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Recovery Potential Modelling of Hickorynut (*Obovaria olivaria*) in Canada

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Foreword

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

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ABSTRACT

The Committee on the Status of Endangered Wildlife in Canada (COSEWIC) has assessed Hickorynut (*Obovaria olivaria*) as *Endangered* in Canada (COSEWIC 2011). In support of a recovery potential assessment (RPA) we present population modelling of Hickorynut, including its dependence on a host fish (Lake Sturgeon) for its parasitic phase. Species and population specific information on the life history of Hickorynut was not sufficient to parameterize a species specific model of Hickorynut. Instead we used general knowledge of the life cycle and vital rates of unionid mussels to estimate the sensitivity of population growth to changes in the survival, growth, and fecundity of Hickorynut. We also explored how host-dependence affects mussel population abundance. Model results show that Hickorynut population growth is likely most sensitive to proportional perturbations that affect juvenile or adult survival. Modelling showed that when a mussel population is stable or growing, mussel population abundance is determined by: host abundance (if stable), host population trajectory, the life history of the mussel, and host-specific probability of glochidial attachment. When the host population was stable, a predictable, stable mussel abundance was reached. This equilibrium was sensitive to the life history of Hickorynut, and was very sensitive to the availability of juvenile Lake Sturgeon as hosts but less so to the availability of adult hosts.

RÉSUMÉ

Le Comité sur la situation des espèces en péril au Canada (COSEPAC) a évalué l’obovarie olivâtre (*Obovaria olivaria*) comme étant espèce *en voie de disparition* au Canada (COSEPAC 2011). Afin d’appuyer l’évaluation du potentiel de rétablissement (EPR), nous présentons ici une modélisation de la population d’obovarie olivâtre, y compris sa dépendance à son poisson hôte (esturgeon jaune) au stade parasitaire. L’information sur le cycle biologique de l’espèce et des populations n’a pas suffi pour paramétrer un modèle propre à l’obovarie olivâtre. C’est pourquoi nous nous sommes appuyés sur des données générales concernant les indices et le cycle vital des unionidés pour estimer la sensibilité de la croissance de la population aux changements de la survie, de la croissance et de la fécondité de l’obovarie olivâtre. Nous avons également examiné les effets de la dépendance à l’hôte sur l’abondance de la population de moules. Les résultats du modèle montrent que la croissance de la population d’obovarie olivâtre est probablement plus sensible aux perturbations proportionnelles affectant la survie des juvéniles et des adultes. La modélisation a montré que si une population de moule est stable ou croissante, son abondance est déterminée par : l’abondance de l’hôte (si elle est stable), la trajectoire de la population hôte, le cycle biologique de la moule et la probabilité de fixation des glochidies sur l’hôte en question. Quand la population hôte est stable, l’abondance de la moule est stable et prévisible. Cet équilibre est sensible au cycle biologique de l’obovarie olivâtre et très sensible à la disponibilité d’esturgeons jaunes juvéniles hôtes, alors qu’il est moins sensible à la disponibilité d’hôtes adultes.

INTRODUCTION

In 2011, Hickorynut (*Obovaria Olivaria*) was designated as *Endangered* by the Committee on the Status of Endangered Wildlife in Canada (COSEWIC 2011), due to a decline in the species' distribution, a continued threat from invasive dreissenid mussels, and potential threats to its host fish, Lake Sturgeon (*Acipenser fulvescens*). 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 from Canada, Fisheries and Oceans Canada (DFO) has developed the recovery potential assessment (RPA) (DFO 2007a; 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. This last component requires the identification of recovery targets and timeframes for recovery, and measures of uncertainty associated with the outcomes of recovery efforts. Species and population specific information on the life history of Hickorynut was not sufficient to parameterize a species specific model of Hickorynut. Instead we used general knowledge of the life cycle and vital rates of unionid mussels to estimate the sensitivity of population growth to changes in the survival, growth, and fecundity of Hickorynut. We also explored how host-dependence affects mussel population abundance. These results will help to identify the most important knowledge gaps, and contribute to recovery planning for Hickorynut.

METHODS

Our analysis consisted of three parts: (i) information on vital rates for unionid mussels was compiled and used to build 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 following Vélez-Espino and Koops (2007; 2009a; 2009b); (iii) a two species model was built to simulate the dependence of Hickorynut on its host species. Model sensitivity to host abundance, host population trajectory, mussel life history, and host attachment probability were explored.

THE MODEL

Hickorynut

Using a matrix approach, the life cycle of Hickorynut was represented with annual projection intervals and by a pre-breeding stage-structured projection matrix (Caswell 2001). The life cycle was divided into three stages: brooding glochidia, juveniles, and mature adults (Figure 1). This model assumes that fertilized adult females brood glochidia over the winter and release them the next spring. The released glochidia must then successfully metamorphose on a host fish, settle as juveniles, and survive the next winter to be counted as 1 year old juveniles in the next census. Mussels remain in the juvenile stage until the age of maturity, when they are classed as adults.

