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Recovery Potential Modelling of Wavy-rayed Lampmussel (*Lampsilis fasciola*) in Canada

Modélisation du potentiel de rétablissement de la lampsile fasciolée (*Lampsilis fasciola*) au Canada

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ABSTRACT

The Committee on the Status of Endangered Wildlife in Canada (COSEWIC) had assessed the Wavy-rayed Lampmussel (*Lampsilis fasciola*) as Endangered in Canada; in 2010 the Wavy-rayed Lampmussel was re-assessed as Special Concern. Here we present population modelling of two populations to assess allowable harm, determine population-based recovery targets, and conduct long-term projections of population recovery in support of a recovery potential assessment (RPA). Our analyses demonstrated that the dynamics of Wavy-rayed Lampmussel populations are particularly sensitive to perturbations that affect survival of adult mussels, and potentially sensitive to survival at the larval (glochidia) and early juvenile stage. Harm to these portions of the Wavy-rayed Lampmussel life cycle should be minimized to avoid jeopardizing the survival and future recovery of Canadian populations. Based on an objective of demographic sustainability (i.e., a self-sustaining population over the long term), we propose abundance recovery targets of at least 1500 adult female mussels. In the absence of mitigating efforts or additional harm, we estimate that it will take a growing Wavy-rayed Lampmussel population up to 60 years to reach this recovery target. However, by affecting at least a 10% increase in survival rates, recovery strategies such as habitat rehabilitation or enhancement can reduce the recovery time of a heavily impacted population by more than half.

RÉSUMÉ

Le Comité sur la situation des espèces en péril au Canada (COSEPAC) a évalué que la lampsile fasciolée (*Lampsilis fasciola*) avait le statut en danger au Canada; celle-ci a été réévaluée en 2010 en tant qu’espèce préoccupante. Ce document présente la modélisation de deux populations afin d’évaluer les dommages tolérables, d’établir les objectifs de rétablissement en fonction de la population et d’effectuer des projections à long terme du rétablissement de la population en vue d’appuyer l’évaluation du potentiel de rétablissement (EPR). Nos analyses ont mis en évidence que la dynamique des populations de la lampsile fasciolée est particulièrement sensible aux perturbations qui ont des répercussions sur la survie des moules adultes et potentiellement sensible à la survie du stade larvaire (glochidie) et du stade juvénile précoce. Les dommages à ces parties du cycle de vie de la lampsile fasciolée doivent être réduits le plus possible afin d’éviter de mettre en péril la survie et le rétablissement futur des populations du Canada. En nous basant sur un objectif de durabilité démographique (c.-à-d., une population autonome à long terme), nous proposons des cibles de rétablissement de l’abondance d’au moins 1 500 moules femelles adultes. Faute de mesures d’atténuation ou de dommages supplémentaires, nous estimons qu’une population de lampsile fasciolée pourra atteindre cette cible de rétablissement dans une période de 60 ans. Cependant, en présumant une augmentation des taux de survie d’au moins 10 %, les stratégies de rétablissement telles que l’amélioration ou la remise en état de l’habitat peuvent diminuer de plus de la moitié la période requise pour le rétablissement d’une population lourdement touchée.

INTRODUCTION

The Wavy-rayed Lampmussel (*Lampsilis fasciola*, Rafinesque 1820) is a small sexually dimorphic mussel recognized by its yellow or yellowish-green rounded shell. The edge of the mantle of the female has evolved into a minnow-shaped "lure", which is waved to attract potential fish hosts before the glochidia are released. The glochidia is a parasitic phase of the Way-rayed Lampmussel life cycle and once expelled into the water must attach to an appropriate fish host to complete metamorphosis. The two known fish hosts for this species are the Smallmouth Bass (*Micropterus dolomieu*) and Largemouth Bass (*Micropterus salmoides*). The Wavy-rayed Lampmussel is typically found in small to medium, clear, hydrologically stable rivers where it inhabits clean sand/gravel substrates in and around shallow riffle areas. The Canadian distribution is restricted to Ontario where it was likely always a rare species. Current distributions are limited to a small portion of the Lake St. Clair delta and the Ausable, Grand, Thames and Maitland rivers with only the Grand, Thames, and Maitland populations believed to be healthy. This species is considered imperiled (N1) in Canada where it was listed as Endangered by COSEWIC, but has now been downlisted to Special Concern.

In accordance with the *Species at Risk Act* (SARA), which mandates the development of strategies for the protection and recovery of species that are at risk of extinction or extirpation in Canada, Fisheries and Oceans Canada has developed the recovery potential assessment (RPA; DFO 2007) 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 (DFO 2007). This last component requires the identification of recovery targets and timeframes for recovery, and measures of uncertainty associated with the outcomes of recovery efforts. Here, we contribute to components two and three by assessing allowable harm, identifying recovery targets, projecting recovery timeframes and identifying mitigation strategies for Canadian populations of the Wavy-rayed Lampmussel. This work is based on a demographic approach developed by Vélez-Espino and Koops (2007, 2009a, 2009b), which uses a population-based recovery target, and provides long-term projections of population recovery under a variety of feasible recovery strategies.

METHODS

Our analysis consisted of four parts: (i) information on vital rates was compiled and used to build stage-structured projection matrices, using uncertainty in life history to represent variation in the life cycle for stochastic simulations; (ii) we used these matrices in a stochastic perturbation to determine the sensitivity of the population growth rate to changes in each vital rate, as well as to determine allowable harm. This analysis was conducted following Vélez-Espino and Koops (2007; 2009a; 2009b); (iii) the projection matrices were used to simulate risk of extinction, and to estimate the minimum viable population (MVP); and (iv) using the MVP as a recovery target, we simulated the effects of potential recovery efforts on time to recovery of a typical population.

SOURCES

Life history estimates for the Wavy-rayed Lampmussel were based on sampling data from populations in the Grand and Thames rivers in Ontario (T.J. Morris, Unpubl. data). These data were supplemented by experimental data which used mussels from the Grand River (K. McNichols, Unpubl. data) and from Virginia (Hanlon and Neves 2000). Where data for *L. fasciola* were not available, estimates based on other *Lampsilis* species were borrowed from the literature.

MATRICES

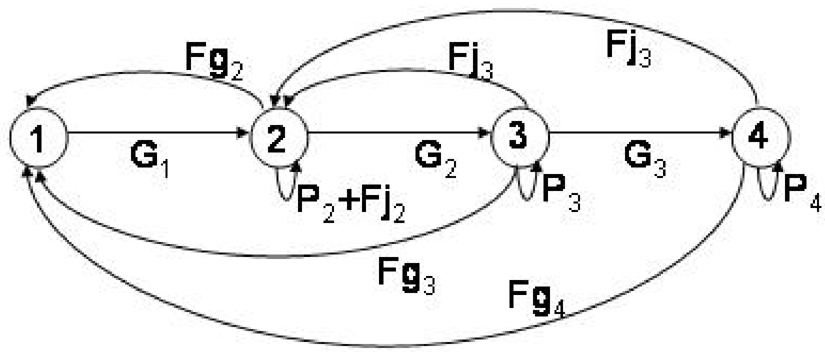
Using a matrix approach, the life cycle of Wavy-rayed Lampmussel was represented with annual projection intervals and by a pre-breeding stage-structured projection matrix (Caswell 2001) with four life stages: glochidia, juveniles, early adult, and late adult (Figure 1). Note that there are two paths from adult to juvenile mussel: i) glochidia are released, metamorphose, and drop from the host as juveniles before winter, or ii) glochidia remain on the host through the winter and drop off early in the spring. The former will be counted as 1 year old juveniles in the next census, while the latter will be counted as glochidia which will not be counted as 1 year old juveniles for another year (effectively introducing a one year time delay). Individuals were classed as juveniles until age 3, the age of first maturity (COSEWIC 2010). Mussels from ages 3 to 32, the maximum age reported in Canada (COSEWIC 2010), were divided evenly between early and late adult stages.

