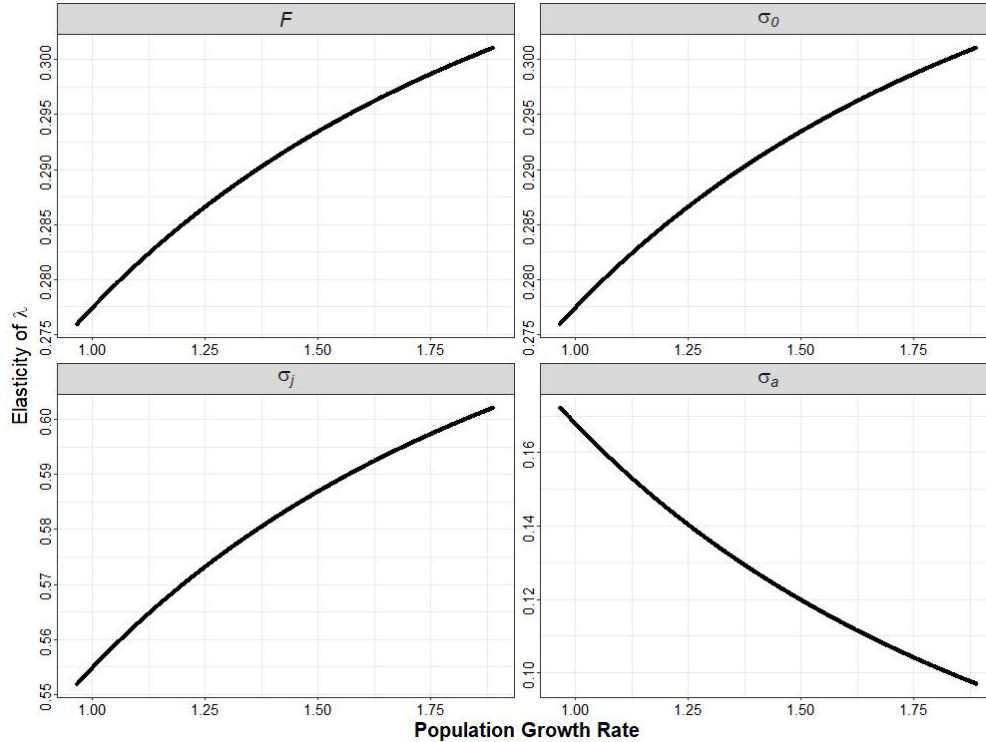


Figure 5. Elasticity of λ analysis with elasticity values as a function of the current population growth rate (λ). F represents the total fertility across all stages and σ represents survival for the YOY (σ_0), juvenile (σ_j) and adult (σ_a) stages.

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.

Figure 6 depicts the results of the elasticity of N_s analysis. For Northern Madtom, all elasticity values are positive and increases in any vital rates lead to an increase in density. The pattern of sensitivity is generally similar across the juvenile and adult life-stages and the combined total population with the exception of their sensitivities to juvenile survival (σ_j) and adult survival (σ_a). Across all three categories (Juvenile, Adult, Total) the median elasticity values for fertility (F), equilibrium YOY survival ($\sigma_{0,1}$) and egg carrying capacity (K_e) are the same, with the values being $F = 0.324$, $\sigma_{0,1} = 1.324$ and $K_e = 1$. For the median elasticity values for the juvenile life-stage, $\sigma_j = 0.881$ and $\sigma_a = 0.196$. For the median elasticity values for the adult life-stage, $\sigma_j = 2.648$ and $\sigma_a = 0.802$. For the median elasticity values for the total population $\sigma_j = 1.168$ and $\sigma_a = 0.294$. Values are tabulated in Table 3.

Due to the changes in juvenile and adult survival elasticities for different life-stages, adult abundance is most sensitive to juvenile survival followed by equilibrium YOY survival ($\sigma_{0,1}$). Juvenile abundance is most sensitive to equilibrium YOY survival followed by egg carrying capacity.

