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Recovery Potential Modelling of Northern Brook Lamprey (*Ichthyomyzon fossor*) – Saskatchewan-Nelson River Populations

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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) assessed the Saskatchewan – Nelson River populations of Northern Brook Lamprey (NBL, *Ichthyomyzon fossor*) as Endangered. Here population modelling is presented to assess the impacts of harm, determine abundance and habitat recovery targets, and conduct long-term projections of population recovery in support of a recovery potential assessment (RPA). The model incorporated parameter uncertainty, environmental stochasticity, and density-dependence into population projections. The analysis revealed that NBL populations were highly sensitive to perturbations in vital rates that affect recruitment such as survival to the larval stage, fecundity, and survival during metamorphosis, as well as ages 1–3 larval survival. As the population growth rate (λ) increased, the sensitivity of all vital rates to perturbation, except for the survival rates of age 4+ larvae, also increased. Population viability analysis was conducted to determine potential recovery targets with demographic sustainability, defined as a self-sustaining population over 60 years, which was achievable with a population size (MPV) of approximately 2,569 [95% confidence interval: 1,110, 4,950] adult females. The current population size, growth rates, and density was unknown for these populations; therefore, a range of initial population sizes and growth rates was used to estimate recovery times and minimum area for population viability (MAPV). The mean recovery time for the lowest initial population sizes and growth rates was 51 years, and the mean MAPV was 6.3 km^2 for the lowest density and highest MPV estimates.

INTRODUCTION

Northern Brook Lamprey (NBL, *Ichthyomyzon fossor*) is a freshwater fish endemic to eastern North America. In Canada, NBL occur in National Freshwater Biogeographic Zones (NFBZs) that span Quebec, Ontario, and Manitoba; the Great Lakes - Upper St. Lawrence NFBZ and the Saskatchewan - Nelson River NFBZ. The Committee on the Status of Endangered Wildlife in Canada (COSEWIC) has assessed the Saskatchewan - Nelson River NFBZ population as Endangered due its very limited distribution in the Winnipeg River watershed in southeastern Manitoba, the declining number of mature individuals, the reductions in extent of occurrence, area of occupancy, and number of locations, and an inferred decline in quantity and quality of aquatic habitat (COSEWIC 2020).

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, Fisheries and Oceans Canada (DFO) has developed the recovery potential assessment (RPA; (DFO 2007a, DFO 2007b) 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, that are further broken down into 22 elements. This report contributes to the RPA through the use of population modelling to assess the impact of anthropogenic harm to populations, identify recovery targets, and project population recovery with associated uncertainties. This work is based on a demographic approach developed for this process (Vélez-Espino and Koops 2009, 2012; Vélez-Espino et al. 2010) and built upon in recent analyses (e.g., van der Lee and Koops 2021).

METHODS

Information on vital rates was compiled to build a matrix population model (Caswell 2000) that incorporates parameter uncertainty, environmental stochasticity, and density-dependence. The impact of anthropogenic harm to populations was quantified with 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). Finally, simulation analysis was used to make estimates of potential recovery time frames. All analyses and simulations were conducted using the statistical program R version 4.1.3 (2022-03-10) (R Core Team 2022), including the R packages: popbio (version 2.7), ggplot2 (version 3.4.1), parallel (version 4.2.1), tidyr (version 1.3.0), data.table (version 1.14.8), dplyr (version 1.1.2), and stringr (version 1.5.0).

THE POPULATION MODEL

The NBL life cycle was modelled using a female only, density-dependent, birth-pulse, pre-breeding, stage-structured population matrix model with an annual projection interval (see Figure 2.1 in Caswell 2000).

The matrix consisted of eight stages (Figure 1), the first seven stages representing larvae from ages one to seven, and the last stage incorporating all NBL after metamorphosis into sexually immature juveniles until maturation and spawning as adults. NBL pass through a protracted larval (ammocoete) phase, that typically lasts five years, but ranges from three to seven years, until metamorphosis (COSEWIC 2020). NBL do not have a parasitic phase and do not feed while undergoing metamorphosis. The juvenile stage lasts for six to eight months, and adults typically spawn within three months of maturation and die within a month of spawning (COSEWIC 2020).

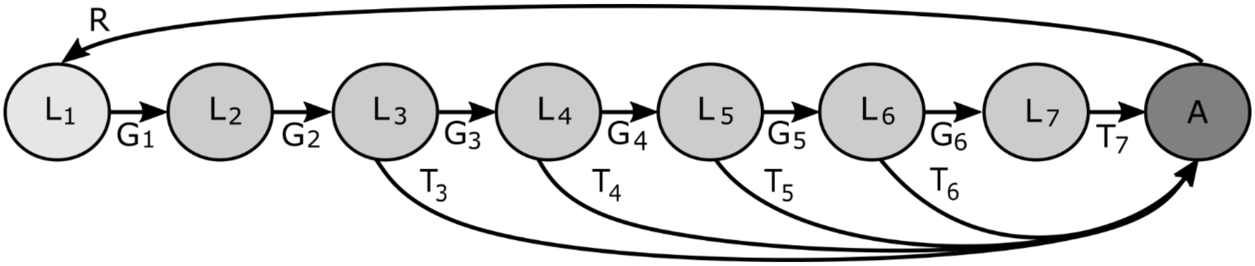

Figure 1. Generalized life cycle used to model the population dynamics of Northern Brook Lamprey. R *represents recruitment including newborn survival,* G_i *represents the probability of surviving and moving to stage* $i + 1$ *each month, and* T_i *represent the probability of transitioning to the final stage, and includes mortality during metamorphosis. There are seven larval stages (*L_1*-*L_6*), and one final stage (A) that represents individuals from metamorphosis until spawning.*

The projection matrix **A** is the product of the transition matrix **B**, consisting of the life-history characteristics and the density-dependence matrix **D** (see Equation 8) representing the density-dependence effects, where:

$$B = \begin{pmatrix} 0 & 0 & 0 & 0 & 0 & 0 & 0 & R \\ G_1 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & G_2 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & G_3 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & G_4 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & G_5 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & G_6 & 0 & 0 \\ 0 & 0 & T_3 & T_4 & T_5 & T_6 & T_7 & 0 \end{pmatrix} \quad (1)$$

and,

$$A = B \odot D \quad (2)$$

where the symbol $\odot$ represents the Hadamard product or the element-by-element multiplication of the matrices. Stage-specific abundance, n, each year, y, is calculated from:

$$n_{y+1} = A_{n,y} n_y \,, \quad (3)$$

where *n* is a vector of stage-specific abundance and the population projection matrix *A* varies among years due to environmental conditions and population size impacting vital rates.

The stage-based matrix model incorporates estimates of R, recruitment, G_i, the probability of surviving and moving to the next stage, and T_i, the probability of surviving and metamorphosizing into the adult stage. Recruitment, R, represents the number of female offspring produced per adult female and includes all reproductive parameters including fecundity (F), offspring sex ratio (SR), and survival from the egg state to the first year of the larval stage (s_0). G_i and T_i are both functions of stage-specific survival, σ_i, T_i also includes stage-specific transition probabilities and survival through metamorphosis, where:

$$G_i = \sigma_i (1 - \tau_i) \quad (4)$$

and

$$T\_i = \sigma\_i \; \tau\_i \quad (5)$$

The proportion of individuals in stage i that will move to the final stage, τ_i, can be estimated from:

$$\tau_i = \frac{\sigma_m}{\left(1 + e^{-t_1(i-t_2)}\right)}, (6)$$

where σ_m is the survival rate through metamorphosis; t_1 and t_2 dictate the shape of the curve (Table 1). Equation 6 is adapted from the equation generally applied to estimate transition probability for lamprey based on length (Slade et al. 2003).