Elements of the stage-structured matrix included the fecundity coefficient of stage class *i* (F_i), the probability of surviving stage *i* and remaining in stage *i* (P_i), and the transition probability of surviving one stage and moving to the next (G_i, Figure 1). P_i and G_i are subdivided into the probability of an individual remaining in stage *i*, or moving from stage *i* to *i*+1, and the annual survival probability of that individual; $P_i=\sigma_i\,(1-\gamma_i)$ and $G_i = \sigma_{i+1}\,\gamma_i$ (except for $G_1=\sigma_0$, the survival of overwintered glochidia through their first winter as juveniles). The term γ_i is calculated from a geometric distribution of $1/T_i$ in which T_i is the duration of stage *i* in years. Fecundity coefficients (F_i) depend on stage specific fertility, f_i, as well as the survival of offspring to the next census. In addition, a proportion of glochidia are assumed to overwinter on the host fish, while the remainder develop into juveniles before winter (and thus before a year has passed). Contributions of adult mussels to the overwintering glochidia and juvenile stages are defined respectively as:

$$(1) \qquad Fg_i = \left[(1-\gamma_i)\,f_i + \gamma_i\,f_{i+1}\right]\omega\sigma_g\sigma_h$$

$$(2) \qquad Fj_i = \left[(1-\gamma_i)\,f_i + \gamma_i\,f_{i+1}\right](1-\omega)\sigma_g\sigma_1$$

where f_j is the product of a stage's average number of glochidia, and the proportion of females in the populaiton. ω is the proportion of glochidia that overwinter on the host, σ_h is the survival of those glochidia through the winter, and σ_1 is the survival of non-overwintered juvenile mussels through their first winter. Finally, σ_g is the probability that a glochidium attaches to a host, metamorphoses into a juvenile, and drops off into a suitable habitat. Note that within a census interval, individuals in stage *i* can either stay in stage *i* and reproduce with fecundity f_i, or graduate to stage *i*+1 and reproduce with fecundity f_{i+1}.



$$M = \begin{pmatrix} 0 & Fg_2 & Fg_3 & Fg_4 \\ G_1 & P_2 + Fj_2 & Fj_3 & Fj_4 \\ 0 & G_2 & P_3 & 0 \\ 0 & 0 & G_3 & P_4 \end{pmatrix}$$

$$M_{(Grand)} = \begin{pmatrix} 0 & 0.10 & 0.34 & 0.65 \\ 0.17 & 0.42 & 0.57 & 1.08 \\ 0 & 0.26 & 0.74 & 0 \\ 0 & 0 & 0.05 & 0.74 \end{pmatrix} \qquad M_{(Thames)} = \begin{pmatrix} 0 & 0.10 & 0.34 & 0.87 \\ 0.17 & 0.42 & 0.58 & 1.49 \\ 0 & 0.30 & 0.83 & 0 \\ 0 & 0 & 0.06 & 0.83 \end{pmatrix}$$

Figure 1. *Generalized life cycle (a), corresponding stage-structured projection matrices (b), and mean values of matrix elements (c) used to model the population dynamics of the Wavy-rayed Lampmussel. Fg_i and Fj_i represent fecundities, P_i is survival in stage i, and G_i is transition from stage i to stage i+1. Note that fertility is positive for the juvenile stage since some juveniles may mature during the interval from t to t+1 and produce offspring at t+1 (Caswell 2001).*

VITAL RATE ESTIMATES

Parameter estimates for vital rates in the Grand and Thames rivers were estimated as follows (Table 1). Where data were lacking, the same rate was used for both populations. Age at maturity was assumed to be 3 years, and was varied uniformly between 2 and 4 years for stochastic simulations. Length-at-age curves, developed in COSEWIC (2010), were used to estimate mean sizes for the two adult stages in each river. Mean numbers of glochidia per adult female (f_i) were calculated using a glochidia-at-length relationship derived by combining fecundity data for *L. fasciola* (K. McNichols, unpubl. data) with data for *L. ornata* (Haag and Staton 2003):

(3) $$f_i = R \cdot 0.00145 L^{4.405}$$

where *R* is the proportion of females in the population, and *L* is mean adult length in mm. Mean and variance of the logged fecundities for each age in the stage class were used to generate a lognormal distribution of fecundities for stochastic simulations.

We performed a catch curve analysis (Hilborn and Walters 1992) on age frequency data from COSEWIC (2010) to estimate adult female survival. This yielded annual survival rates (σ_i) of 79.36% and 88.77% for Grand and Thames mussels respectively. Stochastic survival rates were generated by drawing mortality rates from a normal distribution around the instantaneous mortality rates (0.231 and 0.119), using the standard error of the catch curve regression as an estimate of variance. Random mortality rates were converted back to annual survival rates. Survival of juveniles through the first winter was assumed to be 16.8% (Hanlon and Neves 2000). Stochastic estimates were drawn from a beta distribution with mean 0.168 and variance 0.0279 (based on 5 replicates). It has been suggested that first winter juvenile survival may be higher for juveniles that spend a winter on the host fish, since they drop off earlier in the season and have a longer growth period than juveniles that drop off later in the summer (Watters and O'Dee 1999). For this model we considered the two survival rates as separate terms (σ_0, and σ_1 for overwintered and non-overwintered juveniles respectively) to assess differences in elasticity, but assigned the same values to both as we had no data to suggest separate values. Mean survival for the remainder of the juvenile stage (σ_2) was taken to be the geometric mean of 0.168 and adult survival. Stochastic values were also drawn from a beta distribution using as variance the standard error of survival estimated for ages 1 to first maturity, where juvenile survival was assumed to increase linearly from 0.168 to adult survival. Survival of overwintering glochidia while on the host fish (σ_b) was estimated as 10%, with a maximum of 30%, based on Watters and O'Dee (1999), which tested glochidial survival as a function of months spent on the host in cold temperatures.

To estimate the proportion of glochidia that overwinter on the host (ω) we examined display patterns of female mussels in both rivers. Display frequency distributions showed two distinct peak display times during the season (one in May/June, and the other in July/August). We assumed that glochidia released during the first peak had time to metamorphose, drop from the host, and grow to a sufficient size to survive the winter, while those in the second peak either overwintered on the host, or did not survive the winter. If we assume that glochidia releases are of similar size throughout the season, then we can use the frequency distributions to estimate the proportion of glochidia that overwinter. Using the date of lowest display frequency as the dividing point, we estimated a maximum proportion of ω=0.67 (Grand), or ω=0.69 (Thames). To estimate the minimum proportion we assumed that glochidia released less than approximately 60 days before October 1, when water temperature begin to drop below 15ºC, would be forced to overwinter on the host (i.e., they would not have time to metamorphose and grow to a sufficient size to survive winter conditions). This gives minimum proportions of ω=0.33 (Grand) and ω=0.30 (Thames). Deterministic values were taken as the mean of these ranges, with stochastic values drawn from a uniform distribution between them.

To estimate the probability of a glochidium encountering and attaching to a host, we assumed that hosts are infested in accordance with a Poisson process, and that the time a fish remains infested is exponentially distributed. The expected number of host encounters per mussel per season can be estimated as (Ross 2007):

$$E = \frac{iD_b\left[t_1 - \mu\left(1 - e^{-t_1/\mu}\right)\right]}{D_m \mu\left(1 - e^{-t_0/\mu}\right)} \tag{4}$$

where i is the proportion of bass infected at sampling time t_0 (in days), t_1 is the length of the season (in days), D_m and D_b are the densities of mussels and bass respectively, and μ is the mean infestation time. Mean infestation time was estimated as 67 days, with a 95% confidence interval of 58 to 77 days (K. McNichols, unpubl. data). The start date for the season was assumed to be May 15, the first recorded observation of a displaying female in 2008 (T.J. Morris, unpubl. data). Morris and Granados (2007) sampled Smallmouth Bass in the Grand River from July 1 to October 31, 2006, and found that 41/124 (i=0.33) bass were infested with at least 1 glochidium. This rate was relatively consistent for all sampling months except October. We therefore set the sampling date, t_0, to be 84.5 days, an approximate midpoint in the sampling experiment. The last infested fish was caught on October 10, which gives a season length of 184 days. We assume a mussel density of 0.28 m^{-2}, which gives a female density of 0.12 m^{-2} when multiplied by the proportion of females in the Grand river (COSEWIC 2010). Finally, bass density was calculated as the inverse of required area-per-individual (API), which was estimated using a length-to-API allometry for freshwater fishes in rivers (Randall *et al.* 1995):

$$API = e^{-13.28} \cdot TL^{2.58} \quad (5)$$

where TL is the average total length of an adult in mm. Using the mean length of Smallmouth Bass from Morris and Granados (2007), API was estimated to be 7.4 m^2. We then multiplied the expected number of host encounters per female per season (E) by the estimated number of successfully attached glochidia per encounter (n_g). The mean number of glochidia found by Morris and Granados (2007) per infected bass host was 33.22 (95% confidence interval of 16.42 - 50.02). Dividing by the mean number of glochidia per female in the Grand River (f_{grand}=65 921) gives a probability of attachment of 0.035%. Stochastic estimates were drawn from a uniform distribution in the range 0.000151 - 0.000616, based on the combined ranges for infestation time and successfully attached glochidia. Note that since the mussel density includes buried individuals, this estimate is averaged over all female individuals, including those who do not reproduce in a given season. This rate was also used for the Thames river populations since infestation rates were only available for the Grand populations.