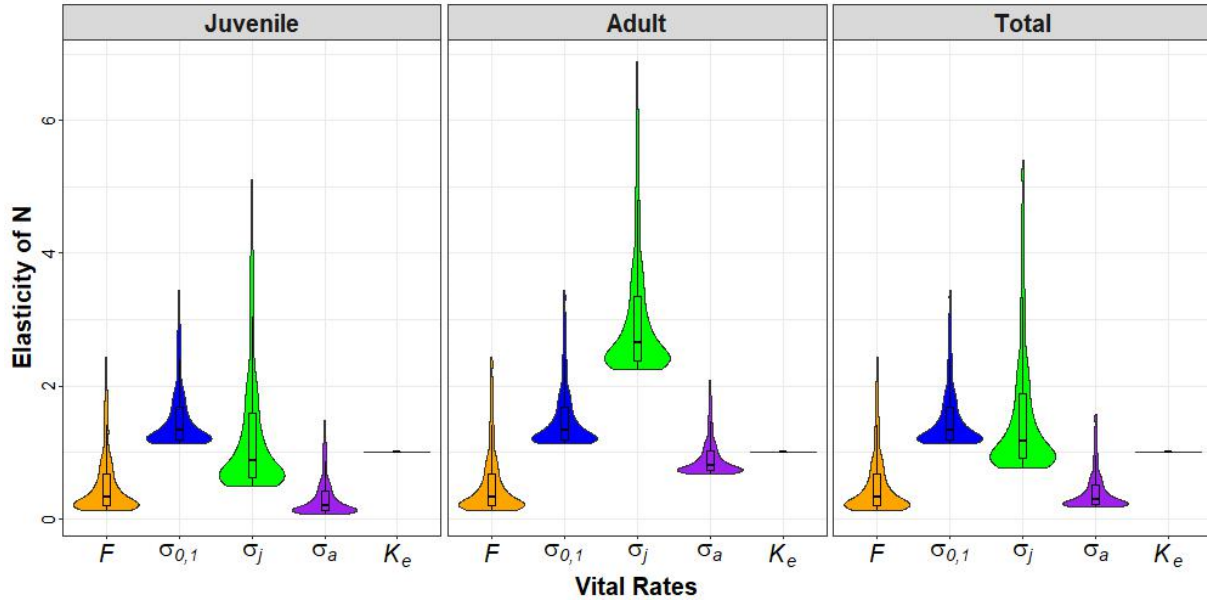


Figure 6. Elasticity of N_s analysis results for Northern Madtom. The three panels shows the results for the juvenile population, the adult population and the total population. The x-axis represents the model parameter (i.e., vital rate) that is perturbed; the y-axis represents the resultant proportional change to life-stage-specific density. F represents total fertility, $\sigma_{0,1}$ represents YOY survival at population equilibrium, σ_j represents juvenile survival, σ_a represents adult survival and K_e represents egg carrying capacity.

Table 3. Median values for elasticity of N_s analysis results for Northern Madtom. The columns represent the vital rates and the rows represent the life-stages considered separately, or in aggregate.

	F	$\sigma_{0,1}$	σ_j	σ_a	K_e
Juvenile	0.324	1.324	0.881	0.196	1
Adult	0.324	1.324	2.648	0.802	1
Total	0.324	1.324	1.168	0.294	1

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 an adult female Northern Madtom population. Harm has the strongest impact when applied to all life-stages. When harm is applied to only a single life-stage, perturbations to the juvenile stage produce the largest impact on density, followed by harm to the YOY stage and, finally, harm to the adult stage. These results are consistent with the elasticity analyses.