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 ($1-\gamma_i$), or moving from stage i to $i+1$ (γ_i), and the annual survival probability of that individual (σ_i); $P_i = \sigma_i (1-\gamma_i)$ and $G_i = \sigma_{i+1} \gamma_i$. The term γ_i is calculated as:

$$\gamma_i = \frac{(\sigma_i)^{T_i} - (\sigma_i)^{T_i - 1}}{(\sigma_i)^{T_i} - 1} \quad (1)$$

where T_i is the duration in years of stage i , and the age distribution within stages is assumed to be stable (Caswell 2001).

Elements of the stage-structured matrix include the fecundity coefficient of age class i (F_i), and the age-specific annual probability of surviving from age i-1 to age i (σ_i). Fecundity coefficients (F_i) are calculated as the annual number of glochidia per female (f), times the survival of offspring to the next census. Since the model is female based, fecundity values were multiplied by 0.5 to count only female offspring (1:1 sex ratio assumed). Since the first life stage consists of glochidia brooding within the female, this survival is represented by annual adult survival. The transition from the glochidial stage to the juvenile stage (σ_{gloch}) incorporates the probabilities of successful attachment, metamorphosis, settling in suitable substrate, and surviving the first winter as a juvenile.

Parameter estimates

Fecundity of Hickorynut was estimated based shell length (L) using the following fecundity-at-size relationship for the related species, *Obovaria unicolor*, presented in Haag (2013).

$$f = 572.16L^{1.31}. \quad (2)$$

The mean shell length of Hickorynut from sampling in the St. Lawrence River was used (47.7 mm ± 2.2 mm SD; A. Paquet, MNRF, unpubl. data). This yields a fecundity estimate of ~90,000 glochidia (95% CI: 85,000 – 96,000). Other estimates of Hickorynut fecundity based on observation (i.e., they were not counted directly) include 40,000 – 80,000 (N. Eckert, Genoa National Fish Hatchery, pers. comm.) and 50,000 – 500,000 (A. Martel, Canadian Museum of Nature, Pers. Comm.). We used 90,000 glochidia as the base estimate for all model exploration.

Longevity and age at maturity were based on samples from the Ottawa River. The ages of approximately 15 adult mussels were estimated to be between 7 and 14 years old based on dark external bands (COSEWIC 2011), however Hickorynut can likely live 20 or more years (A. Martel, pers. comm.). The base estimate of age at maturity was assumed to be 7 years, with a possible minimum of 4 years (B. Sietman, Minnesota Department of Natural Resources, pers. comm.). Maximum age was assumed to be between 14 and 20 years, with a mean of 17 years.

Annual survival for all stages was assumed to be consistent with generalized values for unionid mussels as reported in Young and Koops (2011). All analyses and simulations were conducted using the statistical program R (R Development Core Team 2012). All model parameters are defined in Table 1.

Lake Sturgeon

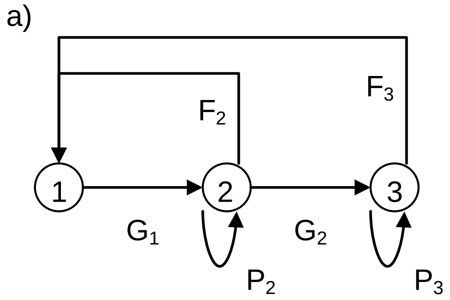
The life cycle of Lake Sturgeon was represented by the projection matrix model developed in Vélez-Espino and Koops (2009b). Parameter values corresponding to the St. Lawrence River population of Lake Sturgeon (Designatable Unit (DU) 8c) were used.

Host-Dependence

Hickorynut glochidia have been reported to transform successfully on Lake Sturgeon as young as 1 year, and as small as ~ 10 cm (N. Eckert, pers. comm.). We therefore assumed that all Lake Sturgeon > 1 year were susceptible to infestation. The probability of glochidial attachment (i.e., survival in the first year, σ_{gloch}) was assumed to be determined by the rate of host-mussel encounters. In particular, the probability of attachment was reduced as a function of the ratio between the abundance of age 1+ Lake Sturgeon (*H*) and adult mussel abundance (*M*), as follows:

$$\sigma'_{gloch} = \begin{cases} \sigma_{gloch} c \dfrac{H}{M} & if \quad cH \le M \\ 1 & if \quad cH > M \end{cases} \tag{3}$$