The probability that an attached glochidium metamorphoses into a viable juvenile mussel was estimated as 0.65 (K. McNichols, unpubl. data), with a variance of 0.014. Stochastic values were drawn from a beta distribution. Finally, we estimated the probability of a transformed juvenile dropping from the host into a suitable habitat as the approximate proportion of suitable habitat within the ranges of the Wavy-rayed Lampmussel. The terms for attachment, metamorphosis, and dropping into habitat always appear together in the projection matrix, and so were considered components of a single glochidial survival term:

$$\sigma_g = p_{\text{att}} \cdot p_{\text{meta}} \cdot p_{\text{hab}} \quad (6)$$

where $p_{\text{att}}=E \cdot n_g / f_{\text{grand}}$ is the attachment rate, p_{meta} is the proportion that metamorphose, and p_{hab} is the probability of dropping into suitable habitat.

Table 1. *Mean, variance and range of parameters pertaining to the life cycle of Wavy-rayed Lampmussel populations in the Grand (G) and Thames (T) rivers. *95% confidence interval; ** Standard error of the logs*

Rate	Sym.	Pop.	mean	Var.	Min.	Max.	Distribution	source
Proportion of overwintering glochidia	ω	G	0.5014		0.3344	0.6684	uniform	T.J. Morris, unpubl. data
		T	0.4949		0.3045	0.6852		
Glochidial survival	σ_g	G	0.000143					
		T	0.000123					
Attachment	p_{att}	G/T	0.000352		0.000151	0.000616	uniform	Ross 2007
(infestation time: days)	μ	G	67		58	77*		K. McNichols, unpubl. data
(infestation rate)	i	G	0.33					Morris and Granados 2007
(mussel density: m^2)	D_m	G	0.28					COSEWIC 2010
(bass area/individual: m^2)	*API*		7.4					COSEWIC 2010
(glochidia per host)	n_g	G	33		16	50*		Morris and Granados 2007
(mean adult fecundity)	f_{grand}	G	65921					K. McNichols, unpubl. data, Haag and Staton 2003
Metamorphose	p_{meta}	G/T	0.65	0.014		0.95	beta	K. McNichols, unpubl. data
Proportion suitable habitat	P_{hab}	G	0.625		0.5	0.75	uniform	T. Morris (DFO) and Art Timmerman (MNR) pers. comm.
		T	0.55		0.5	0.6		John Schwindt (Upper Thames River Conservation Authority) pers. comm.
Overwinter survival on host	σ_b	G/T	0.1			0.3	uniform	Watters and O'Dee 1999
Juvenile first year survival	$\sigma_{0,1}$	G/T	0.168	0.0279		0.495*	beta	Hanlon and Neves 2000
Juvenile 1+ survival	σ_2	G	0.365	0.018		0.794	beta	
		T	0.386	0.024		0.888		
Adult survival	$\sigma_{3,4}$	G	0.794	0.041**		1	lognormal	COSEWIC 2010
		T	0.888	0.024**		1		COSEWIC 2010
Early adult fecundity (f3)	f_3	G	44062	0.144**		83708	lognormal	K. McNichols, unpubl. data, Haag and Staton 2003
		T	47180	0.141**		101623		
Late adult fecundity (f4)	f_4	G	97769	0.020**		107481		
		T	150184	0.057**		207968		
(proportion female)	R	G	0.42					COSEWIC 2010
		T	0.48					
Generation time		G	6.3					COSEWIC 2010
		T	10.4					
Age of maturity	T_{mat}	G/T	3		2	4		COSEWIC 2010
Maximum age	T_{max}	G/T	32					COSEWIC 2010
von Bertalanffy growth curve			L_∞	k	t_0			
		G	75.3	0.121	-4.97			COSEWIC 2010
		T	98.3	0.043	-12.47			

ALLOWABLE HARM AND REQUIRED RECOVERY EFFORTS

We assessed allowable harm and minimum recovery effort within a demographic framework following Vélez-Espino and Koops (2007; 2009a; 2009b). Briefly, we focused on estimates of annual population growth rate (λ) as determined by the largest eigenvalue of the projection matrix (Caswell 2001). Setting equilibrium (i.e., λ = 1) as the minimum acceptable population growth rate, allowable harm (τ_v) and maximum allowable harm ($\tau_{v,\ max}$) were estimated analytically as:

$$(7) \qquad \tau_v < \left(\frac{1}{\varepsilon_v}\right)\left(\frac{1-\Lambda}{\Lambda}\right) \text{ and } \tau_{v,\max} = \left(\frac{1}{\varepsilon_v}\right)\left(\frac{1-\Lambda}{\Lambda}\right).$$

where ε_v is the elasticity of vital rate *v*, and Λ is population growth rate in the absence of additional harm (see below). Elasticities are a measure of the sensitivity of population growth rate to perturbations in vital rate *v*, and are given by the partial derivatives of λ with respect to e_{kl}, the individual elements of the matrix ($\varepsilon_{kl} = \partial \log \lambda / \partial \log e_{kl}$).

In addition to calculating the elasticities of vital rates deterministically, as described above, we also incorporated variation in vital rates to determine effects on population responses from demographic perturbations. We used computer simulations (R, version 2.9.2: R Development Core Team 2009; code modified from Morris and Doak 2002) to (i) generate 5000 matrices, with vital rates drawn from distributions with means and variances as described above (see Velez-Espino and Koops 2007); (ii) calculate λ for each matrix; (iii) calculate the ε_v of σ_i and f_i for each matrix; and (iv) estimate mean stochastic elasticities and their parametric, bootstrapped 95% confidence intervals. We estimated Λ as the geometric mean of the λ values of the 5000 matrices, which gave population growth rates of approximately Λ=1.08 (Grand River) and Λ=1.18 (Thames River). We then calculated the maximum allowable harm for each vital rate at its mean, maximum (upper 95% CI), and minimum (lower 95% CI) sensitivity value.

Because human activities often impact multiple vital rates simultaneously, we also used elasticities to approximate allowable simultaneous harm to survival or fertility rates. Cumulative harm (or recovery effort) was estimated as

$$(9) \qquad \Psi \approx \left(\frac{1-\Lambda}{\Lambda}\right) \Big/ \sum_{v=1}^{n} \varepsilon_v$$

where *n* is the number of vital rates that are simultaneously harmed (or improved), ε_v is the elasticity of vital rate *v*, and Ψ is allowable harm expressed as a single multiplier of all vital rates of interest.

RECOVERY TARGETS

Consistent with the preconditions of SARA section 73(3), we used demographic sustainability as a criterion to set recovery targets for the Wavy-rayed Lampmussel. 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 (see below) over 250 years (approximately 24-40 generations). Note that our model is based on female individuals and assumes that dynamics are mirrored for male individuals. Therefore, all potential recovery targets (MVPs) are expressed in terms of a number of *female* individuals, and must be divided by the proportion of females in the population to obtain MVP total.

We estimated recovery targets as follows. (i) 50 000 projection matrices were generated using the means, variances, and distributions as in the allowable harm analysis, and based on a geometric mean growth rate of λ=1 (the range for probability of attachment was adjusted to achieve this value); (ii) projection matrices were drawn at random from these to generate 5000 realizations of population size per time step (i.e., over 250 years); (iii) These realizations were used to generate a cumulative distribution function of extinction probability, where a population was said to be extinct if it was reduced to one adult (female) individual; (iv) this process was repeated 10 times, giving an average extinction probability per time step. Catastrophic decline in population size was incorporated into these simulations, and occurred at a probability (P_k) of 0.05 or 0.15 per generation. Two catastrophic scenarios were simulated for comparison: A) a catastrophe was defined as a 50% reduction in abundance of all life stages (full catastrophe); B) 20% of catastrophes resulted in a 50% decline in abundance of all stages, while the remainder affected only glochidia and juvenile individuals (partial catastrophe). The latter case was designed to simulate catastrophic events that are more likely to affect younger individuals. We used these simulations to determine the number of adults necessary for the desired probability of persistence (see Results) over 250 years.