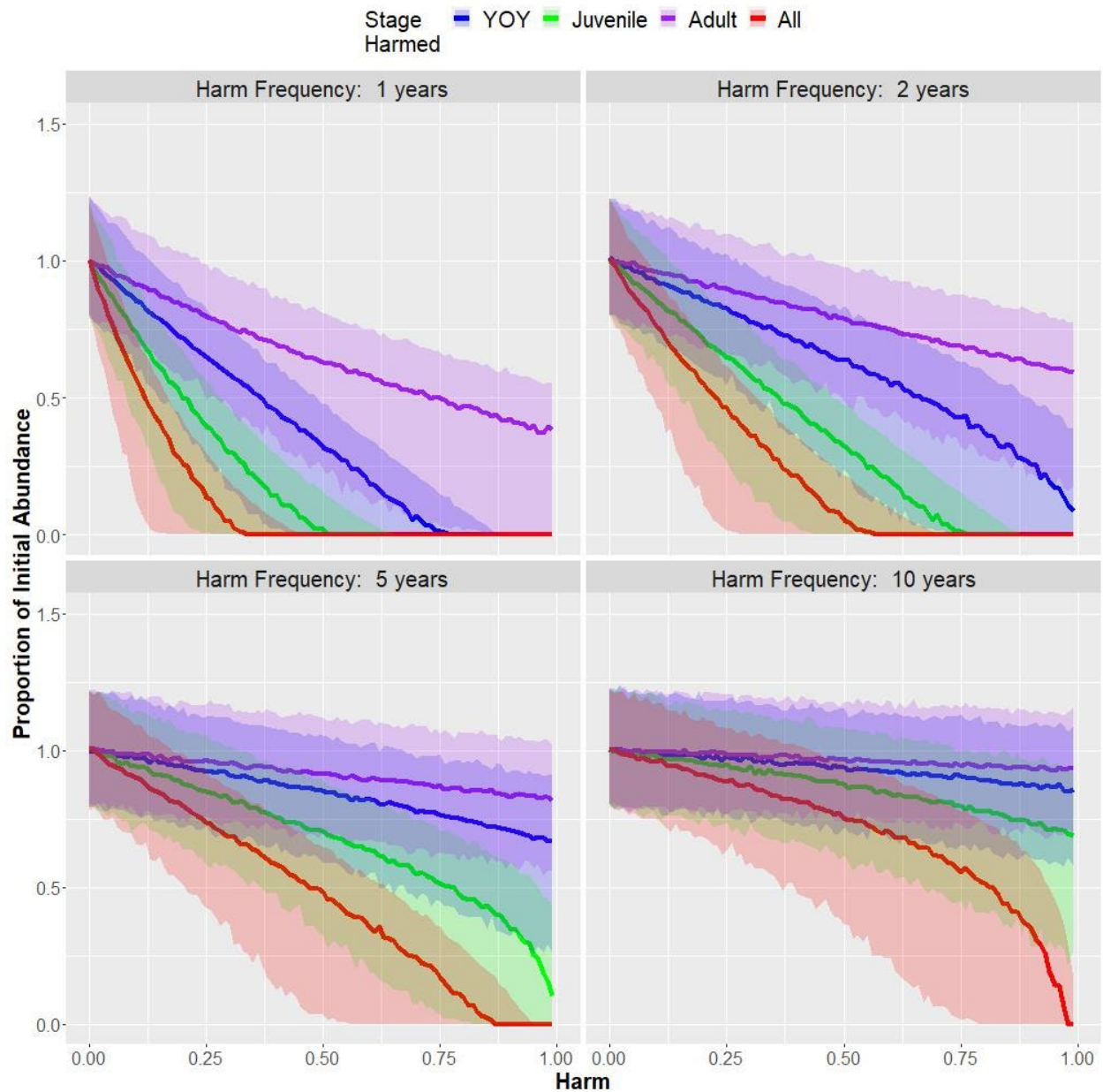


Figure 7. Results from harm simulation analysis where harm is applied at different frequencies to a Northern Madtom population. The colors represent the life-stage(s) harmed: YOY, juvenile, adult, and total population. The x-axis represent the proportional harm (e.g., annual mortality) applied to the 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: MVP

Demographic sustainability was assessed using stochastic, density-dependent population simulations. Simulation outputs of binomial quasi-extinction (1: extinct, 0: extant) were fitted using a logistic regression as a function of adult female abundance, generational catastrophe rate and maximum population growth rate (λ'_{max}). All three parameters were significant. Sub-

models containing subsets of the three covariates were compared with the full model using the Akaike information criterion (AIC) method. The full model with all covariates was chosen as the best model due to having the lowest AIC score (Table 4; Figure 8).

Table 4. Logistic regression model results for Northern Madtom extinction probability. K_a represents adult female population size, P_{cat} represents catastrophe rate per generation and (λ'_{max}) represents maximum population growth rate.