Density-dependence

Density-dependence was assumed to act on recruitment. Density-dependence would affect the survival up until burrowing due to limitations on habitat availability (Dawson et al. 2015). Although there is some evidence in lamprey species that there is density-dependence in larval growth (Dawson et al. 2015) which might have implications for larval survival and transformation probability, the experiments were performed on densities much higher than expected for this population. Density-dependence was implemented using a Beverton-Holt function:

$$d = \frac{\left(\frac{\sigma_{max}}{\sigma_0}\right)}{\left(1 + \left({}^{b}/_{K}\right)N_l\right)}, \qquad (7)$$

where N_l is larval density (all stages), K is carrying capacity, b is the density-dependence coefficient, σ_0 is survival until recruitment when the population is stable and σ_{max} is survival until recruitment when the population is at maximum population growth rate (λ_{max}) (van der Lee and Koops 2021).The density-dependence parameter represents the negative effects of high density, with d decreasing with increasing larval density (N_l). The value of b dictates the shape of the curve, with higher values resulting in quicker declines in density dependence.

The density-dependence matrix, D, was structured as:

$$D = \begin{pmatrix} 1 & \cdots & 1 & d \\ 1 & \cdots & 1 & 1 \\ \vdots & \ddots & \vdots & \vdots \\ 1 & \cdots & 1 & 1 \end{pmatrix} \quad (8)$$

and incorporated into Equation 2.

PARAMETERIZATION

There is incomplete understanding of many important characteristics of the life-history and population ecology of NBL. Model parameters were estimated from different populations of NBL, similar lamprey species, common relationships, or solved for to provide a certain population state (e.g., population growth rate $\lambda = 1$) (Table 1). Uncertainty was incorporated into model runs by drawing the unknown parameter from a specified probability distribution providing a range of plausible values. Uncertainty was applied in the model for the majority of parameters including survival rates, metamorphosis parameters, and fecundity.

Table 1. Parameter values incorporated in the matrix population model for Northern Brook Lamprey. Fixed parameters were held constant across model runs, uncertain parameters were sampled randomly from the specified distributions (B= beta, N = normal, and U = uniform), and estimated parameters were estimated from combinations of other parameters, or solved for to provide a certain population state (e.g., $\lambda = 1$). Sources: 1. Docker et al. (2019), 2. COSEWIC (2020), 3. *Vélez-Espino et al. 2008*, 4. *Morman 1979*, 5. *Reed et al. 2003, 6. Multiple sources, see text for details.*

Parameter	Definition, Source	Value or Distribution
Fixed Parameters		-
f_1, f_2	Fecundity parameters for fecundity-length relationship[1,2]	3.104, -3.461
SR	Sex ratio at recruitment[1]	0.5
Uncertain Parameters		-
λ_{max}	Maximum population growth rate[3]	U(*min* =1.21, *max* =1.43)
σ_L	Larval survival rate[6]	B($\alpha =$, β = 38)
σ_m	metamorphosis survival rate[6]	B(α = 49.5, β =38)
TL	Adult total length[4]	N(μ = 115, sd = 5.5)
t_1	Transition scale parameter[6]	N(μ = 2, sd = 0.1)
t_2	Transition shape parameter[6]	N(μ = 5, sd = 0.1)
P_{cat}	Probability of a catastrophe occurring per generation[5]	U(*min* =0.5, max = 0.20)
Estimated Parameters		-
λ	Population growth rate	-
R	Recruitment to the first larval stage (age 1)	-
F	Fecundity	-
G_i	Probability of survival and moving to the next stage	-
L_i	Larval stage i	-
A	Adult stage; includes juveniles	-
T_i	Probability of transitioning into A at L_i	-
N_i	Abundance of stage i	-
ξ	Generation time	~6 years
b	Density dependence coefficient	-
σ_0	Survival rate at recruitment for a stable population	-
σ_{max}	Survival rate at recruitment at maximum population growth	-
K	Carrying capacity	-

Recruitment

The matrix model requires an estimate of recruitment (R) per female. Recruitment represents the number of female offspring surviving to the first larval stage and includes all aspects of reproduction including fecundity, offspring sex ratio, and survival. The relationship between fecundity (F, number of eggs) and total length (TL) for NBL has been calculated as:

$$log_{10}(F) = 3.104 \cdot log_{10}(TL) - 3.461 \quad (9)$$

This significant relationship explained about 66% of the variation in fecundity ($p < 0.05, R^2 = 0.661, n = 9$; Vladykov (1951) in Docker et al. (2019)). Adult NBL length is unknown for these populations; however, the average length for 156 NBL adults in the Lower Peninsula of Michigan was 115 mm (range 86–166 mm) (Morman 1979), which results in an average fecundity of 862 eggs (CI: 350, 2693). To represent parameter uncertainty in fecundity, adult NBL TL used in Equation 9 was estimated using a normal distribution (μ = 115, sd = 5.5).

The sex ratio of lamprey species in the larval stage is typically at or near parity (Docker et al. 2019). It is reasonable to assume that the sex ratio at recruitment to age 1 is not significantly different from 1:1, as ovarian differentiation may not be fully complete until around 1 year of age in non-parasitic lamprey species (Docker et al. 2019). Lamprey females appear to, however, have higher mortality just prior to, or during, metamorphosis leading to adult sex ratios skewed in favour of males. NBL populations with measured adult sex ratios range from 25–46% females (COSEWIC 2020).

Survival until age 1 is unknown for NBL but is considered to be the lowest of all NBL stages. The value of survival that would result in a stable population (population growth rate ($\lambda = 1$) was solved for a given combination of life-history parameters. This provides an estimate of the average number of female recruits that is needed to survive for the population to be stable.

Stage transitions

Survival

Stage-specific NBL survival rates (σ_i) are unknown. Lamprey mortality is generally considered to be the highest from the egg phase until larvae reach suitable burrowing larval habitat (see above), and then again at metamorphosis. Burrowed lamprey ammocoetes, however, are thought to experience relatively low and uniform mortality across ages, with estimated annual survival rates ranging from 56.8% to 77% (Table 2). Annual survival rates used for the juvenile stage in two Sea Lamprey (*Petromyzon marinus*) population models ranged from 35% to 53%; however, it was unclear if these were based on data from the juvenile stage. Due to these uncertainties, the values for σ_i were allowed to vary in the model. For the larval stage, σ_i was drawn from a beta distribution, with shape parameters α = 57 and β= 38 derived from mean of 0.6 and standard deviation of 0.05 to represent parameter uncertainty. For the juvenile survival, which was included in the transition equation between larvae and adults, survival was drawn from a beta distribution, with shape parameters α = 49.5 and β= 38 derived from a mean of 0.5 to represent a higher mortality and standard deviation of 0.05 to represent parameter uncertainty.

Table 2. Estimates of stage-specific survival for different lamprey species from the literature. Sources: 1. Kelso and Todd (1993), 2. Johnson et al. (2014), 3. Weise and Pajos (1998), 4. Howe et al. (2012), 5. Vélez-Espino et al. (2008).

Age/Stage	Annual Survival (%)	Error /[CI]	Species	Source
age 0–1	47	-	*Geotria australis*	*1*
age 1–2	77	-	*Geotria australis*	*1*
larval	57.6	3.2%	*Petromyzon marinus*	*2*
larval	56.8	3.2%	*Petromyzon marinus*	*2*
larval	57.1	3.6%	*Petromyzon marinus*	*2*
larval	61	-	*Petromyzon marinus*	*3*
juvenile	35	0.029%	*Petromyzon marinus*	*4*
juvenile	53	[0.3,0.7]	*Petromyzon marinus*	*5*

Stage duration

Larvae remain burrowed until they start metamorphosis, beginning at approximately three years and up to seven years, with three years being mainly males, and five years being the most typical (COSEWIC 2020). To achieve the above stated population characteristics, along with a generation time of approximately six years (COSEWIC 2020) the τ parameters t_1 and t_2 were drawn from a normal distribution with mean two and five respectively, and a standard deviation of 0.1 representing parameter uncertainty. For age seven, τ was set to one as this was the last larval stage and all individuals left would transition to adults. NBL go through metamorphosis in their last year, remaining as a juvenile for six to eight months prior to maturation and spawn within three of maturation. Although not documented for NBL, adult lampreys typically die within a month of spawning (COSEWIC 2020). The adult stage represented juveniles and adults, and only lasted for one year.