RECOVERY STRATEGIES AND RECOVERY TIMES

We set recovery targets as MVPs to determine recovery timeframes of individual populations under three hypothetical recovery strategies. Each strategy consisted of improving target vital rates by 10% and 20%, and focused on improving either glochidial survival (σ_g), juvenile survival (σ_0, σ_1 and σ_2), or adult survival (σ_3 and σ_4). Recovery time was defined as the number of years required to achieve a 95% probability of reaching the recovery target. The initial size of the adult female population ranged from 2 to 20% of the recovery target, and was distributed among age classes according to the stable stage distribution. The stable stage distribution is represented by the dominant right eigenvector (w) of the mean projection matrix ($\mathbf{M}\ w = \lambda \cdot w$)(De Kroon *et al.* 1986). For each initial population size and recovery strategy, probability of recovery was calculated as for the recovery targets (including variability and catastrophic events). For the status quo projection (recovery in the absence of improvement or additional harm), random projection matrices were based on a geometric mean growth rate of 1.08 (Grand) and 1.18 (Thames). For each strategy the mean (and min/max) of the associated vital rates were increased by 10% or 20% before randomly generating projection matrices. We then used 3 000 realizations of population size over 250 years to generate a cumulative distribution function for the time to reach the recovery target, and averaged the results over 5 runs. The probability of recovery at time t was equal to the proportion of realizations of population size that met or exceeded the recovery target at time t.

RESULTS

SENSITIVITY AND ALLOWABLE HARM

According to the elasticities of the mean vital rates of the Wavy-rayed Lampmussel life cycle, population growth rate for both the Grand and Thames populations is most sensitive to perturbations of annual adult survival, followed by glochidial survival, juvenile first winter survival, and fecundity (Figure 2). Notice that a negative elasticity for the term ω means that increasing the proportion of overwintering glochidia will negatively impact the population growth rate. If, however, the true survival of juveniles that overwintered on the host is larger compared to the survival of non-overwintered juveniles, then the sign of ω can be positive (see positive upper confidence limit). While the means of the stochastic elasticities do not differ largely from the deterministic elasticities, wide confidence intervals suggest that elasticities are sensitive to changes in vital rates. Comparing correlations shows that the results of the sensitivity analysis are most influenced by uncertainty in juvenile first year survival, and somewhat by uncertainty in glochidial survival (specifically, the attachment rate). While the population growth rate is most sensitive to proportional changes in adult survival, juvenile first year survival explains roughly 60% of the variation in the growth rate. More accurate estimation of these parameters would refine the sensitivity analysis for both the Grand and Thames populations.

Estimates of the maximum allowable harm to individual vital rates depended on the stochastic element (e.g., mean or upper or lower 95% CL; Table 2 and 3). From a precautionary perspective (i.e., assuming an upper 95% CL), our results suggest for Grand River populations a maximum allowable reduction of 14% in glochidial survival, juvenile first year survival, or fecundity, 9% in combined juvenile survivals, and only 6% in adult survival (Table 2). If human activities are such that harm exceeds just one of these thresholds, the future survival of individual populations is likely to be compromised. Furthermore, recovery time can be severely delayed by any level of harm, particularly to the more sensitive vital rates. Allowable harm for Thames River populations is approximately twice that of the Grand (Table 3).

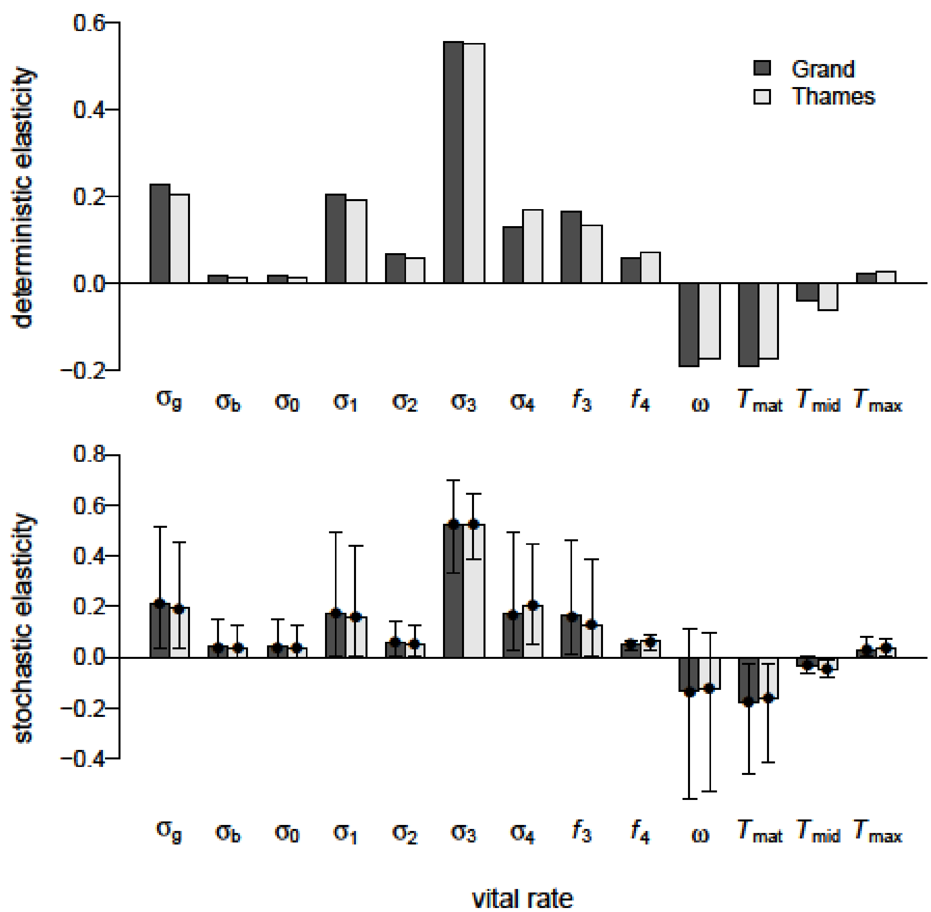


Figure 2. *Results of the deterministic and stochastic perturbation analyses showing elasticities (ε_v) of the vital rates: annual survival of stage i (σ_i, see text and Table 1), fertility of stage i (f_i), probability of overwintering on the host (ω), age at maturity (T_{max}), dividing age between early and late adult stages (T_{mid}), and maximum age (T_{max}). Stochastic results include associated bootstrapped 95% confidence intervals.*

Table 2. *Summary of maximum allowable harm ($\tau_{v,max}$) estimates for individual and combined vital rates of Wavy-rayed Lampmussel in the Grand River, based on a stochastic perturbation analysis and a population growth rate (Λ) of 1.08. σ_g = survival of glochidia; $\sigma_{0,1,2}$ = first winter survival of overwintered and non-overwintered glochidia, and annual survival of juveniles respectively; $\sigma_{3,4}$ = annual survival of two adult stages; $f_{3,4}$ = adult fertility. Consistent with the precautionary approach, bold values indicate the maximum allowable harm recommended for management decisions.*

Level of Allowable Harm	Vital rate			
	σ_g	$\sigma_{0,1,2}$	$\sigma_{3,4}$	$f_{3,4}$
mean (deterministic)	-0.310	-0.240	-0.102	-0.310
mean (stochastic)	-0.343	-0.271	-0.106	-0.343
+95% CL	**-0.144**	**-0.095**	**-0.061**	**-0.138**
-95% CL	-2.212	-6.720	-0.210	-2.370

Table 3. *maximum allowable harm ($\tau_{v,max}$) estimates for individual and combined vital rates of Wavy-rayed Lampmussel in the Thames River, based on a stochastic perturbation analysis and a population growth rate (Λ) of 1.18.*

Level of Allowable Harm	Vital rate			
	σ_g	$\sigma_{0,1,2}$	$\sigma_{3,4}$	$f_{3,4}$
mean (deterministic)	-0.751	-0.587	-0.216	-0.751
mean (stochastic)	-0.790	-0.629	-0.219	-0.790
+95% CL	**-0.330**	**-0.218**	**-0.145**	**-0.315**
-95% CL	-4.379	-15.08	-0.373	-4.499

RECOVERY TARGETS

Probability of extinction decreases as a power function of population size (Figure 3). Functions of the form $y = a \cdot x^{-b}$ were fitted, using least squares and the logged values of *x* (population size) and *y* (extinction probability), to the simulated extinction probabilities for each catastrophe scenario; estimated values of *a* and *b* are summarized in Table 4.