Parameter	Value	Standard error	p-value
Intercept	6.87	0.07	<0.001
$\log_{10}(K_a)$	-3.13	0.02	<0.001
P_{cat}	17.28	0.19	<0.001
λ'_{max}	-1.1	0.03	<0.001

The MVP size was estimated from the logistic regression model using randomly selected generational catastrophe rates between 5% and 20% and maximum population growth rates between 1.1 and 1.89. The MVP size of adult females, which corresponds to a 5% extinction risk, was ~2,400 (CI: 700 – 5,600) and to a 1% extinction risk was ~7,900 (CI: 2,400 – 18,600). Extinction probability of any adult female population size can be estimated from the fitted logistic relationship with a given catastrophe rate and maximum population growth as:

$$P_{ext} = \frac{1}{1 + e^{-(6.87 - 3.13 \log_{10}(K_a) + 17.28 P_{cat} - 1.1 \lambda'_{max})}}. \quad (20)$$

The stable age distribution for Northern Madtom consists of 84% juveniles (ages 1 and 2) and 16% adults (ages 3-5). Assuming a stable age structure and a 1:1 sex ratio, the maturity schedule can be used to convert the number of adult females to a population size consisting of all juvenile and adult individuals of both sexes. The MVP for Northern Madtom adults and juveniles combined is ~29,000 (CI: 8,900 – 68,000) under a 95% chance of persistence over 100 years and ~97,000 (CI: 29,000 – 230,000) under a 99% chance of persistence over 100 years. These MVP values were estimated for an isolated population. If the Northern Madtom in the three locations were assumed to be reproductively isolated from each other, then the MVP value should be applied to each individual population.

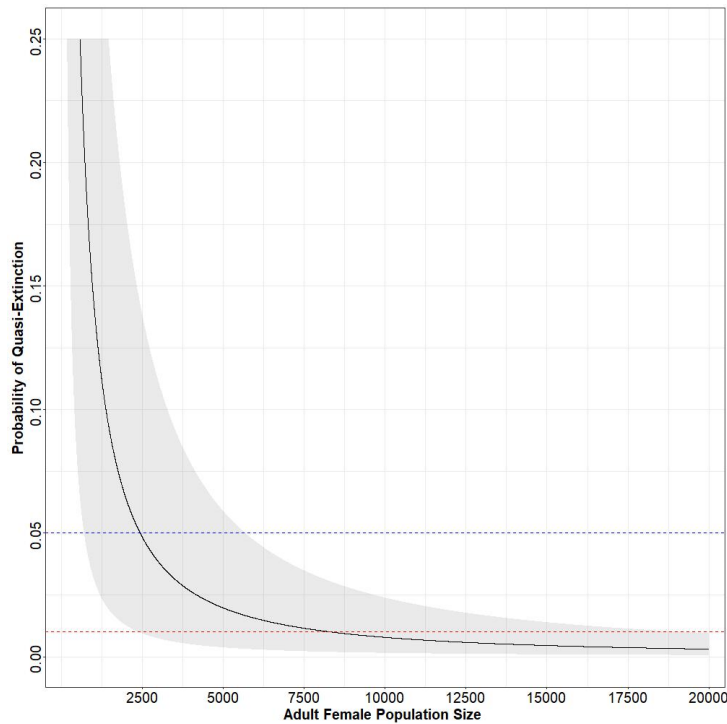


Figure 8. The probability of quasi-extinction within 100 years as a function of adult female population size. The solid black line represents the logistic regression trend with the grey region representing the confidence intervals (for P_{cat} ranging from 5% to 20% per generation and λ'_{max} ranging from 1.1 to 1.89). The horizontal blue and red dashed lines represent the 5% and 1% threshold for quasi-extinction respectively.

Two additional alternative life-history scenarios were explored using MVP simulations to account for uncertainties about Northern Madtom life-history. The two alternate scenarios examined include lowering the age-at-maturity from age-3 to age-2 and increasing the longevity from age-5 to age-6. The MVP values along with 95% CI for 99% persistence over 100 years are shown in Table 5. For the age-2 maturity scenario, the MVP in terms of adult females is higher than the standard life-history scenario and this is due to counting an extra age class as adults. When the MVP is converted to include all individuals age-1 and higher, the MVP becomes lower than the standard scenario. The MVP values for the age-6 longevity scenario are also lower than the standard life-history scenario.