Here, σ_{gloch} is survival of mussels in the first year supposing that host availability is not a limiting factor, *c* is a scaling constant that represents the mean annual probability of one host encountering each mussel, and σ'_{gloch} is the effective mussel survival in the first year (after host-dependence reductions). The constant *c* can also be interpreted as a scaled carrying capacity for mussels based on host abundance. Namely, survival of mussels is affected only if $H < M/c$. In the absence of any data on infestation-induced fatality of host fish, the rate of fatality was assumed to be negligible to preserve the simplicity of the model.



b) $$A = \begin{pmatrix} 0 & F_2 & F_3 \\ G_1 & P_2 & 0 \\ 0 & G_2 & P_3 \end{pmatrix}$$

c) $$A = \begin{pmatrix} 0 & 2080 & 32764 \\ 2.55e^{-5} & 0.69 & 0 \\ 0 & 0.05 & 0.73 \end{pmatrix}$$

Figure 1. Generalized life cycle (a), corresponding stage-structured projection matrix (b), and mean values of matrix elements (c) used to model the population dynamics of Hickorynut. F_i represents annual effective fecundities, and σ_i the survival probabilities from stage i-1 to stage i. Note that fecundity is positive for juveniles since in a pre-breeding census, these individuals are about to mature and produce offspring (Caswell 2001).

Table 1. Values, symbols, descriptions, and sources for all parameters used to model Hickorynut and Lake Sturgeon.

Category	**Description**	**Symbol**	**Estimate**	**Source / Reference**
Mussel Parameters	Glochidial survival	σ_{gloch}	2.55 E-5 (1.8 E-5 – 3.3 E-5)	(Young and Koops 2011)
	Host-dependent glochidial survival	σ'_{gloch}	$\sigma'_{gloch} = \sigma_{gloch} c \frac{H}{M}$	Equation (3)
	Host encounter per mussel scaling constant	c	Unknown	
	Juvenile survival	σ_{juv}	0.74 (0.54 – 0.93)	(Young and Koops 2011)
	Adult survival	σ_{adult}	0.75 (0.51 – 0.99)	(Young and Koops 2011)
	Fecundity	f	90,000 (85,000 – 96,000)	
	Age at maturity	T_{mat}	7 (4 – 7)	(COSEWIC 2011)
	Maximum age	T_{max}	17 (14 – 20)	
	Mean shell length	L	47.7 mm (45.5 - 49.9)	A. Paquet, MNRF
Host Parameters	First year survival	σ_1	0.00082	(Vélez-Espino and Koops 2009b)
	Juvenile survival (2 stage classes)	σ_2, σ_3	0.28, 0.71	
	Adult survival (2 stage classes)	σ_4, σ_4	0.90, 0.90	
	Fecundity (2 stage classes)	f_4, f_5	24,361, 33,667	
Matrix Elements	Effective mussel fecundity (female offspring from surviving adults)	F_i	Figure 1c	(Caswell 2001)
	Rate of remaining in stage *j*	P_i		
	Transition from stage *j*-1 to stage *j*	G_i		
Analysis	Annual population growth rate	λ	NA	(Caswell 2001)
	Generic vital rate (survival, maturity, fertility)	v		
	Elasticity (proportional sensitivity of rate *v*	ε_v		
Population Abundance	(Equilibrium) adult mussel population abundance	$(M^*)\ M$	Dependant on model parameters	
	(Equilibrium) abundance of available hosts (age 1+ fish)	$(H^*)\ H$		

POPULATION SENSITIVITY

We examined the sensitivity of this model in two ways. We first considered the scenario where host abundance exceeded the requirements of the mussel population. That is, host abundance did not affect the attachment (and therefore survival) of mussel glochidia (H is sufficiently large that $\sigma'_{\text{gloch}} = \sigma_{\text{gloch}}$ in equation (3) for all H). We call this the host-independent model. We also explored the sensitivity of the host-dependent model, where host abundance affects glochidial survival ($\sigma'_{\text{gloch}} < \sigma_{\text{gloch}}$ for some or all H).

Host-independent model

We are interested in the sensitivity of the estimated annual population growth rate (λ) to perturbations in vital rate v. Annual population growth rate can be estimated as the largest eigenvalue of the projection matrix (Caswell 2001). Model sensitivity is quantified by elasticities, which are a measure of the sensitivity of population growth rate to perturbations in vital rate v, and are given by the scaled partial derivatives of λ with respect to the vital rate:

$$\varepsilon_v = \frac{v}{\lambda} \sum_{i,j} \frac{\partial \lambda}{\partial a_{ij}} \frac{\partial a_{ij}}{\partial v} . \tag{4}$$

Here, a_{ij} are the matrix elements.

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 to (i) generate 5,000 matrices, with vital rates drawn from distributions with means and ranges as described above (Table 1) (see Vélez-Espino and Koops 2007); (ii) calculate λ for each matrix; (iii) calculate the ε_v of σ_j and f_j for each matrix; and (iv) estimate mean stochastic elasticities and their parametric, bootstrapped 95% confidence intervals.