Density dependence

Maximum population growth rates (λ_{max}) are not available for NBL. Maximum population growth rates estimated from analyses of Sea Lamprey time series in the Great Lakes ranged from 1.21 to 1.43 (Vélez-Espino et al. 2008). To account for the uncertainty in NBL maximum population growth rate, λ_{max} was drawn from a uniform distribution with a minimum value of 1.21 and maximum value of 1.43. σ_{max} was solved for in the same manner as σ_0 to find the value that results in a population growing at its maximum rate. The value b was then calculated by rearranging the density dependence equation as: $b = \sigma_{max} \ / \ \sigma_0 - 1$. The value for carrying capacity (K) was set or optimized in the model for a desired λ, depending on the analysis performed (as described below).

IMPACT OF HARM

The impact of anthropogenic harm to a NBL population was assessed with deterministic elasticity analysis of the projection matrices and stochastic simulations.

Elasticity analysis of matrix elements provides a method to quantify the impact of changes to vital rates on a population. Specifically, elasticities measure the proportional change to population growth rate (λ) that results from a proportional change in a vital rate (ν). For example, a λ elasticity of 0.2 for survival during metamorphosis indicates that a 10% increase in survival rate (e.g., 0.5·(1+0.1) = 0.55) would cause a 2% increase in population growth rate (e.g., 1·(1+0.1·0.2) = 1.02).

Elasticities are useful as they allow for assessment of how impactful changes to vital rates and other model parameters are to a population and 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 (i.e., $< 30\%$ changes), and assume all other model parameters remain unchanged. Therefore, simulation analysis, which can provide better predictions in the presence of non-equilibrium dynamics, was also used to compare the effects of transient or periodic harm to a population.

Elasticity of population growth rate

Elasticities of λ (ϵ_λ) are calculated by taking the scaled partial derivatives of λ with respect to a vital rate (ν, Caswell 2000):

$$\varepsilon_\lambda = \frac{\nu}{\lambda}\sum_{i,j}\frac{\partial\lambda}{\partial a_{i,j}}\frac{\partial a_{i,j}}{\partial \nu}, \qquad (10)$$

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

A range of potential vital rate elasticities were estimated by allowing uncertain parameters to vary. As well, population growth rate was allowed to vary by incorporating the effect of density on recruitment. This was accomplished by randomly generating larval density as a proportion (0 to 1000%) of carrying capacity using a draw from a uniform distribution on a log scale. $\lambda = 1$ when $N_l = K$, $\lambda < 1$ when $N_l > K$ and $\lambda > 1$ when $N_l < K$. The elasticity analysis was replicated 5,000 times.

The maximum allowable harm can be estimated from elasticities by calculating the change in a vital rate that allows a population to maintain a $\lambda > 1$. Allowable harm applies when a population has an initial $\lambda > 1$. Maximum allowable harm is estimated as (Vélez-Espino and Koops 2009):

$$\text{Maximum allowable harm } = (1/\epsilon_\lambda)\big((1-\lambda)/\lambda\big) \quad (11)$$

Since λ is unknown for NBL, maximum allowable harm was not estimated for this population.

Simulation

Simulation analysis was used to investigate the impacts of periodic stage-specific harm on population density. The larval ages 1–7 were combined since, due to their similar survival rates and habitat use, they would have similar susceptibility to anthropogenic harm. The final (adult) stage lasts for only one year with 100% mortality (i.e., semelparous); instead impact of harm was assessed for recruitment which accounts for both survival through metamorphosis and survival until the first larval stage. Life-stages were affected by harm ranging from zero to 99%, drawn from a uniform distribution at different frequencies: one, two, five, and ten years, over a 100-year simulation. The initial carrying capacity was then compared to the mean population size over the final 15 years of the simulation to determine the long term effect of the harm, quantified as the proportion of initial *K*. It is important to note that transient dynamics, which may result in a varied and greater effect on abundance, would be captured if a time period closer to when harm was applied as opposed to the last 15 years. The frequency indicates how often harm was applied. A frequency of 1 indicates that harm is constant and applied every year, where a frequency of 10 indicates that harm is periodic and applied once every 10 years. Since the model incorporates density-dependence, it is assumed that the population is able to recover in between applications of harm as conditions are returned to the initial state. The simulations incorporated parameter uncertainty by varying uncertain parameters (Table 1), and were replicated 1,000 times.

RECOVERY TARGETS

Abundance: Minimum Viable Population (MVP)

The concept of demographic sustainability was used to identify potential minimum recovery targets for NBL. 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 60 years (10 NBL generations, where generation time (ξ) estimated from stochastic projection matrices (Caswell 2000) with $\lambda = 1$, was 5.97 (CI: 5.72–6.20)). MVP was estimated using simulation analysis which incorporated parameter uncertainty, 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 rationale. It must be long enough to be of consequence for the population examined but not so long as to be an unreasonable time frame for management considerations. Sixty years was selected as it equates to approximately ten NBL generations.

Catastrophes represent an event that causes greater than a 50% decrease in population size. A NBL population may be impacted by catastrophes such as severe drought or a rise in water temperatures (COSEWIC 2020). The rate that severe catastrophes impact NBL populations is unknown. Based on a meta-analysis, Reed et al. (2003) determined that among vertebrate populations, catastrophic die-offs (defined as a one-year decrease in population size >50%) occurred at a rate of $14\%\xi^{-1}$ on average. The impact of a catastrophe affects all life-stages simultaneously and was drawn randomly from a beta distribution scaled between 0.5 and one with shape parameters of 0.762 and 1.5 (Reed et al. (2003), $\beta(0.762,1.5) \cdot (1 - 0.5) + 0.5$), representing the probability of a 50 to 100% decline in population size.

Quasi-extinction represents the compounding impacts 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).

Simulations were conducted for populations with various initial abundances of adult females, ranging from 50 to 5,000 (initial density represented carrying capacity, K, where $\lambda = 1$) and catastrophe rates of 5 - 20% per generation (drawn from a uniform distribution). The simulations were conducted for 60 years and replicated 20,000 times. The number of quasi-extinctions was tracked across simulations and the probability of extinction (P_{ext}) was modelled with a logistic regression that was a function of $log10$ transformed initial female density, catastrophe rate (P_{cat}), and all uncertain population model parameters where:

$$P_{ext} = \frac{1}{1 + e^{-X\beta}}, \qquad (12)$$

and X is a matrix of all covariates and β is a vector of coefficients including the intercept. Because regression analysis is sensitive to sample size, which in this case is the number of simulations, the process was repeated for MVP estimates from simulations with 5,000, 10,000, and 15,000 replications. The best model was chosen by removing all insignificant population model parameters along with those that were inconsistently significant across simulation sample sizes.

Habitat: Minimum Area for Population Viability (MAPV)

Minimum area for population viability (MAPV) represents the quantity of habitat required to support a population of MVP size. MAPV was estimated by dividing the MVP estimate by density. In optimal habitats, larval NBL densities can be very high (e.g., up to 126 NBL larvae m^{-2}) although, when density is averaged over larger areas, <1 to 20 larvae m^{-2} is more typical for other lamprey species (COSEWIC 2020). These density data estimates represent potential larval population density, whereas MVP is specific to adult females. To determine the number of larval NBL that corresponds to the female adult MVP, the stable stage distribution was calculated for the population matrix, incorporating parameter uncertainty, and repeated 10,000 times to determine the mean and 95% confidence interval.

RECOVERY TIMES

There are no current estimates of NBL population abundances or growth rates. To determine a range of recovery times, population sizes starting from 10% of the MVP, and growth rates ranging from 1 to λ_{max} were used. Carrying capacity of the available habitat was solved for using the projection matrix given the estimated abundance and λ. The time taken for the population to exceed MVP for a given catastrophe rate was recorded. Simulations were replicated 10,000 times.

RESULTS

IMPACT OF HARM

The impact of anthropogenic harm to NBL populations was assessed with two analyses: deterministic elasticities and simulations.