Table 5. MVP and 95% CI values for two alternative life-history scenarios (age 2 maturity and age 6 longevity) compared with the standard scenario. MVP values were estimated for a 99% chance of persistence over 100 years. Values are presented for adult females and for all age-1 and older individuals.

Scenarios	MVP – Adult Females	MVP – Age 1+ individuals
Age 3 maturity, Age 5 longevity (standard)	7,900 (2,400 – 18,600)	97,000 (29,000 – 230,000)
Age 2 maturity	9,400 (2,500 – 24,000)	52,000 (14,000 – 133,000)
Age 6 longevity	7,000 (2,100 – 17,000)	80,000 (24,000 – 193,000)

Habitat: MAPV

Under a 1% extinction risk, the target MVP is ~97,000 juveniles and adults of both sexes. With the density estimates from Smyth and Drake (2021), the MAPV for such a population would be ~1,700 hectares for the Detroit river, ~1,900 ha for the St. Clair river and ~1,600 ha for the Thames river.

Using the theoretical density estimates from Randall et al. (1995), the MAPV is ~4.5 ha for riverine habitats and ~13.9 ha for lacustrine habitats.

RECOVERY TIMES

Although Northern Madtom 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 9. The median time to recovery is 17 years and 95% percent of populations reached recovery in 58 years or less. This recovery time is the time it takes for a Northern Madtom population to reach its carrying capacity from 10% of carrying capacity. Given the model, parameters and initial population, this recovery time would be the same regardless of the chosen carrying capacity. The MVP value was chosen as the carrying capacity for the simulations since that would produce the longest amount of time to reach MVP. If MVP was lower than the carrying capacity, the population would pass the MVP value in less than the simulated recovery time as the population trajectory moves towards carrying capacity.

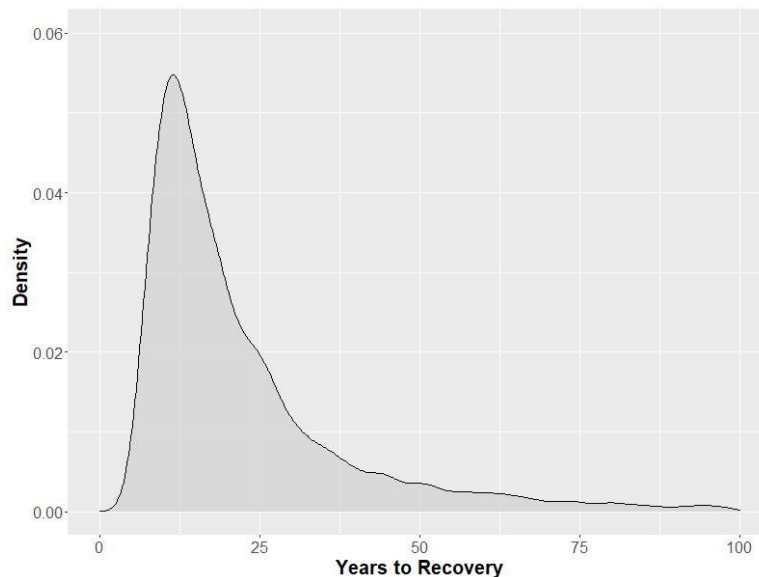


Figure 9. Distribution of recovery time-frames for all simulations of Northern Madtom given a recovery target of MVP and initial population of 10% of MVP.

DISCUSSION

A population model for Northern Madtom was developed to make predictions on how the population may respond to anthropogenic harm and to estimate recovery targets for abundance

and habitat. Limited information on Northern Madtom life-history characteristics has been published. The available information was compiled and additional parameters estimated using MDNR and DFO survey data.

Multiple methods were used to assess the impacts of harm to a Northern Madtom population. Most results show that Northern Madtom are most sensitive to changes in juvenile survival. For the elasticity of λ (population growth rate), the highest impact on population growth rate was juvenile survival, followed by fertility and YOY survival; adult survival had the least impact. The patterns of these results do not change under different population growth rates, in that the elasticity values differ slightly but the ranking of sensitivity for the vital rates remains the same.