Host-dependent model

Both mussel and host populations were projected forward in time using the mean parameter values in Table 1. At each time step, glochidial survival was adjusted according to equation (3). Projection continued until population dynamics remained constant (i.e., both populations had reached extinction, stability, or a constant growth rate). Sensitivity of these trajectories and equilibria (if they existed) were compared by (i) adjusting the trajectory of host and/or mussel populations to test different combinations of growth, stability, or decline; (ii) adjusting vital rates in the case of stable trajectories to determine sensitivity of equilibria to these changes; and (iii) availability or effectiveness of hosts of different life-stages were reduced.

The latter case was included because the model assumes that each host fish is equally susceptible to glochidia regardless of size or age. However, it is possible that older fish are less susceptible because of acquired immunity, or that younger fish are able to hold fewer glochidia due to their smaller size. We considered the following four host-availability scenarios where availability of each of four stages of host (early juvenile, late juvenile, early adult, late adult) was weighted accordingly:

i. Size- or age- related differences in susceptibility to glochidia either do not exist, or counter balance one another such that all age 1+ Lake Sturgeon are equally susceptible; weights = (1, 1, 1, 1).
ii. The larger the host, the more glochidia it can hold. Weights were chosen arbitrarily to approximate fish growth patterns; weights = (0.5, 0.75, 0.95, 1).
iii. The inverse of ii; the older the host, the less susceptible it becomes to infestations; weights = (1, 0.95, 0.75, 0.5).

iv. Assumptions ii and iii are both true; the smallest and the oldest hosts can accommodate fewer glochidia than hosts of medium size and age. Weights are equal to the product of scenarios ii and iii; weights = (0.5, 0.7, 0.7, 0.5).

ALLOWABLE HARM

Allowable harm is defined as harm to the population that will not jeopardize population recovery or survival. Chronic harm refers to a negative alteration to a vital rate (survival, fecundity, etc.) that reduces the annual population growth rate permanently or over the long term. Transient harm refers to a one-time removal of individuals such that survival (and therefore population growth rate) is only affected in the year of the removal.

Estimates of allowable harm are very dependent on population trajectory and on species specific vital rates. Because there are so many unknown elements of Hickorynut life history, we do not provide specific allowable harm values here. Instead, we rely on model sensitivity to provide allowable harm advice; the more sensitive the model is to changes in a particular parameter, the more susceptible the population will be to harm affecting that life stage.

RESULTS

POPULATION SENSITIVITY

Host-independent model

Hickorynut population growth rate is expected to be most sensitive to proportional changes in juvenile or adult survival, moderately sensitive to the age at maturity, and relatively insensitive to proportional changes in glochidial survival, fecundity, or maximum age (Table 2; Figure 2).This holds true not only for the mean estimated parameter values, but also for any values within the ranges tested (Table 1). This is of particular importance given the uncertainty surrounding estimates of survival for all Hickorynut life stages. The uncertainty in elasticities (confidence intervals) can be explained by the correlation between vital rates and elasticity values for other rates. The importance (elasticity) of adult survival is negatively correlated with the value for juvenile survival (r = -0.67), while the importance of juvenile survival is negatively correlated with the value of adult survival (r = -0.66) and also age at maturity (r = 0.47). In other words, the lower the survival of either stage (juvenile or adult), the more sensitive the population will be to survival of the other stage.

Table 2. Summary of elasticities of Hickorynut vital rates (ε_v) in the host-independent model. Shown are elasticities for: annual survival probabilities for each stage, fecundity, age at maturity, and maximum age.

	σ_{gloch}	σ_{juv}	σ_{adult}	f	T_{mat}	T_{max}
Stochastic mean	0.11	0.73	0.48	0.11	-0.24	0.05
Deterministic mean	0.14	0.57	0.50	0.14	-0.20	0.03
Lower 95% confidence	0.18	0.67	0.69	0.18	-0.17	0.06
Upper 95% confidence	0.06	0.38	0.44	0.06	-0.24	0.00