While choosing a larger recovery target will result in a lower risk of extinction, there are also costs associated with an increased target (increased legislation, time, etc.). When determining MVP from the fitted power curves, we attempted to balance extinction risk and recovery effort with the following algorithm. (i) We assumed that the maximum allowable risk of extinction is 10% based on COSEWIC's quantitative criteria (E) that a risk of extinction greater than or equal to 10% within 100 years constitutes Threatened status. We define a maximum MVP (i.e., maximum feasible effort) to be the population that would result in a 0.1% probability of extinction; (ii) using these as boundaries, we calculate the average decrease in probability of extinction per individual increase in population size; (iii) finally, we choose as MVP the population size that would result in this average (i.e., the point on the power curve at which the slope equals the average % decrease in extinction risk per increase in target). We compare MVPs for the following catastrophic scenarios: 5% probability per generation, full catastrophe; 15% probability per generation, full catastrophe; 15% probability per generation, partial catastrophe. Calculated in this way, MVPs for the Grand River were, respectively, 2204, 83050, and 1504 adult females. These targets all result in probabilities of extinction of approximately 0.01 (Figure 3, left). The Thames River has significantly smaller MVPs: 35, 421 and 31 adult females respectively (Figure 3, right). Notice that a 5% probability of full catastrophe gives a similar result to a 15% partial catastrophe scenario; consistent with the results of the elasticity analyses (Figure 2).

These simulations assume an extinction threshold of 1 adult female. We observed that increasing the extinction threshold (i.e., if the population is considered effectively extinct before it declines to 1 female) results in an approximately linear increase in MVP. If the extinction threshold is defined as 10 female individuals, assuming 15% partial catastrophe, the Grand River MVP increases from 1504 to over 17000 adult females, and the Thames River MVP increases from 31 to 200 adult females. Given that mussels are sessile, these higher MVP values may be more appropriate.

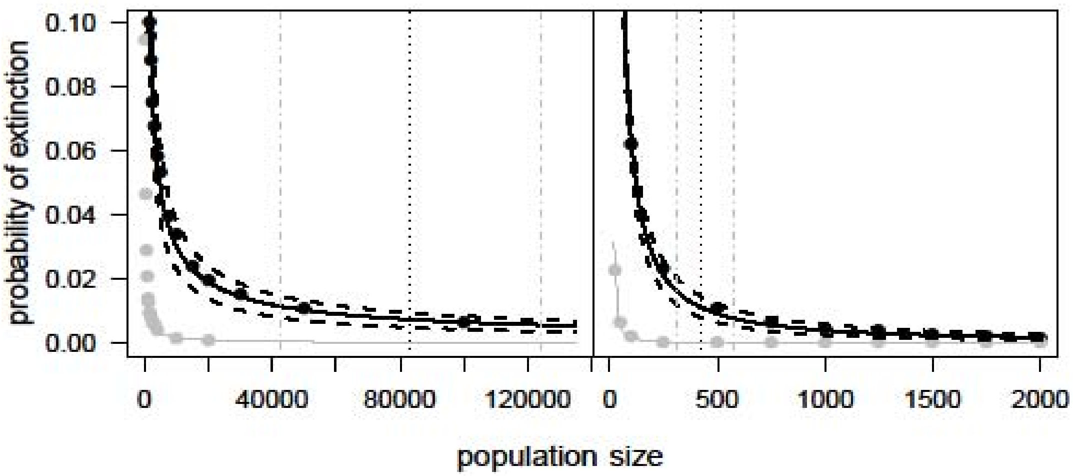


Figure 3. *Probability of extinction of 10 simulated Wavy-rayed Lampmussel populations from the Grand (left panel) and Thames rivers (right panel) as a function of population size. Assumes the population is at equilibrium (λ=1) and is without additional harm or recovery efforts. Bolded black curves assume a 15% probability of a full catastrophe (solid = mean, dashed = max and min of 10 runs). Solid grey curve represent 15% probability of a partial catastrophe. Vertical dashed lines show mean MVP (dotted black) and MPVs associated with max and min curves (dashed grey). Note the difference in scale of population size.*

Table 4. *Coefficients of fitted power curves for probability of extinction as a function of population size (Figure 3). Also shown are associated minimum viable population sizes (MVP) and the probability of extinction for that population size.*

Catastrophe	**Grand**				**Thames**			
	a	**b**	**MVP**	**p. ext.**	**a**	**b**	**MVP**	**p. ext.**
5% full	1.21	0.78	2204	0.008	1.54	1.64	35	0.013
15% full	2.61	0.66	83050	0.007	2.78	1.20	421	0.011
15% partial	1.95	0.91	1504	0.009	1.97	1.81	31	0.014

RECOVERY TIMES

Under current conditions, and in the absence of recovery efforts, a Grand River population of Wavy-rayed Lampmussels that was at 10% of the above recovery targets was predicted to take anywhere from 57-72 years (depending on the assumed catastrophe scenario) to reach a 95% probability of recovery (Figure 4). Three recovery strategies were simulated, and each involved increasing the associated vital rates by 10% and by 20%. Strategies included 1) improving glochidial survival (either through an increase in the attachment rate, the metamorphose rate, or the proportion of suitable habitat), 2) improving survival in all juvenile stages, or 3) improving survival in both adult stages. Increasing adult survival was the most effective strategy, improving recovery time to approximately 30 years (10% increase) or 20 years (20% increase). A 10-20% increase in juvenile survival resulted in recovery times of 30-40 years (for 5% full catastrophe or 15% partial) or 34-47 years (15% full catastrophe). Proportionally similar improvements to glochidial survival were the least effective, taking 39-46 years or 43-54 years respectively.

Recovery times for Thames River populations were predicted to be considerably shorter (Figure 5). A population that is at 10% of the MVP targets and experiencing status quo conditions is expected to take between 20 and 25 years to recover (depending on catastrophe scenarios). An improvement in adult survival of 10% reduced this prediction to approximately 15 years. An increase of 20% in adult survival was not measured since this would result in a survival rate greater than 100%. A 10-20% increase in juvenile or glochidial survival resulted in recovery times of less than 20 years or 22 years, respectively.

The times to recovery reported above assume that the population is at 10% of the target. These times varied with initial population size and recovery efforts invested (Figure 6). The Thames River populations, with the current positive population growth, are expected to recover with minimal or no effort, even if starting from low initial population sizes. The Grand River populations are also expected to recovery with minimal effort, but will need active recovery efforts to reach recovery targets within the same timeframe as Thames river populations. In general, the choice of strategy and of catastrophe scenario was of lesser importance for the Thames populations (Figure 6).

If harm is allowed, time to recovery is predicted to increase exponentially (Figure 7). This is particularly important when harm affects the more sensitive vital rates. If the survival of adults in the Grand River is decreased to the allowable harm indicted in Table 2, populations are expected to take more than twice as long to recover. The pattern of increase in recovery time was similar for Thames river populations.