Elasticity of Population Growth Rate

Elasticities demonstrate which vital rates, if changed, have the greatest impact on a population's growth rate. Most individual vital rates had similar elasticities of 0.17 including survival to age one, larval survival of ages 1–3, fecundity, and survival through metamorphosis (Figure 2). NBL populations were least sensitive to changes in the survival of larval ages 4+, with a combined median elasticity of 0.08, and transition probability with median elasticities of 0.01, 0.02, 0.04, and 0.02 for ages three, four, five, and six respectively. Transition probability had the greatest variability in elasticity.

The elasticity values for vital rates were influenced by population state (λ) and other life-history parameter values (Figure 3). The most influential parameters were population growth rate, age five transition probability, and larval survival. The elasticity values of all vital rates, except for the survival of older (ages 4+) larvae, increased with λ while that of older larvae survival decreased. The transition probabilities had the greatest change in elasticities across λ, followed by older larval survival. In addition, the elasticities of the transition probability of age five larvae had a non-linear relationship with λ with an inflection point at $\lambda > 1$ after which the elasticities stopped increasing with increases in λ.

The elasticities of all the recruitment and survival parameters were influenced by the age five transition probability, with higher elasticities for all vital rates at higher transition probabilities, except for ages 4+ larval survival where the elasticity decreased with increasing probability for the full range. The elasticities of the transition probabilities were influenced by larval survival, with lower elasticities at higher survival rates for the full range for ages three, four, and five and only for $\lambda < 1$ for age six.

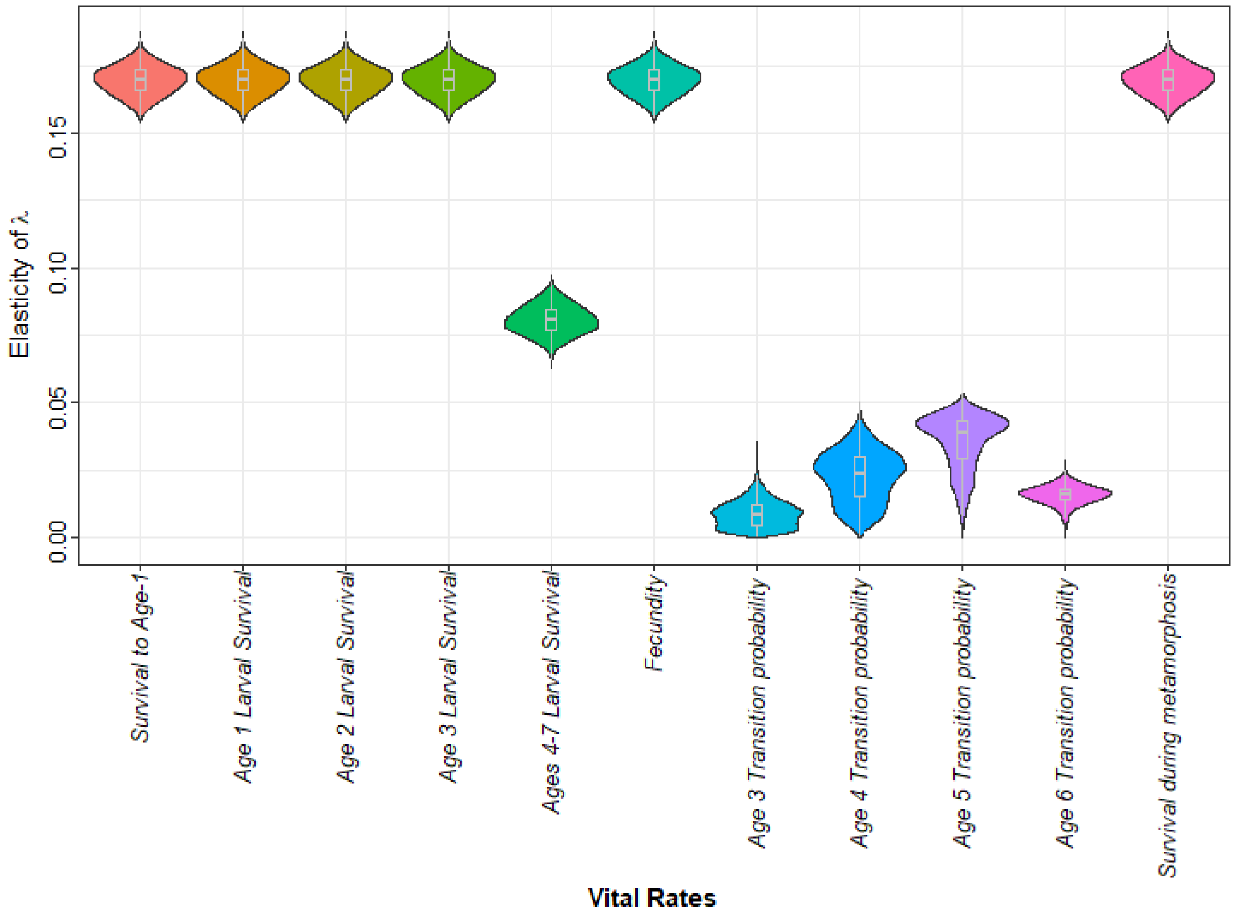

Figure 2. Elasticity of population growth rate analysis results for Northern Brook Lamprey populations represented with violin and box plots. Results reflect uncertainty in life-history characteristics and different values of population growth rates.