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. For the adult life-stage, juvenile survival once again had the highest impact. Based on the median elasticity value of juvenile survival on the adult population, a reduction in the juvenile survival rate by ~9% 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 ~10% to juvenile survival leads to a 25% decline in adult abundance. Both the elasticity analysis and the harm simulations show the order of sensitivity goes from juvenile survival to YOY survival to adult survival.

Long tails of elasticity of N values are exhibited by fertility and the three survival rates. These are a result of when the randomly chosen value for the maximum population growth rate (λ'_{max}) is very low ($\lambda'_{max} < \sim 1.2$). These tails would disappear if a higher minimum limit for λ'_{max} was set for the elasticity calculations. The elasticity value of N for carrying capacity (K_e) is 1 for all λ'_{max} values which indicates that it is not impacted by changes in maximum population growth. This is possibly due to K_e having its impact on the population when the population is at carrying capacity. When the population is at equilibrium, the population growth will always be stable ($\lambda = 1$) and hence the elasticity value for K_e is not affected by what value was chosen for λ'_{max} .

Estimates of recovery targets for abundance were made based on simulation analysis to determine the population sizes required for demographic stability through estimates of MVP size. Persistence probability depends on population size, catastrophe rate and maximum population growth. For a 99% persistence probability, Northern Madtom requires ~7,900 (CI: 2,400 – 18,600) adult females, which translates to ~97,000 (CI: 29,000 – 230,000) adults and juveniles of both sexes. As a comparison to the previous model results in DFO (2012), MVP was estimated to be ~2.7 million age-1+ individuals. The inclusion of density-dependence effects in the current model greatly reduced the MVP. The upper confidence interval is associated with higher catastrophe rates and lower maximum population growth while the lower confidence interval is associated with lower catastrophe rates and higher maximum population growth.

To explore the implications of uncertainties in longevity and age-at-maturity, alternate life-history scenarios where longevity was increased to age-6 and where age-at-maturity was reduced to age-2 were investigated using MVP simulations. Both alternate scenarios produced MVP values which were lower than the MVP under the standard life-history scenario, with reducing age-at-maturity having a stronger impact than increasing longevity. The MVP value from the standard scenario is the most conservative value when considering a recovery target. Elasticity analysis was not conducted on the alternate scenarios; however, it is possible to make some educated guesses on their impacts. An increase in longevity by one year does not have a great impact on the Northern Madtom lifecycle and the elasticity analysis of this scenario should resemble the standard scenario. Earlier maturity will reduce the length of the juvenile life stage and will likely

reduce the importance of juvenile survival while increasing the importance of fecundity, YOY and adult survival.

Estimates of MVP were converted to habitat requirements by dividing the MVP by mean estimates of density. Based on the density estimates from Smyth and Drake (2021), the habitat required would be ~1,700 hectares for the Detroit River, ~1,900 ha for the St. Clair River and ~1,600 ha for the Thames River. In comparison, based on the body-size and population density relationships found in Randall et al. (1995), the habitat requirement would be ~4.5 ha for riverine habitats and ~13.9 ha for lacustrine habitats. As a comparison, the endangered Neosho Madtom (*Noturus placidus*) was estimated to have a density ranging from 3.3 to 11.7 individuals per 100 m² (Moss 1983, Wenke et al. 1992, Fuselier and Edds 1994), which is about five to twenty times the density estimates for Northern Madtom from the three rivers.

The large discrepancy between the MAPV results derived from field sampled density estimates and the theoretical density estimates are driven by both low current densities of Northern Madtom populations in those rivers and the theoretical density estimate assuming that the area will solely be Northern Madtom habitat. The theoretical estimate also assumed a Northern Madtom population will be at full productive capacity. These assumptions may not hold true for an impaired population and the theoretical MAPV estimate could be overly optimistic. Based on these factors and other uncertainties, the larger MAPV calculated via sampling density should be used until more refined density estimates become available.