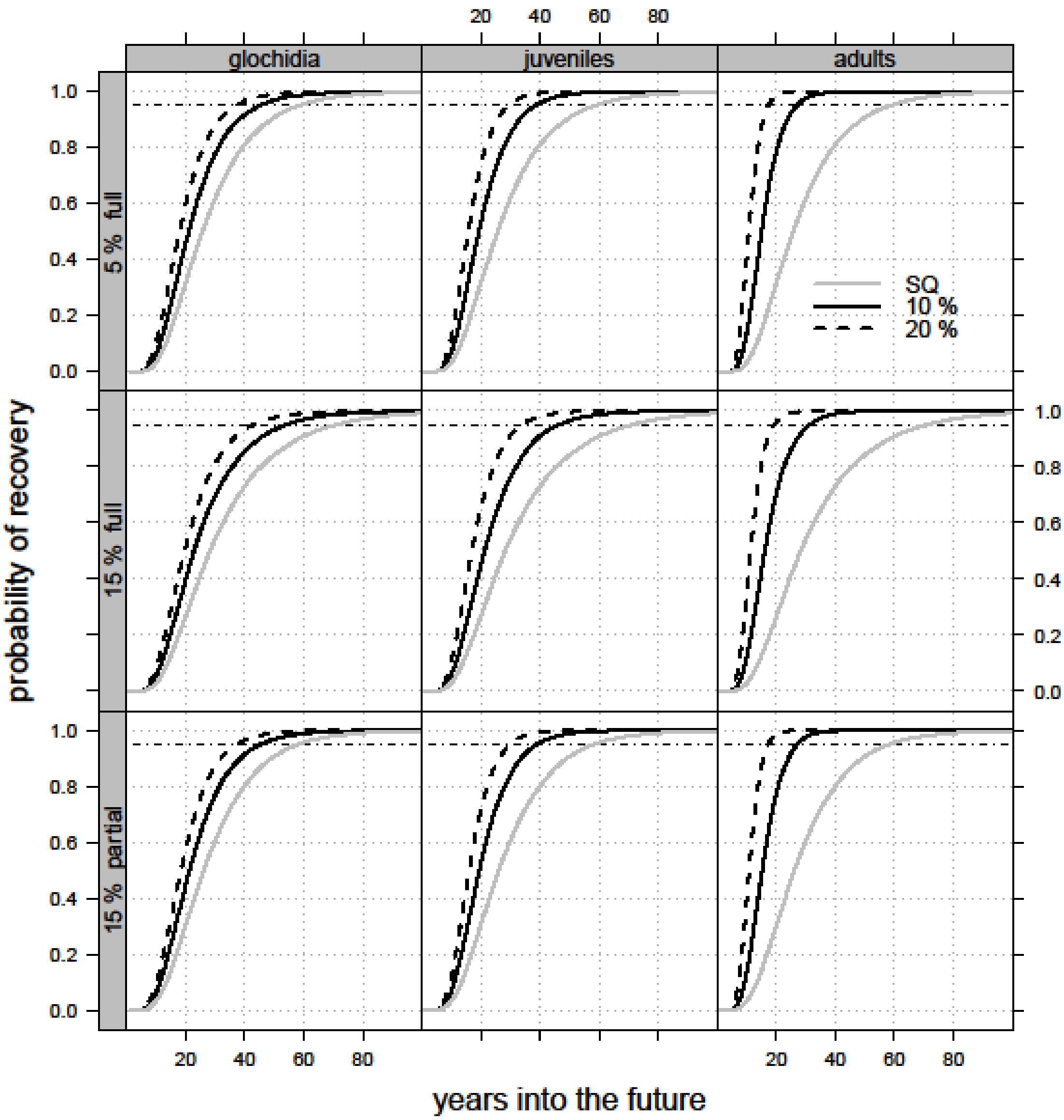


Figure 4. *The probability of recovery of 10 simulated Wavy-rayed Lampmussel populations in the* ***Grand River*** *under 3 hypothetical recovery strategies and 3 catastrophic scenarios, based on an initial adult population size that was 10% of the recovery targets (2204, 83 050, and 1504 for 5% full, 15% full, and 15% partial catastrophe scenarios respectively). Grey line shows recovery under status quo (SQ) conditions, assuming no harm and a population growth rate of 1.08. Solid and dashed lines represent improvement of 10% and 20% in glochidial, juvenile, or adult survival.*

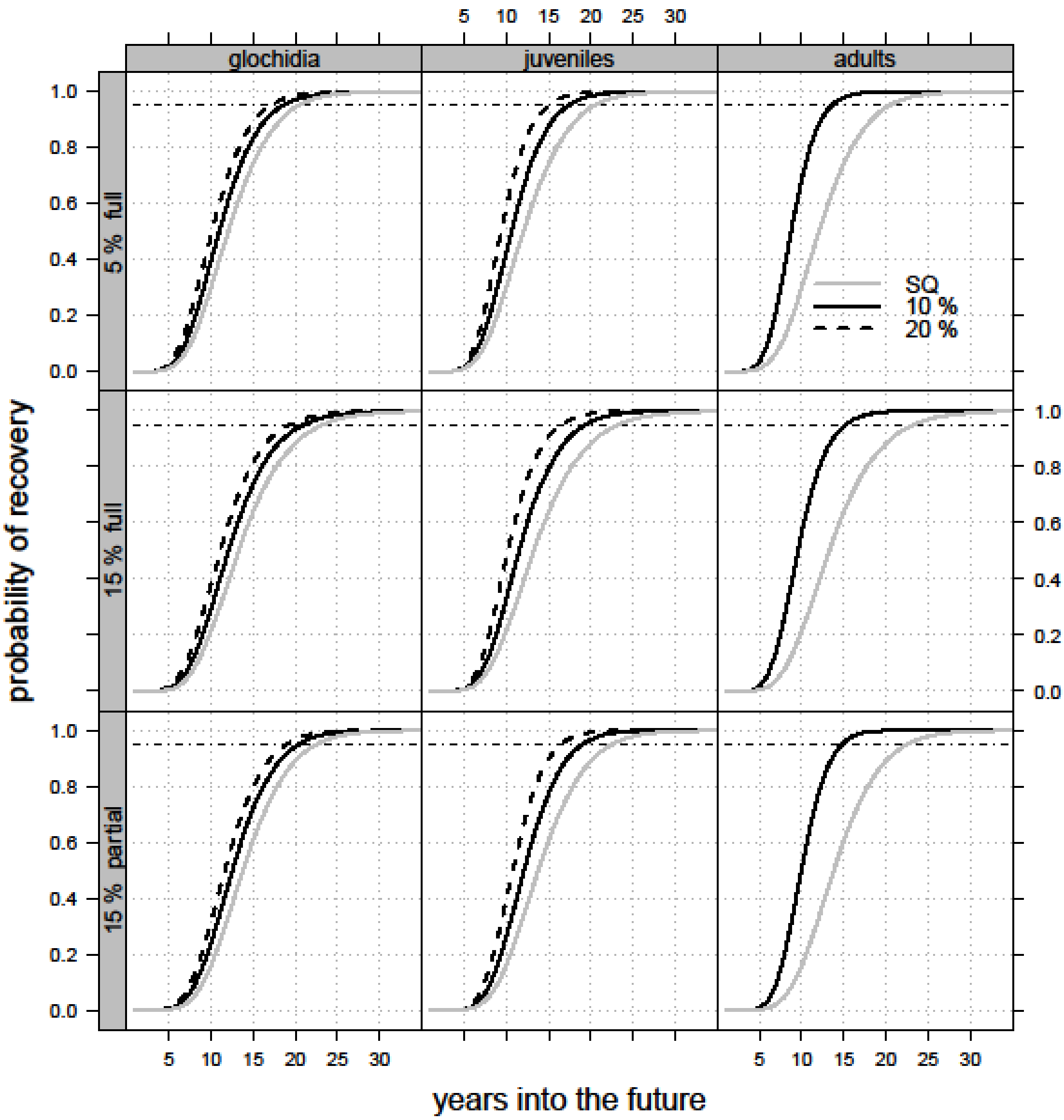


Figure 5. *The probability of recovery of 10 simulated Wavy-rayed Lampmussel populations in the* ***Thames River*** *under 3 hypothetical recovery strategies and 3 catastrophic scenarios, based on an initial adult population size that was 10% of the recovery targets (35, 421, and 31 for 5% full, 15% full, and 15% partial catastrophe scenarios respectively). Grey line shows recovery under status quo (SQ) conditions, assuming no harm and a population growth rate of 1.18. Solid and dashed lines represent improvement of 10% and 20% in glochidial, juvenile or adult survival. Note the difference in time scale from figure 4.*