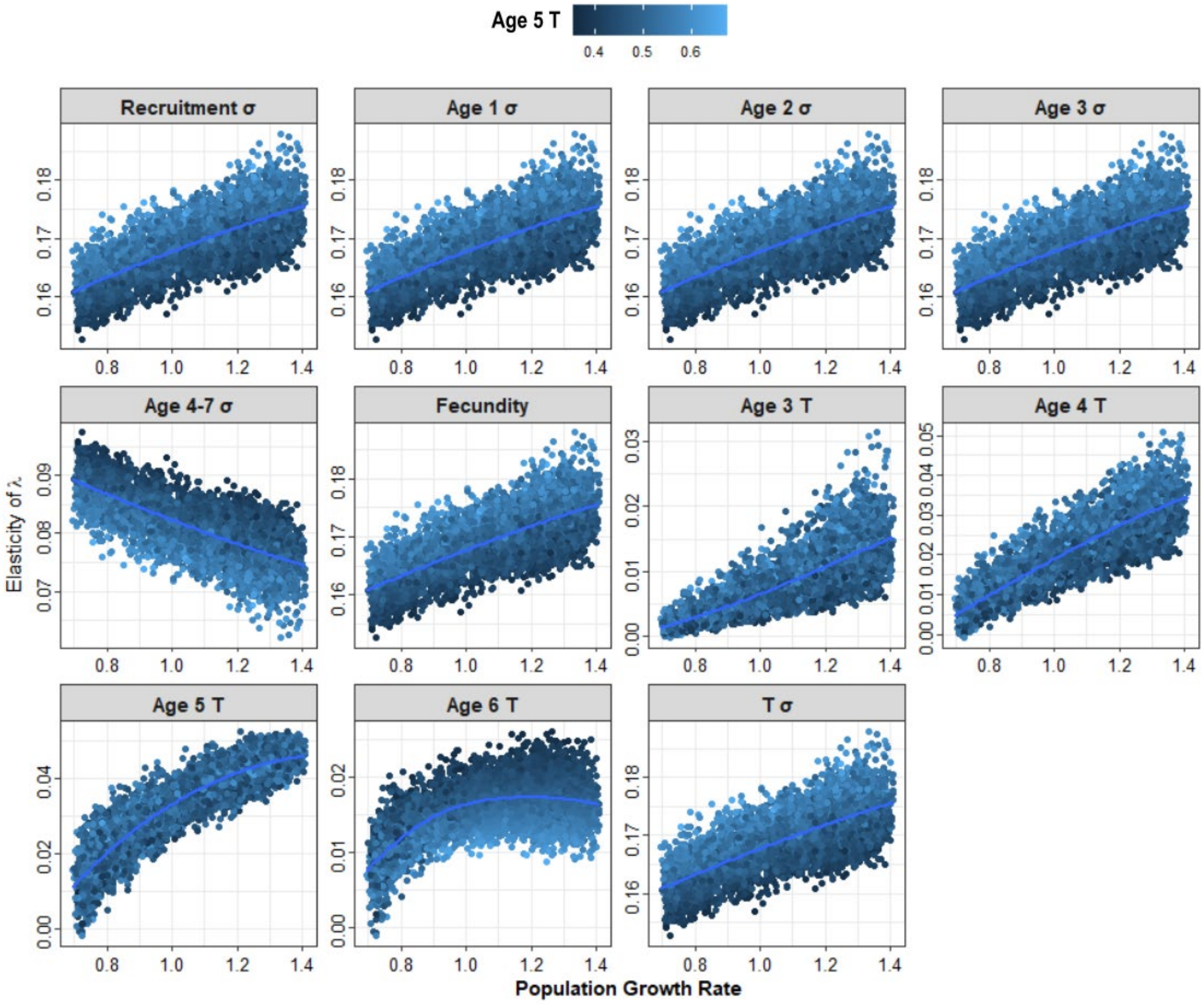

Figure 3. Elasticity of population growth rate analysis results for Northern Brook Lamprey populations plotted against population growth rates. Panels represent the vital rate elasticities (sigma = survival, T = transition probability). Colour indicates the age five transition probability, NOTE different y-axis scales

Simulation

Simulation analysis was used to investigate the impact of anthropogenic harm to stable population size and investigate the effects of periodic perturbations occurring annually (for comparison to elasticity analysis), every second year, fifth year, and tenth year (Figure 4).

Harm (i.e., proportional increase in stage specific mortality) applied to the larval stage or both larval stage and recruits had a larger impact on abundance than harm only applied to recruitment. Small amounts of mortality had large impacts on population size. When harm was applied annually, a harm of ~ 0.06 to the larval stage, ~ 0.2 to recruitment, or ~ 0.05 to both stages resulted in a 25% reduction in population size; with biennial harm, this increased to a harm of ~ 0.1 to the larval stage, ~ 0.4 to recruitment, or ~ 0.09 for both. When harm was applied every five years, the amount of harm required to reduce the population size by 25% increased to ~ 0.1 when applied to the larval stage and both stages, and ~ 0.9 when applied to just the recruits. And finally, when harm was applied every 10 years, the amount of harm required to reduce the population size by 25% increased to ~ 0.45 when applied to the larval stage and ~ 0.3 for both stages; almost no level of harm to recruitment reduced the population below 25%. When harm was applied to the larval or both stages every one to two years the population trended towards zero, however, when harm was applied every five or 10 years, which was just less than equal or double NBL generation time, the NBL populations were unlikely to crash except at the highest levels of harm (i.e., > 70%).

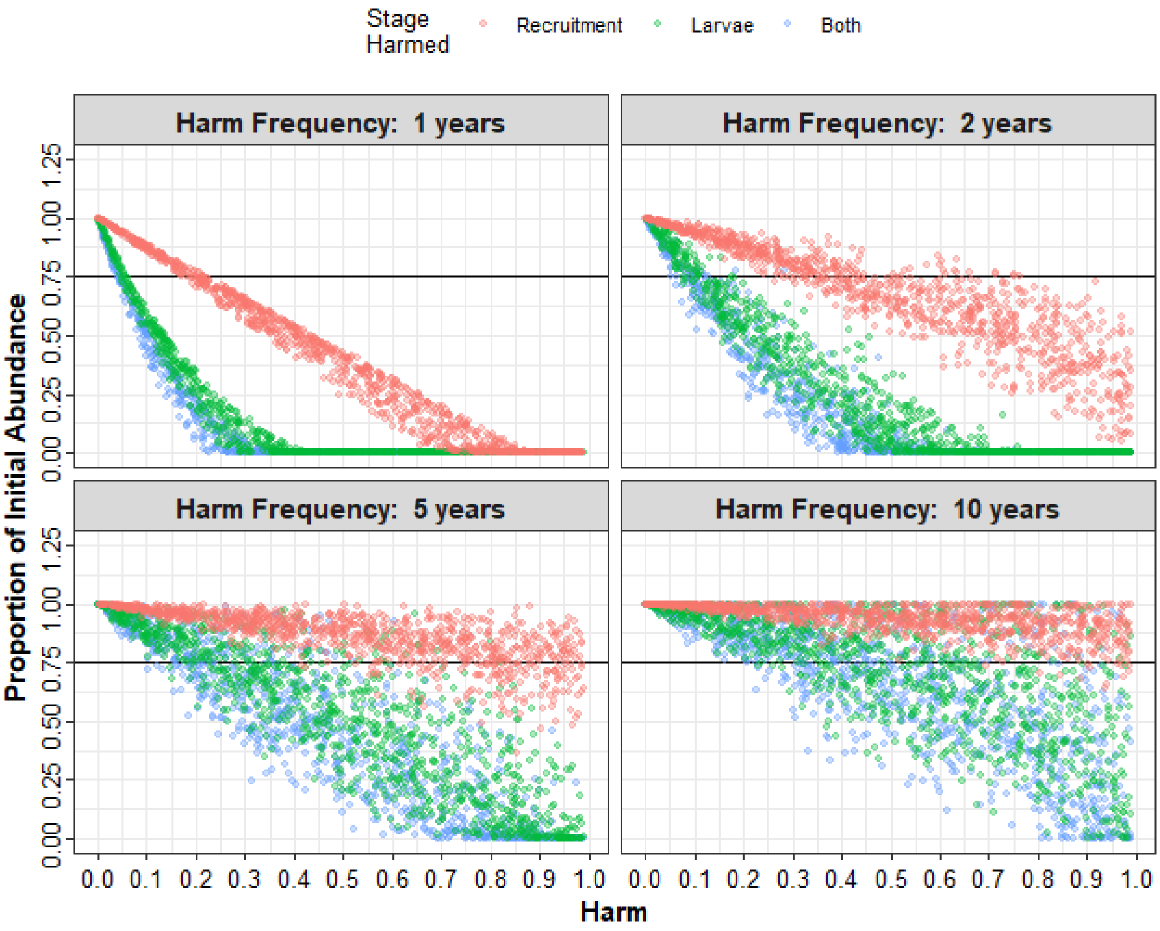

Figure 4. Results of simulation analysis examining the proportional change in stable Northern Brook Lamprey population size that resulted for anthropogenic harm occurring at different frequencies (1-, 2-, 5-, and 10-year intervals). Harm (i.e., proportional increase in stage specific mortality) was applied to recruitment (red), larval stage (green), and both (blue). The horizontal line indicates a 25% reduction in population size.

RECOVERY TARGETS

Abundance: Minimum Viable Population (MVP)

Demographic sustainability was assessed using simulation analysis which incorporated parameter uncertainty, environmental stochasticity and density-dependence. Simulation outputs, binomial quasi-extinctions (1: extinct; 0: extant), were fitted using a logistic regression as a function of adult female population size, catastrophe rate and uncertain life-history parameters.

Only population size and probability of catastrophe had a significant effect on extinction probability (Table 3, Figure 5). None of the other life-history parameters consistently influenced extinction risk over the range of values included (Table 1) and over the length of time (60 years; ~ 10 generations) simulated, and the number of replications in the simulation. The scale parameter for the transition probability equation (Equation 9), was however significant for the simulation with only 5,000 replications (Figure 6).