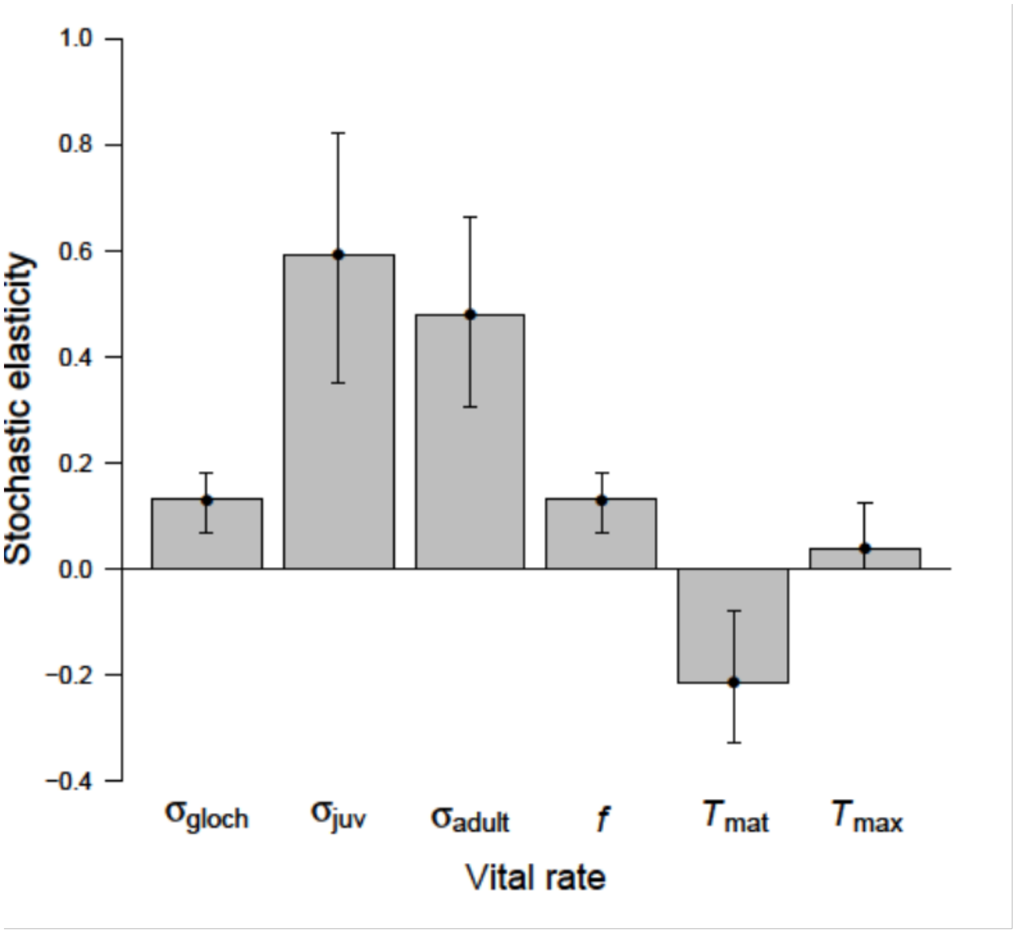


Figure 2. Results of the stochastic perturbation analysis showing elasticities (ε_v) of vital rates (annual survival probability for each stage, fecundity, age at maturity, and maximum age) for the host-independent model of Hickorynut. Results include associated bootstrapped 95% confidence interval. Exact values listed in Table 2.

Host-dependent model

All simulations, except where otherwise indicated, assumed mean parameter values for Hickorynut and Lake Sturgeon as stated in Table 1, constant *c* = 1, and host-availability scenario i (weights = (1, 1, 1, 1).)

Given a declining host population, both host and mussel populations decreased until extinct regardless of mussel population trajectory (Figure 3a). Notice, however, that the adult mussel population may increase before it declines if the initial host abundance exceeds mussel requirements, or if there are large numbers of juveniles moving into the adult stage. In the latter case, the total mussel population is in decline even though adult numbers are temporarily increasing. Reducing the constant *c* results in a faster reduction in mussel abundance, but does not change the pattern of population trajectory (Figure 3a). This was the case for all explored trajectories.

Given a stable host population, a growing mussel population (i.e., a population that would continue to grow in the absence of host limitations) will stabilize to an equilibrium abundance (*M**) that is determined by the stable host abundance (*H**), the constant *c*, and the mussel's life history parameters (equation (5)). This relationship was determined by finding the equation for the dominant eigenvalue of the generic mussel population matrix (including host density dependence), setting this equal to 1 (equilibrium), and solving for *M*.

$$M^* = \frac{f\sigma_{gloch}\sigma_{adult}\gamma_{juv}cH^*}{(\sigma_{juv}\gamma_{juv} - \sigma_{juv} + 1)(\sigma_{adult}\gamma_{adult} - \sigma_{adult} + 1)} \qquad (5)$$

It is important to note that equation (5) is valid only if $M^* > cH^*$. Otherwise, the parameter values are such that the growth rate $\lambda < 1$, and the mussel population will decline to zero ($M^* = 0$). Assuming a stable host population, the expected equilibrium for a growing mussel population increases linearly with changes in fecundity, and exponentially with changes in adult or juvenile survival (Figure 4, equation (5)). The equilibrium abundance is independent of initial mussel population (Figure 3b), but dependent on the mussel'8s life history and natural growth rate (Figure 3c).