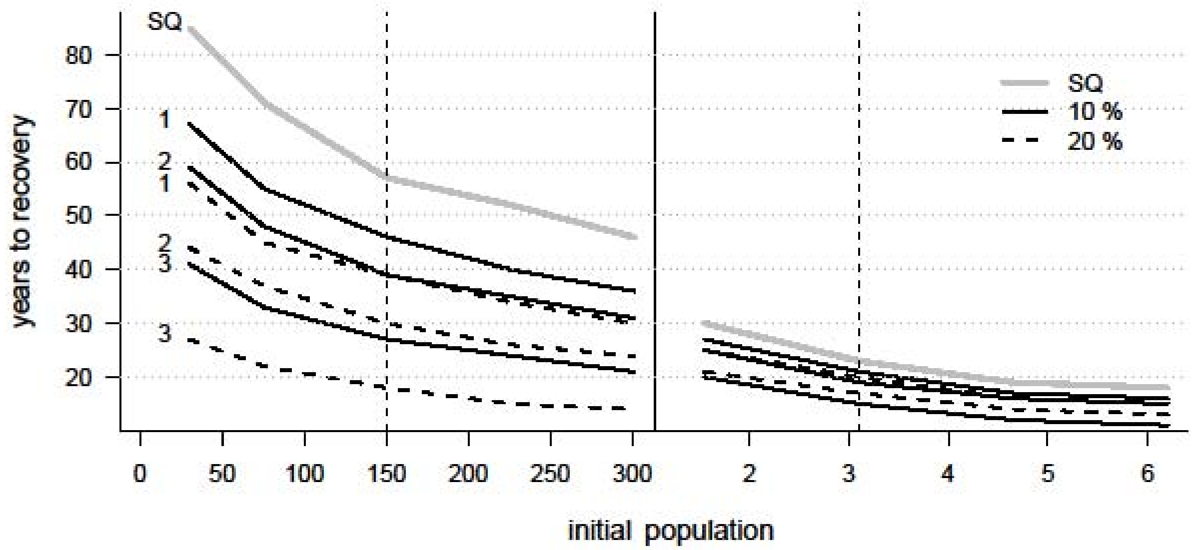


Figure 6. *Stochastic projections of mean Wavy-rayed Lampmussel recovery times for the Grand (left panel) and Thames (right panel) river populations. Figure shows predicted recovery times as a function of population size. Simulations assume 15% probability of partial catastrophe, and a recovery target of 1504 and 31 adult females for the Grand and Thames respectively. Initial populations range from 2-20% (Grand) or 5-20% (Thames) of these targets. Grey line shows recovery times in the absence of mitigation or additional harm (status quo; SQ), and numbered lines correspond to strategies influencing glochidial survival (1), juvenile survival (2), and adult survival (3). Proportions of increase for each strategy are as in Figure 4 and 5. Vertical line shows recovery times given 10% of the target (Figures 4 and 5).*

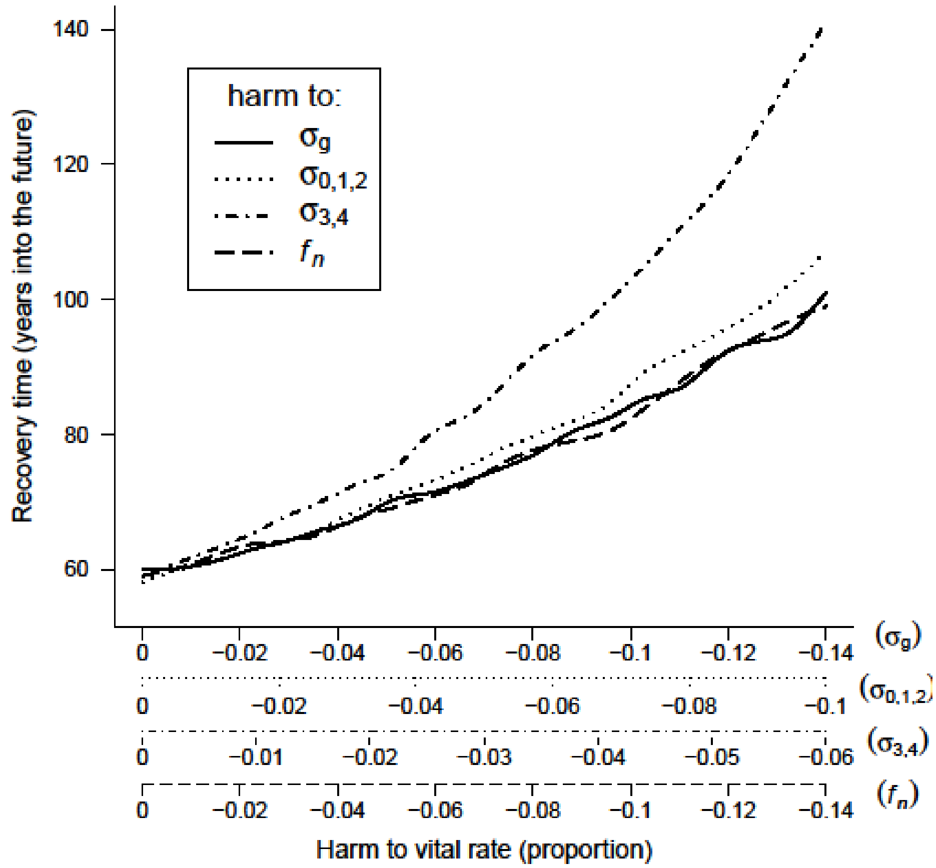


Figure 7. *Stochastic projections of mean Wavy-rayed Lampmussel recovery times for Grand River populations under additional harm. Each curve shows recovery times under harm to one vital rate or combination of rates. Levels of harm range from 0 harm (status quo conditions) to the maximum allowable harm as recommended in table 2. Simulations assume 15% probability of partial catastrophe, and a recovery target of 1504 adult females*

DISCUSSION

Our results show that human-induced harm should be minimal to avoid jeopardizing the survival and future recovery of the Wavy-rayed Lampmussel. This is true for both Grand and Thames River populations, but particularly for the Grand. Specifically, our modelling suggests that annual survival rates of Wavy-rayed Lampmussel populations in the Grand (Thames) River cannot be reduced by more than 14 (33)% for glochidia, 9 (22)% for juveniles, or 6 (14)% for adults. Any harm beyond just one of these thresholds is expected to compromise the future survival and recovery of a population.

In addition to providing estimates of allowable harm, this work also provides recovery targets based on the concept of MVP (i.e., a population with a high probability of persistence over the long-term). Methods used to determine MVP assume random mating and complete mixing of the population (i.e., all individuals interact and can reproduce with one another). Given that mussels are sessile, this assumption is unlikely to hold for the full reach of the Wavy-rayed Lampmussel in either the Grand or the Thames River. Targets will likely need to be applied to smaller subsections of the rivers in which the assumption of complete mixing can be met. Targets were estimated at 2204, 83 050, and 1504 *female* adults (Grand populations) or 35, 421, and 31 female adults (Thames populations), given catastrophic scenarios of: 5% probability per generation and 50% full decline; 15% probability and 50% full decline; or 15% probability and 50% full decline in 1/5 events, with the remainder resulting in 50% decline in juveniles and glochidia only. Larger MVP targets are recommended if mussel populations are considered effectively extinct at thresholds greater than 1 adult female. Recovery targets based on MVP can be easily misinterpreted (Beissinger and McCullough 2002) as a reference point for exploitation or allowable harm. A recovery target is neither of these things because it pertains exclusively to a minimum abundance level for which the probability of long-term persistence within a recovery framework is high. Therefore, abundance-based recovery targets are particularly applicable to populations that are below this threshold, and are useful for optimizing efforts and resources by selecting those populations that are in the greatest need of recovery.

Our analyses show that, in the absence of recovery efforts and harm and assuming a 15% probability of partial catastrophe per generation, a Thames River population that is between 2 and 20% of the recovery target in terms of abundance will take 18-30 years to reach that target with a 95% probability (Figure 6). A Grand River population will take 46-85 years to recover under the same circumstances. To reduce recovery times we recommend recovery actions that give a >10% increase in the survival of adult Wavy-rayed Lampmussels. Alternatively, increases in survival of glochidial or juvenile stages have the potential to recover the species in both populations, but need to be proportionally larger to be as effective as adult survival strategies. Efforts to increase glochidial survival could focus on the Smallmouth Bass population; increased host density could improve attachment rate, and angling restrictions could improve glochidial survival on the host (if removal from the water is traumatic for glochidia). Both glochidial survival and juvenile survival could be effectively improved by stocking of juveniles, particularly if they are released early in the season to allow maximum opportunity for growth. Increases in suitable habitat would improve the probability of dropping into suitable habitat, thus increasing glochidial survival. Finally, survival of all life stages could potentially be influenced by improvements in water quality.