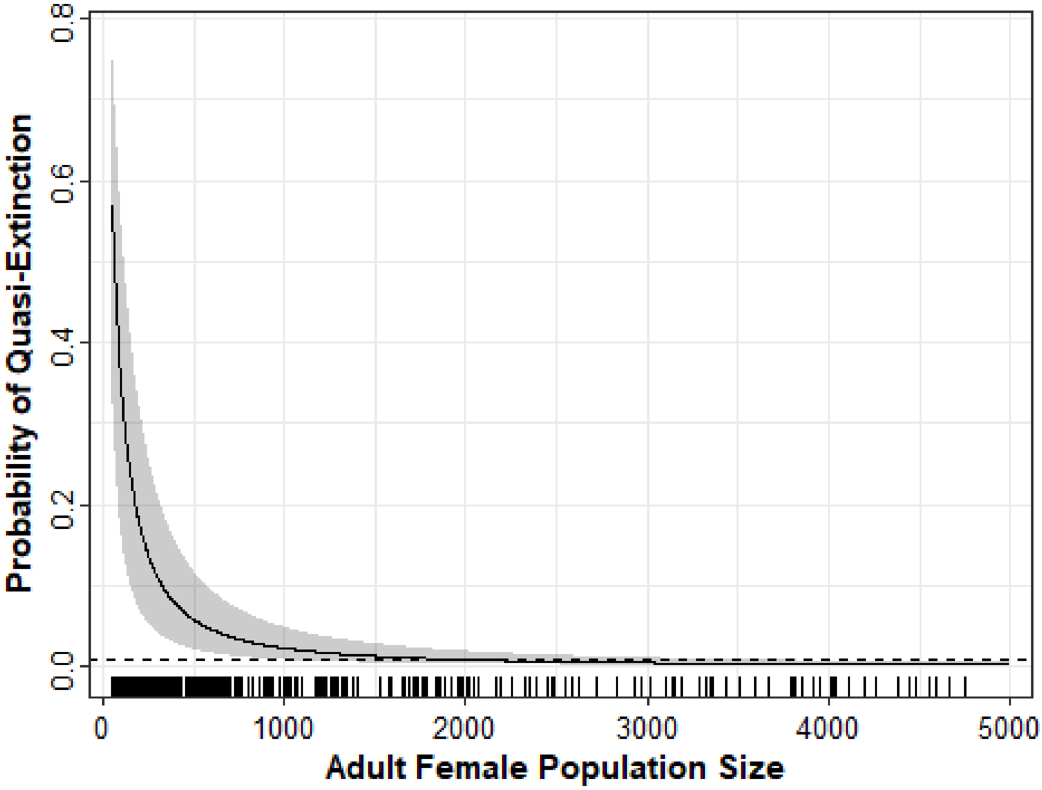

Figure 5. The probably of quasi-extinction as a function of adult female Northern Brook Lamprey population size. The rug plot indicates quasi-extinctions. The solid line represents the logistic regression trend with the grey region representing the confidence intervals (for P_{cat} ranging from 13% to 15% per generation). The dashed line indicates a 1% probability of extinction.

Table 3. Logistic regression model results for NBL extinction probability. N_a represents adult female population size and P_{cat} represents the probability of catastrophe per generation (~ 6 years).

Parameter	Estimate	Std. Error	p-value
(Intercept)	3.28	0.27	< 0.001
$log_{10}(N_a)$	-2.82	0.09	< 0.001
P_{cat}	12.88	1.11	< 0.001

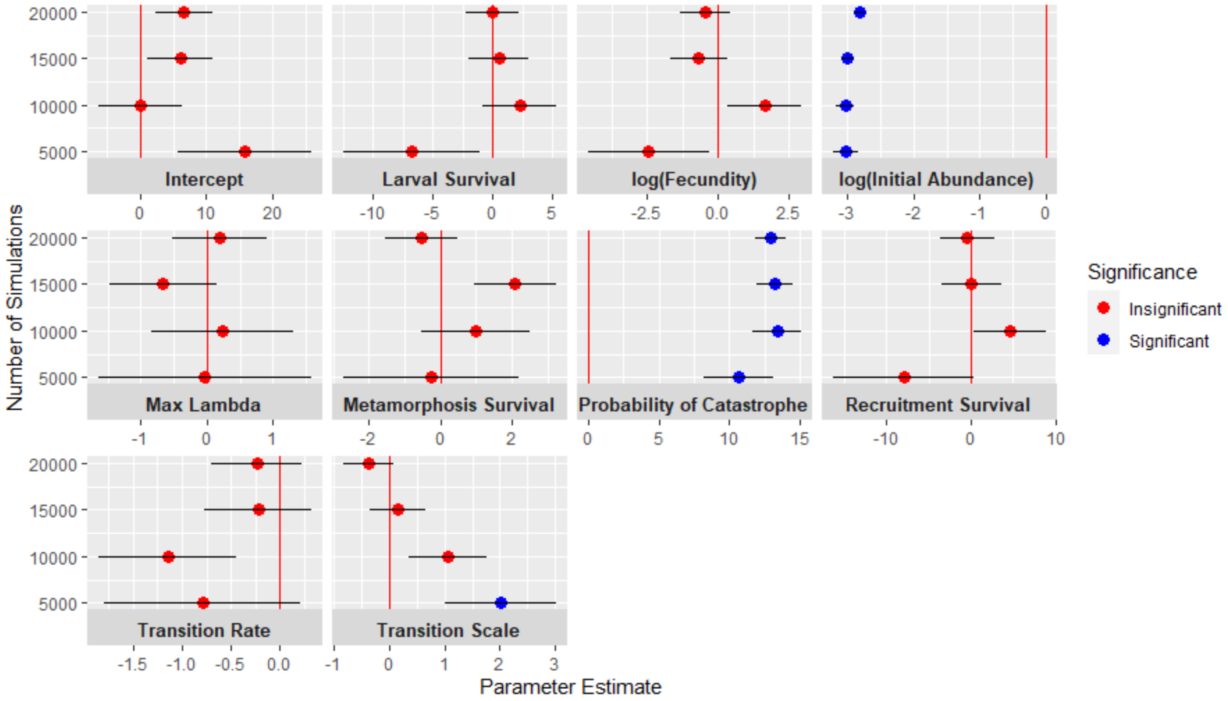

Figure 6. Significance and the range of estimates (with confidence intervals) for life-history parameters considered in the regression analysis to determine the equation for the probability of extinction, across a range of replications used in the simulation analysis.

Minimum viable population (MVP) size was estimated from the logistic regression model to find the adult female population size that resulted in a 1% probability of extinction. This resulted in an MVP estimate of 2,569 [95% confidence interval: 1,110, 4,950] adult females, and using the precautionary adult sex ratio estimate of 25% females (COSEWIC 2020) results in a total adult MVP of 10,276 [95% confidence interval: 4,408, 19,800] adults.

Extinction probability of any adult female population size (N_A) can be estimated from the fitted logistic relationship for a given probability of catastrophe (P_{cat}) as:

$$P_{ext} = \frac{1}{e^{-(3.28-2.82\cdot log_{10}(N_A)+12.88\cdot P_{cat})}} \quad (13)$$

Habitat: Minimum Area for Population Viability (MAPV)

Using the stable stage distribution, the mean number of larvae that corresponds to one adult female was estimated as 64 [95% confidence interval: 36, 139]. Larval density and available suitable habitat is uncertain for NBL, therefore MAPV was estimated for a range of densities from 0.1 to 126 larvae per m^2. Larval abundance estimates were generated for every combination of a subsample of 100 estimates of larvae per adult and a subsample of 500 estimates of MVP, for each density estimate. The estimation of MAPV for bins of larval abundance and density was then summarized in Figure 7. The range of density estimates represent very different methods (e.g., averaged over a reach or habitat type) and habitats (e.g., preferred, marginal); therefore, an average MAPV value is not meaningful and Figure 7 should be used to determine the range of MAPV values for a given density estimate. There is approximately 4.1 km^2 total wetted area available within the known distribution of NBL, with ~ 0.7 km^2 in the Birch River, and ~ 3.4 km^2 in the Whitemouth River; however, it is unknown how much of this habitat is suitable for NBL (D. Watkinson, DFO, unpublished data).