Given a growing host population, the mussel population growth rate cannot exceed that of the host population indefinitely (Figure 3d). That is, the mussel population will grow at the faster rate until it reaches its host-dependent growth capacity, which occurs when the host-dependent reduction in first year survival reduces the mussel population growth rate to the same rate as the host.

Mussel population abundance was very sensitive to the availability of juvenile hosts, and much less sensitive to the availability of adult hosts (Figure 5). In other words, a reduction in a host's capacity to accommodate glochidia due to smaller host size is much more detrimental than a reduction due to older age and/or acquired immunity. Note that these reductions in host availability assume that the hosts are merely unavailable to the glochidia, not removed from the population. Removal of hosts will affect the host population growth rate and its equilibrium abundance; decreases in host equilibrium abundance will affect mussel abundance linearly (equation (5)).

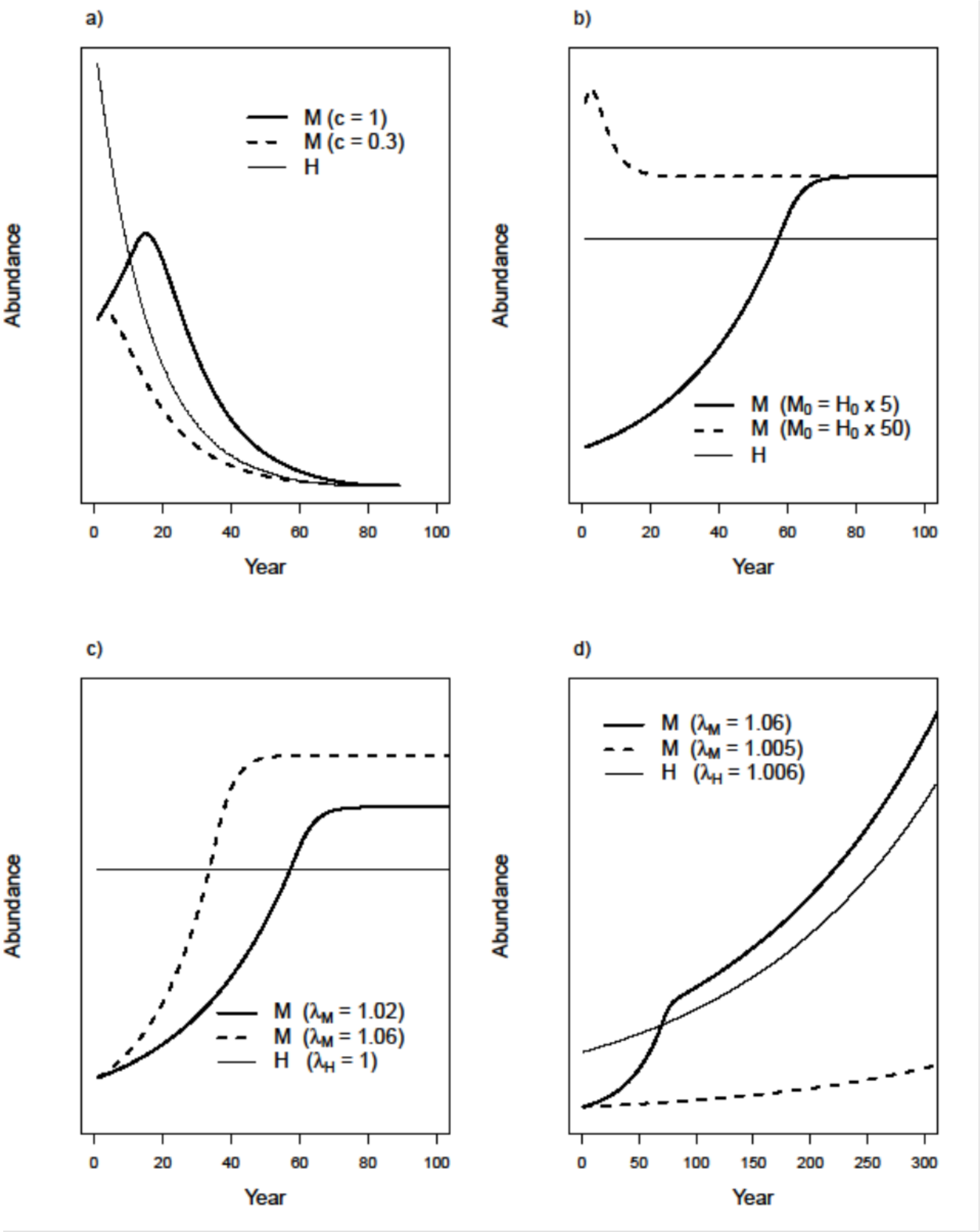


Figure 3. Abundance trajectories of Lake Sturgeon and host-dependent Hickorynut assuming a) a declining host population (λ=0.94), a growing mussel population (λ=1.02), and varying values of the constant c (equation (3)); b) a stable host population (λ=1), a growing mussel population (λ=1.02), and varying initial mussel populations; c) a stable host population, and mussel populations growing at varying rates; and d) a growing host population and mussel populations growing at varying rates.