An implicit assumption when comparing elasticities or recovery strategies is that proportional changes in different vital rates are equivalently feasible, when this may not be the case (Morris and Doak 2002). For instance, according to elasticity values, increasing adult survival from 70% to 84% (a 20% increase) will have a stronger influence on growth rate than increasing glochidial survival from 0.013% to 0.016%, but the latter may be more practical. It is, therefore, important to consider orders of magnitude when interpreting these sensitivity and recovery effort results for application to recovery strategies.

UNCERTAINTIES AND NEED FOR RESEARCH

Consideration of the uncertainty in vital rate estimates for the Wavy-rayed Lampmussel is especially important because of the wide range of population growth rates achieved in stochastic simulations. Annual population growth rates ranged from 0.79-1.89 (Grand River) and 0.88-2.0 (Thames River; 95% bootstrapped confidence interval). Both of these ranges include λ=1. Therefore, if the true values of some (or all) vital rates are in the lower ranges of their confidence intervals, then populations could be experiencing slower growth than suggested above, and may even be in decline. More accurate estimates of uncertain vital rates are needed to confirm the status of the Wavy-rayed Lampmussel populations. In addition, smaller levels of uncertainty could lead to a relaxation of the reported levels of allowable harm.

The most uncertain parameter in the Wavy-rayed Lampmussel life cycle is glochidial survival (σ_g). The estimate of maximum attachment rate was 75% greater than the mean, while the minimum estimate was 57% lower than the mean. If the true attachment rate is equal to the estimated maximum, the suggested recovery strategies are already achieved. Conversely, if the true rate is equal to the minimum estimate, allowable harm for the glochidial stage is already exceeded. Our estimate of attachment rate depends upon an accurate estimate of the bass to mussel density ratio, as well as an estimate of infestation rates in the host fish, which were only available for the Grand River. Different bass to mussel ratios in other locations might result in different infestation rates, affecting the applicability of our estimate to these populations. Another potentially large source of error in this estimate is the number of glochidia per host fish. Given that infected bass were collected from the Grand River, and were not in a controlled environment, it is possible that some glochidia had already matured and fallen off the host fish prior to being counted. It is therefore possible that our estimate of attachment rate is an underestimate of the true success rate. We emphasize the need for experiments that simulate natural conditions as closely as possible to estimate the true success rate of released glochidia. Considerations when designing experiments to determine attachment rate include: incorporating the partial release of glochidia in a given encounter (rather than the whole brood), and the dependence on ratios of mussel to host. Finally, the proportions of suitable habitat used in our model were rough estimates, and could be further refined.

Information is also lacking regarding the overwintering of glochidia of the Wavy-rayed Lampmussel. Our estimate of survival on the bass through the winter (~10%) was based on an experiment that measured the proportion of glochidia that stayed on the host in cold water for 6 months and then matured when waters were warmed. The later survival of these juveniles, or of the juveniles that fell off in the cold water during the 6 months, was not measured. It has also been suggested that since overwintered glochidia drop off the host earlier in the season, they may have higher survival as juveniles than those that did not overwinter. The magnitude of this advantage needs further testing. Note that for our model, the first year survival of both types was assumed to be the same, but differing rates could have significant effects on the results. Our estimate of the proportion of glochidia that overwinter on the host was based on display patterns in the Grand and Thames Rivers. It was assumed that the two distinct peaks in displaying represented glochidia that would overwinter (late peak) or not (early peak). This assumption requires verification; what is the latest date that a newly released glochidium can mature, drop off, and still survive the winter? The assumption that the size of releases is consistent between the two peaks should also be verified. These sources of error could have resulted in an overestimate of the proportion of overwintering glochidia, and/or an underestimate of their survival. In the absence of a more accurate estimate of glochidial survival, the model would benefit from an estimate of population growth rate (which could be used to back calculate, or confirm our estimate of, glochidial survival).

Differences between MVPs and recovery times for Grand and Thames populations are a result of higher adult survival and fecundity estimates in the Thames River, as well as differences in the ranges of uncertainty. Wavy-rayed Lampmussels from the Thames were larger and older, on average, than those from the Grand, which influences both survival and fecundity estimates. In addition, the slightly higher proportion of females in the Thames River contributes to higher fecundity estimates. Our model used the same fecundity-at-size relationship for both populations. True variation in the fecundity and long term survival of different populations should be investigated before applying different management actions.

Estimates regarding catastrophic events are also needed for mussel populations in general. We tested three different scenarios for catastrophic events. To improve the model, and to choose the most relevant results, we need to know i) the frequency of catastrophic events affecting mussel populations, ii) the magnitude of decline in such events, and iii) the life stages affected and the magnitude of the impacts. Estimates of catastrophic scenarios, population growth rate, and glochidial and juvenile survival rates should be a priority for this species and likely for other mussel species.

REFERENCES

Beissinger, S.R., and McCullough, D.R. 2002. Population viability analysis. Chicago: University of Chicago Press.

Caswell, H. 2001. Matrix Population Models: Construction, Analysis, and Interpretation. 2nd Edition. Sunderland, MA: Sinaur Associates, Inc.

COSEWIC (Committee on the Status of Endangered Wildlife in Canada). 2010. COSEWIC assessment and status report on the Wavyrayed Lampmussel, *Lampsilis fasciola* in Canada. Ottawa, Ontario, Canada. xiv + 67 p.

De Kroon, H., Plaiser, A., Groenendael, J.V., and Caswell, H. 1986. Elasticity: the relative contribution of demographic parameters to population growth rate. Ecology 67: 1427-1431.

DFO. 2007. Revised protocol for conducting recovery potential assessments. DFO Can. Sci. Advis. Sec. Sci. Advis. Rep. 2007/039.

Haag, W.R. and Staton, J.L. 2003. Variation in fecundity and other reproductive traits in freshwater mussels. Freshwater Biology 48(12): 2118-2130.

Hanlon, S.D. and Neves, R.J. 2000. A comparison of reintroduction techniques for recovery of freshwater mussels. Blacksburg, Virginia, Virginia Cooperative Fish and Wildlife Research Unit, Department of Fisheries and Wildlife Sciences, Virginia Polytechnic Institute and State University: 129 p.

Hilborn, R. and Walters, C.J. 1992. Quantitative Fisheries Stock Assessment: Choice, Dynamics & Uncertainty. New York: Chapman and Hall.

Morris, T.J. and Granados, M. 2007. Investigating the relationship between the federally endangered Wavy-rayed Lampmussel (*Lampsilis fasciola*) and its glochidial host, the smallmouth bass (*Micropterus dolomeieu*), in the Grand River, Ontario, Canada. Final Report to the Inter-departmental Recovery Fund Project #889. 21 p.

Morris, W.F. and Doak, D.F. 2002. Quantitative Conservation Biology: Theory and Practice of Population Viability Analysis. Sunderland, MA: Sinauer Associates.

R Core Development Team. 2009. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing: Vienna, Austria.

Randall, R.G., Kelso, J.R.M., and Minns, C.K. 1995. Fish production in freshwaters: are rivers more productive than lakes? Canadian Journal of Fisheries and Aquatic Sciences 52: 631-643.

Ross, S.M. 2007. Introduction to Probability Models. 9th Edition. New York: Academic Press.

Shaffer, M.L. 1981. Minimum population sizes for species conservation. BioScience 31: 131-134.

Vélez-Espino, L.A. and Koops, M.A. 2007. Recovery potential assessment of an extirpated population: Lake Ontario Atlantic Salmon (*Salmo salar*). DFO Can. Sci. Advis. Sec. Sci. Res. Doc. 2007/083: 27 p.

Vélez-Espino, L.A. and Koops, M.A. 2009a. Quantifying allowable harm in species at risk: Application to the Laurentina black redhorse (*Moxostoma duquensnei*). Aquatic Conservation: Marine and Freshwater Ecosystems 19: 676-688.

Vélez-Espino, L.A. and Koops, M.A. 2009b. Recovery potential assessment for lake sturgeon in Canadian designatable units. North American Journal of Fisheries Management 29: 1065-1090.

Watters, G.T. and O'Dee, S. 1999. Glochidia of the freshwater mussel Lampsilis overwintering on fish hosts. Journal of Molluscan Studies 65: 453-459.