Density (individuals per m²)	1,060 - 1,557	1,558 - 2,385	2,386 - 3,509	3,510 - 5,132
100 - 126	0.0026km²	0.0043km²	0.0065km²	0.011km²
20-100	0.003km²	0.005km²	0.0075km²	0.013km²
15-20	0.017km²	0.028km²	0.042km²	0.071km²
10-14	0.023km²	0.039km²	0.058km²	0.098km²
5-9	0.039km²	0.064km²	0.096km²	0.16km²
2-4	0.078km²	0.13km²	0.19km²	0.33km²
1-1.9	0.15km²	0.25km²	0.37km²	0.63km²
0.5-1	0.37km²	0.62km²	0.93km²	1.6km²
0.25-0.4	0.78km²	1.3km²	1.9km²	3.3km²
0.1-0.24	1.5km²	2.5km²	3.7km²	6.3km²
Larval MVP	150,717 - 396,311	396,312 - 604,830	604,831 - 910,127	910,128 - 2,990,503

Figure 7. Estimates of the minimum area for population viability (MAPV) for a range of larval densities and MVP estimates (larval and adult).

RECOVERY TIMES

The mean recovery time for the simulations, with population sizes starting from 10% of the MVP, and growth rates ranging from 1 to λ_{max} was 4 years [95% CI: 1, 57]. Recovery times were greatest when the initial population size and growth rates were low and decreased with increasing sizes and rates (Figure 8).

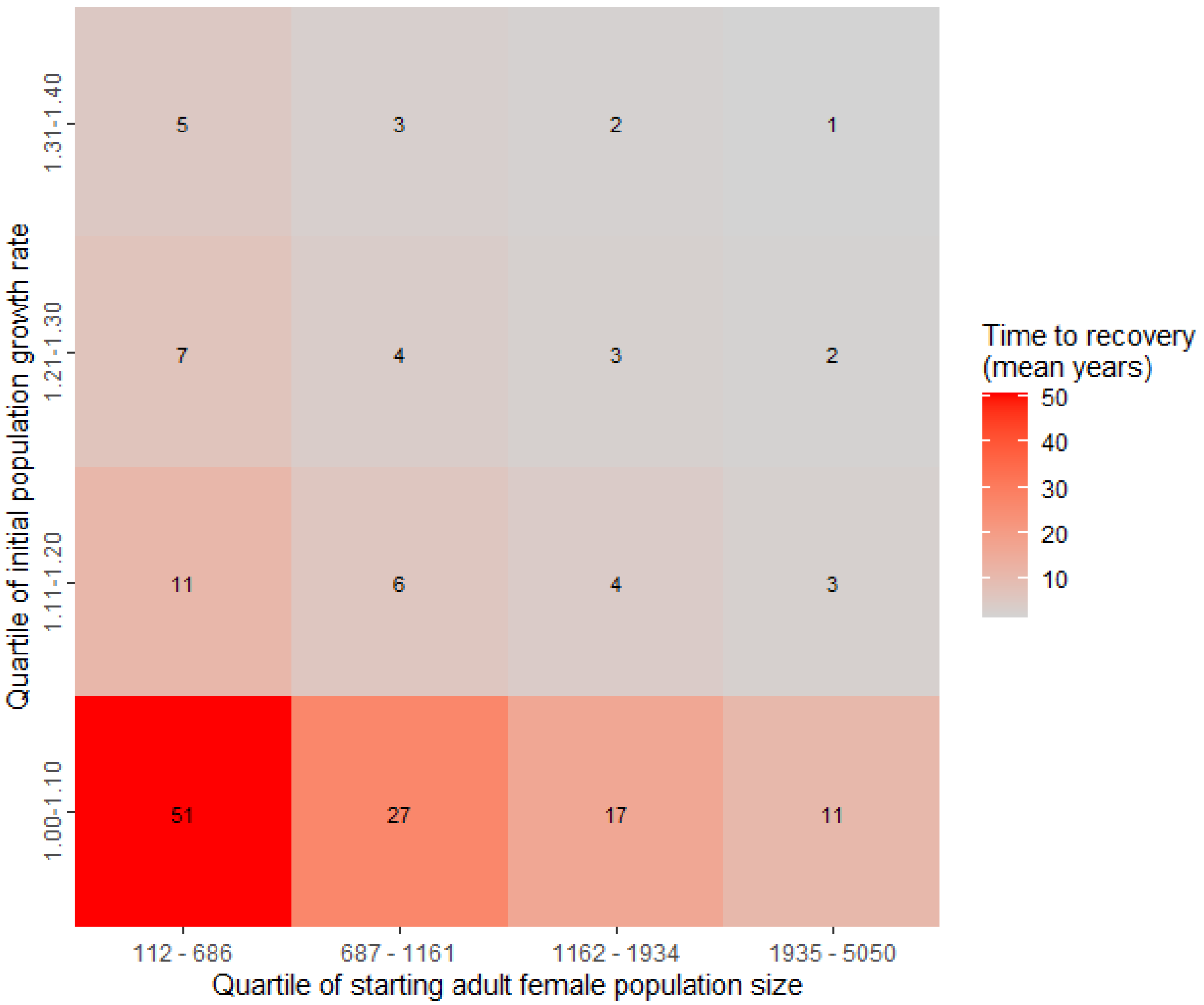

Figure 8. The mean number of years it would take for the Northern Brook Lamprey population to reach the minimum viable population based on the quartile of initial female adult population size and population growth rate.

DISCUSSION

A population model for NBL was created to make predictions on how the population may respond to anthropogenic harm, estimate potential recovery targets for abundance and habitat, and estimate recovery times for depressed populations. The model included parameter uncertainty, environmental stochasticity and density-dependent effects.

Elasticity analysis was used to determine which NBL vital rates were most sensitive to harm. Most individual vital rates had similar elasticities of just under 0.17 including survival to age one, larval survival of ages one to three, fecundity, and transformation survival. This indicates that, for example, a 10% decrease in survival during metamorphosis could result in a stable population growth (λ= 1) decreasing to λ= 0.98 (i.e., 1·(1-0.1·(0.17)) = 0.98). Elasticities are additive, therefore a 10% decrease in survival that would affect all larval ages would result in a larger decrease in λ (i.e., 1·(1-0.1·(0.17+0.17+0.17+0.08)) = 0.94). NBL populations were least sensitive to changes in the survival of larvae ages 4+ and transition probabilities.

When the population was growing ($\lambda > 1$), NBL population growth rate became increasingly sensitive to all vital rates except for the survival of larvae aged 4+, likely due to the majority of larvae having already metamorphosized by age five. This indicates that efforts to improve larval survival, survival through metamorphosis, and recruitment will have the greatest impact on population growth rates and sizes. Elasticity estimates were also affected by the value of uncertain life-history parameters. The elasticities of vital rates generally increased with increasing age-five transition probability, and transition probability elasticities decreased with higher larval survival rates.

Simulation analyses were used to determine the effect of decreasing survival rates on population size while accounting for density-dependence. This information is useful for estimating maximum allowable harm. There was a ~ 25% reduction in population size with only ~ 5% increase in harm applied annually; the population crashed with only a ~ 25% increase in harm applied annually to both the larval stage and recruitment. This is a large effect from a small level of mortality indicating a high degree of population sensitivity to potential harm to the larval stage. Increasing the rate at which harm was applied from annually to biannually had minimal impact on allowable harm, however there was a substantial decrease in the impact of harm when harm was only applied every five or 10 years. When harm was only applied every five or 10 years the population was unlikely to crash, even at the highest levels of harm applied, likely due to the generation time being six years for this population, allowing the population to recover between harm events. Since there are no current estimates of population growth rates, maximum allowable harm was not estimated for the NBL, however Equation 11 can be applied, using the elasticities from the vital rates, when population growth rates are made available, if the population is growing ($\lambda > 1$).