UNCERTAINTIES

The life history characteristics of Northern Madtom were not well-described in the literature. As a result, there is uncertainty in the parameterization of the population model. Data used to inform the von Bertalanffy growth curve was gathered from sampling in the St. Clair River and the growth curve was assumed to apply equally to populations in the other two rivers. The theoretical maximum population growth rate was calculated using general allometric relationships. Fecundity was estimated using a small sample size (n=10). There is also uncertainty as to whether the age-of-maturity is 2 or 3 years. Mortality was estimated from data aggregated from the three rivers. Variations in sampling methodologies and gear could introduce noise which was unaccounted for when estimating mortality. The data were also originally un-aged. An age-key derived from the von Bertalanffy growth curve was used to estimate fish age, adding potential error to mortality estimates.

Other important parameters such as maximum population growth rate and the rate and severity of catastrophes were not known and were included in the model as stochastic parameters. The range of parameter values were chosen to fully explore the range of possible model result. For a small cryptic species such as the Northern Madtom, it is likely that both catastrophe rate and maximum population growth rate would be closer to the high end of the range of examined values.

The density of Northern Madtom is poorly known. Sampling density estimates from the Detroit, St. Clair and Thames rivers were based on limited data and are likely to be biased low due to imperfect detections as a result of low Northern Madtom detection probability. Lamothe et al. (2020) found that it takes 16 repeated trawls with non-detections in the St. Clair river and 12 repeated trawls in the Thames River to achieve 95% confidence that Northern Madtom is not present at a site. Without such intense sampling efforts, it is likely that these current densities are an underestimate. An additional consideration is that the current low densities are the result of a degraded population which may not reflect densities which could be achieved by a recovered population.

Theoretical density estimates were derived from general allometric relationships and may not accurately describe the species. The theoretical habitat estimate from Randall et al. (1995) also assumes all the estimated habitat area is available for Northern Madtom and the population is as productive as it could be while making full use of the habitat. These assumptions may not hold true and this value should only be considered as a possible lower bound for MAPV.

ELEMENTS

Element 3: Estimate the current or recent life-history parameters for Northern Madtom.

The best available data were assembled to provide life-history parameters for Northern Madtom. 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 MVP. Simulations incorporated density-dependence, environmental stochasticity, parameter uncertainty and random catastrophes. Persistence probability is influenced by population size, maximum population growth and catastrophe rates. Under a 99% probability of persistence over 100 years, the MVP target is 97,000 (CI: 29,000 – 230,000) juveniles and adults of both sexes. With a 95% chance of persistence over 100 years, the MVP is 29,000 (CI: 8,900 – 68,000) juveniles and adults of both sexes.

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 Northern Madtom population dynamics parameters.

Limited current Northern Madtom population density estimates are available from the Detroit, St. Clair and Thames rivers but population estimates and trajectory of Northern Madtom are unknown.

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 Northern Madtom with a 1% extinction probability was estimated to be ~1,700 hectares for the Detroit river, ~1,900 ha for the St. Clair river and ~1,600 ha for the Thames river based on sampled densities. However, habitat requirements based on theoretical size-density relationships were estimated to be ~4.5 ha for riverine habitats and ~13.9 ha for lacustrine habitats.

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 Northern Madtom population density estimates are available from the Detroit, St. Clair and Thames rivers 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 Northern Madtom 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 Northern Madtom mortality rates or productivity, this information cannot be provided under mitigation scenarios. Under ideal conditions and from an initial population of 10% of MVP, Northern Madtom are projected to reach MVP 95% of the time in 58 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. Fecundity estimates were based on a small sample size and should be used with caution. Maturity at age-3 should also be used with caution since it is based on the lack of fecundity data for age-2. Furthermore, much of the life-history data was derived from the Northern Madtom populations in Detroit and St. Clair rivers and may not reflect the population in the Thames River.

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 Northern Madtom 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 juvenile stage had the greatest impact on the population.

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

$$\text{Maximum Harm} = \frac{\text{final state} - \text{initial state}}{\text{initial state}} \times \frac{1}{\varepsilon \times \text{frequency}} \quad (21)$$

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 median elasticity of the adult population (N_a) for juvenile survival (σ_j) was ~ 2.648 , if the initial adult population size was 5,000 and one wishes to remain above 4,500 adults then the juvenile survival rate could be reduced by a maximum of $\sim 3.8\%$.

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