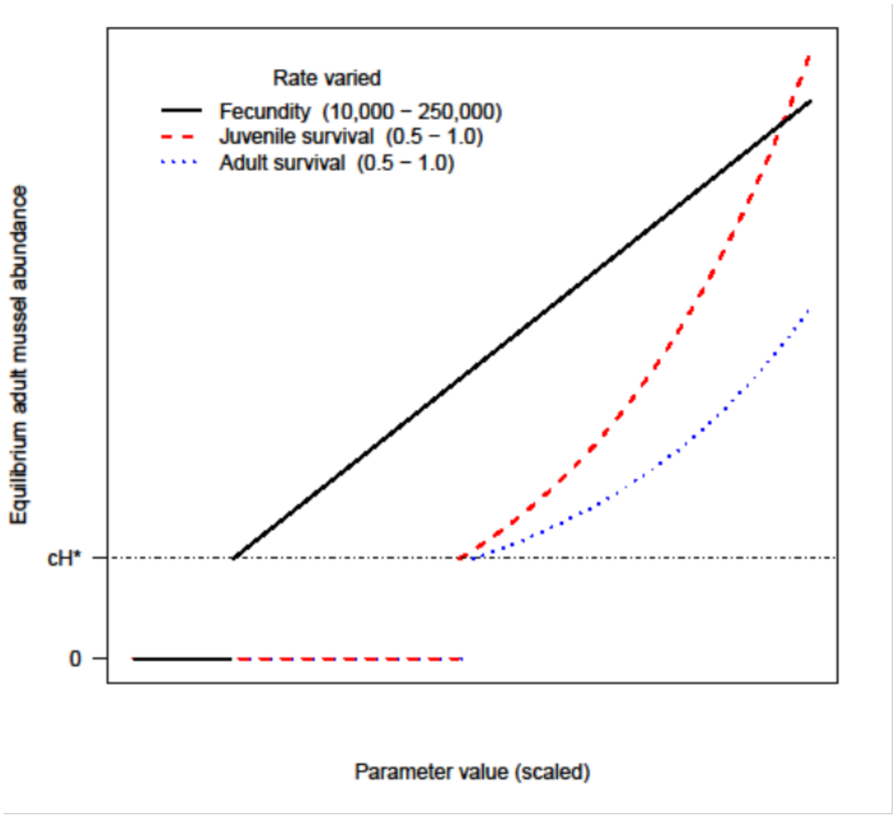


Figure 4. Equilibrium adult mussel abundance (M) as a function of life history parameters: fecundity between 10,000 and 250,000 glochidia, juvenile survival between 50 and 100%, and adult survival between 50 and 100%. All values assume the same stable host population with equilibrium abundance H*. Reference line at cH* shows the dividing line between positive, stable mussel abundance and extirpation (rates that result in a declining population with a 0 equilibrium).*