Estimates of potential recovery targets for population abundance were provided using simulation analysis to determine the population size required for demographic stability through estimates of minimum viable population size. The estimate of the number of adult females required for a 1% chance of extinction over 60 years was 2,569 [95% confidence interval: 1,110, 4,950] which equates to 10,276 [95% confidence interval: 4,408, 19,800] adults if a 3:1 male:female sex ratio is assumed. Uncertain life-history characteristics did not have an impact on MVP estimates, likely due to the manner in which recruitment was determined. Survival until recruitment into the larval stage was determined by finding the value that gave a stable population, therefore the same number of larvae would result regardless of life-history characteristics. When not formulated in this manner, the highest risk of extinction faced by semelparous species has been shown to change depending on developmental rate; with delayed metamorphosis leading to greater sensitivity to variable juvenile survival, and earlier metamorphosis leading to greater sensitivity to variable developmental rate (Jonsson and Ebenman 2001). The MVP simulation only represented ~ 10 generations (60 years) for NBL. With longer simulations (e.g., 500 years) some life-history characteristics, such as maximum population growth rate and transition probability, may influence persistence probability and MVP size as they impact how quickly a population can respond to a perturbation. The mean MAPV was 6.3 km^2 for smallest density estimates paired with the largest MVP estimates, and 0.0026 km^2 for highest density estimates paired with the smallest MVP estimates. The range of MAPV values provided in Figure 7 provides a starting point to work from when determining the amount of habitat required for a MVP sized population, however more work is needed to determine average density estimates for the NBL populations before a specific estimate can be provided.

The current NBL population sizes and growth rates are unknown; therefore, recovery times were estimated for a range of starting female population sizes, from 10% of MVP to MVP, and population growth rates, from one to the maximum population growth rate. The mean recovery time was 51 years for the slowest population growth rates paired with the smallest initial female population sizes, and one year for the fastest population growth rates paired with the highest initial female population sizes. The range of recovery times provided in Figure 8 provides a starting point to work from, however more work is needed to determine average abundance estimates for the NBL populations before a specific estimate can be provided.

UNCERTAINTIES

There were significant uncertainties in the parameterization of the population model for NBL. Uncertain parameters included: nearly all aspects of recruitment, survival, age specific transition probabilities, and maximum population growth rate. Rather than selecting specific values for these parameters that may be representative of NBL, a range of potential values were used represented by probability distributions. This allows for the uncertainty in the NBL parameters to be represented in the simulations by giving a range of results. Incorporating parametric uncertainty can greatly impact the findings derived from population viability analysis (McGowan et al. 2011). More precise results can be extracted from the simulations as additional information about NBL life-history becomes available. In addition the ability to make predictions for allowable harm, recovery times, and MAPV was hindered by a lack of data on 1) current population sizes and growth rates, 2) species density, 3) total availability of suitable habitat within their distribution, and 4) how current threats relate to the probability and size of catastrophes and changes in vital rates.

The density-dependent relationship could have impacted the outcomes of the model. Density-dependence was assumed to follow a Beverton-Holt relationship, act only on the survival of the first year of life, and was a function of larval female density. This was meant to represent burrowing success of larvae recruiting into the population. The assumption made was that density-dependence would have a reduced impact once individuals had secured a burrowing site. Although laboratory experiments have revealed density dependence in lamprey larval growth rates, most of these experiments were conducted at densities considerably higher than those anticipated for the NBL populations under study (Dawson et al. 2015). When estimating MVP, the crucial factor is whether density-dependence occurs and its degree of strength, rather than the manner in which it occurs. As an instance, Lamothe et al. (2021) discovered that the maximum population growth rate had an impact on MVP calculations, while van der Lee and Koops (2021) found that the form of the density-dependence relationship did not. Incorporating density-dependence in population analysis allows for population recovery after major disruptions, resulting in considerably lower MVP estimates compared to scenarios without density-dependence (as demonstrated in studies such as Roberts et al. 2016). Incorporating density-dependence in other model parameters, for example in transition probabilities to incorporate evidence of larval growth rates responding to density (Dawson et al. 2015), would likely lower MVP estimates.

Semelparous organisms invest all of their resources in a single reproductive season making them highly vulnerable to environmental fluctuations or unexpected events that can negatively affect the success of that reproductive event (Stearns 1976). However, semelparity also allows for a burst of reproduction that can take advantage of favorable conditions when they arise, for example, if reproduction is triggered by a combination of environmental cues (e.g., salmon, Quinn et al. 2003). Therefore, the impact of semelparity on extinction risk is context-dependent and can vary depending on the specific ecological and environmental conditions faced. The response of NBL reproductive success to environmental cues and fluctuations requires further investigation in order to assess its effect on minimum viable population sizes and recovery times.

Although NBL was analyzed with a simple population structure, there is a possibility that a more intricate population structure exists, which may have implications for estimating population size and overall persistence probability. A meta-population structure, involving migration or interbreeding among sub-populations, has the potential to significantly increase population persistence. However, this effect may be reduced if stochastic environmental conditions are correlated among populations (Palmqvist and Lundberg 1998, Reed 2004). If there is some level of NBL meta-population structure within the watershed, for example between the Birch and Whitemouth rivers, the persistence probability may be higher than what was estimated in this study. Moreover, NBL was modelled as being independent from Silver Lamprey (*Ichthyomyzon unicuspis*), whereas there is a possibility of a shared gene pool, with no distinct genetic differences between the two species (COSEWIC 2020). This would result in a significant modification of the population model formulation. It is improbable that they form a single freely interbreeding panmictic population, and they are not thought to co-occur in the Birch and Whitemouth Rivers, and thus they are considered distinct species (COSEWIC 2020).

ELEMENTS

Element 3: Estimate the current or recent life-history parameters for NBL

The life-history parameters used for NBL in the population model were derived from literature and are mainly general parameters for lamprey species, as there is limited data available specifically for this species and population. Table 1 provides a summary of the values applied in the model; further description is provided in the Methods section regarding data sources. Many life-history characteristics of NBL still require further research and are associated with uncertainties that were represented using probability distributions to encompass the range of potential values for the species (Table 1). The Methods section elaborates on the selection process of these parameters.

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

Candidate abundance targets were determined using population viability analysis with estimates of minimum viable population (MVP). The simulations took into account density-dependence, environmental stochasticity, and parameter uncertainty. The probability of persistence was influenced by initial population size, with a population size of approximately 9,196 adults needed to achieve a 1% probability of extinction over 60 years given an assumed ratio of 3:1 male-female.

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 current wetted areas within the NBL distribution is ~ 0.7 km^2 in the Birch River and ~ 3.4 km^2 in the Whitemouth River, how much of this habitat is suitable for NBL is poorly understood. The density of NBL within suitable habitat is unknown. Figure 7 can be used to determine the area required to support the MVP (i.e., the MAPV) for a wide range of NBL densities. It is important to note that the MAPV estimate only takes into account the amount of habitat needed to sustain an MVP-sized population and does not consider other factors that may affect the population's persistence.

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

At present, there are no available estimates for the population size or growth rate of these NBL populations. Nonetheless, simulations were conducted to determine the mean recovery time to reach the minimum viable population (MVP) using various starting population sizes and positive growth rates. The results suggest that it would take on average four years to reach the MVP. However, actual recovery times based on the simulation results depend on the initial population size and growth rate, ranging up to an average of 51 years for the lowest population growth rates and initial sizes.

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 the mitigation measures and NBL 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

Population growth rates and sizes of NBL are unknown; therefore, I was unable to provide expected trajectories for this population.

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 incorporated in the population models are based on the best available data for NBL and should be used for any future population modelling. Details regarding how the parameters were estimated are outlined in the Methods section of this report.

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

The impact of anthropogenic harm for NBL was assessed with deterministic elasticity analysis and model simulations. The larval stage was found to be highly sensitive to perturbations, with even a ~ 6% increase to larval annual mortality rate resulting in a 25% reduction in population size. The required increase in larval mortality rates went up to ~ 10% with harm occurring biennially, ~ 30% with harm occurring every five years, and ~ 45% with harm occurring every 10 years, for the same decrease of 25% in population size. When harm occurred every one to two years, the NBL population trended towards zero at increases in larval mortality rates of approximately 35–50%. However, when harm occurred every five or 10 years, which is just less than equal to or double the NBL generation time, the populations were unlikely to crash.

In contrast, harm to recruitment had less of an impact on population size, if it occurred infrequently, and only resulted in a population trend towards zero if harm was applied annually. A 25% reduction in population size was observed with increases to mortality rates of ~ 20% and ~ 35% applied to recruitment every one or two years, respectively.

If the populations have a growth rate less than one, there is no level of human-induced mortality and habitat destruction that the species could sustain without jeopardizing its survival or recovery.

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