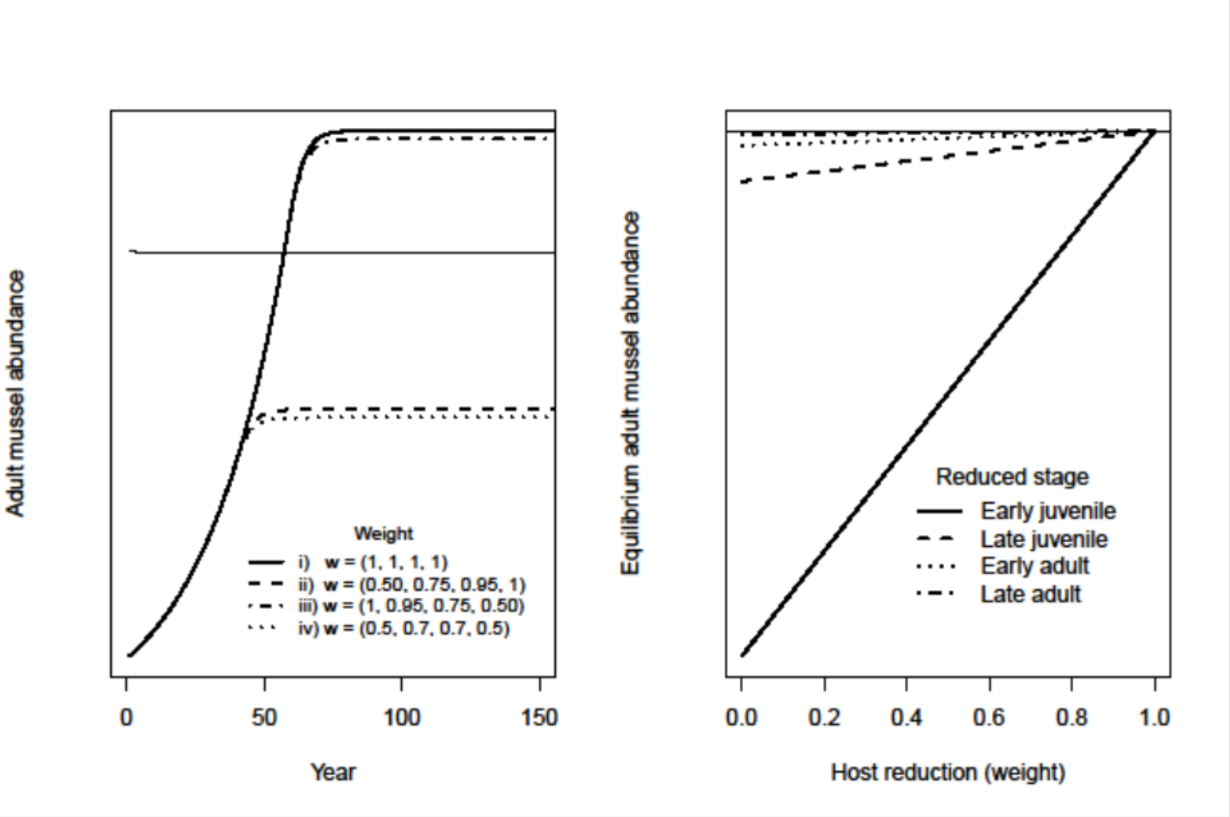


Figure 5. (a) Adult mussel population trajectories for different host availability scenarios: i) no reduction in adult availability; ii) reduction in capacity of smaller fish to host glochidia; iii) reduction in capacity of older fish to host glochidia; iv) reductions due to both smaller size and older age. (b) Equilibrium adult mussel abundance as a function of independent reductions in each host stage.

DISCUSSION

Due to the knowledge gaps in the life history of Hickorynut, the nature of its dependence on its host, Lake Sturgeon, and the abundance of either species, we were unable to construct a model of Hickorynut that would provide meaningful estimates of recovery targets, times to recovery, or allowable harm. Instead, we used all available knowledge of the species, and of mussels in general, to explore the sensitivities of a “best guess” model in hopes of providing insight for management and future research.

Our results show that the survival and future recovery of Hickorynut requires a minimization of human-induced harm to the annual survival of juvenile and adult mussels. While Hickorynut populations were much less sensitive to proportional changes in glochidial survival, we emphasize that proportionally large changes to glochidial survival may be very small in magnitude (i.e., biologically small). Proportional comparisons between stage-specific survival rates may therefore be misleading. For instance, results showed that mussel abundance was potentially very sensitive to reductions in host availability, which affects only the glochidial mussel stage. This was particularly true for younger hosts.

We determined that given a stable host population, the mussel population will either become extinct (if it is in decline) or stabilize at a predictable equilibrium (if it is growing). The equilibrium varies depending on host abundance, host population trajectory, the life history of the mussel, and host-specific probability of glochidial attachment. The equilibrium was sensitive to the life history of Hickorynut, and was very sensitive to the availability of juvenile Lake Sturgeonas hosts but less so to the availability of adult hosts. These findings do not incorporate environmental variation or uncertainty and should be interpreted as expected general patterns and not exact predictions.

UNCERTAINTIES

Annual survival of Hickorynut is unknown for all life stages, and the remainder of Hickorynut life history has been assumed based on sparse data (age at maturity and longevity) or related species (fecundity). These basic life history parameters have potentially large implications for the recovery of the species and should be investigated further.

The nature of the Hickorynut’s dependence on its host is also very uncertain. Accuracy and effectiveness of any host-mussel modeling is especially dependent on understanding this relationship, and further research is needed. The probability of glochidial attachment, and its dependence on the abundance of both hosts and mussels, is poorly understood. Given the paucity of knowledge, we chose the simplest possible relationship and assumed that successful attachment depends on the ratio between hosts and mussels. This assumption needs to be tested through experimentation.

The capacity of Lake Sturgeon to accommodate glochidia is also unknown. To our knowledge, experimental infestation has been performed exclusively on juvenile Lake Sturgeon, and it is unknown how the size of the fish may affect the numbers of glochidia that can attach. In addition, it is speculated that older Lake Sturgeon may be less susceptible to glochidia, but the extent of this is unknown. It should also be confirmed that juvenile Lake Sturgeon habitat (and not just adult habitat) overlaps that of Hickorynut.

If knowledge in the above areas is improved, a more representative model of Hickorynut and Lake Sturgeon can be built and used to determine recovery targets for Hickorynut as well as more detailed host requirements. Abundance estimates and current population trajectories for both mussel and host species will also be important parts of any such model.

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