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Recovery Potential Modelling of Eastern Pondmussel (*Ligumia nasuta*), Fawnsfoot (*Truncilla donaciformis*), Mapleleaf (*Quadrula quadrula*), and Rainbow (*Villosa iris*) in Canada

Modélisation du potential de rétablissement de la ligumie pointue (*Ligumia nasuta*), de la troncille pied-de-faon (*Truncilla donaciformis*), de la mulette feuille d'érable (*Quadrula quadrula*) et de la villeuse irisée (*Villosa iris*) au Canada

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ABSTRACT

The Mapleleaf (*Quadrula quadrula*), Eastern Pondmussel (*Ligumia nasuta*), Rainbow (*Villosa iris*) and Fawnsfoot (*Truncilla donaciformis*) are freshwater mussels that have been assessed as Threatened (Ontario population of Mapleleaf) or Endangered (Manitoba population of Mapleleaf, Eastern Pondmussel, Rainbow and Fawnsfoot) by the Committee on the Status of Endangered Wildlife in Canada (COSEWIC). In support of a recovery potential assessment (RPA), we present population modelling of freshwater mussels and assess the sensitivity of population growth to changes in the model parameter values. Our analyses demonstrated that the population growth rate of freshwater unionid mussels is most sensitive to changes either in juvenile survival, adult survival, or reproduction related vital rates. Which of these rates is most sensitive can be predicted with knowledge of population specific vital rates; predictions are most accurate when fecundity and age at maturity are known. Harm to sensitive portions of the mussel’s life cycle should be minimized to avoid jeopardizing the survival and future recovery of Canadian populations.

RÉSUMÉ

La mulette feuille-d’érable (*Quadrula quadrula*), la ligumie pointue (*Ligumia nasuta*), la villeuse irisée (*Villosa iris*) et la troncille pied-de-faon (*Truncilla donaciformis*) sont des moules d’eau douce que le Comité sur la situation des espèces en péril au Canada (COSEPAC) a désignées comme étant des espèces menacées (population de mulettes feuille-d’érable de l’Ontario) ou en voie de disparition (population de mulettes feuille-d’érable du Manitoba, de ligumies pointues, de villeuses irisées et de troncilles pied-de-faon). À l’appui d’une évaluation du potentiel de rétablissement (EPR), nous présentons la modélisation de la population de moules d’eau douce et nous évaluons quelles sont les incidences sur la croissance de la population des changements pour les valeurs des paramètres du modèle. Selon nos analyses, ce sont les changements de taux de survie des juvéniles, de taux de survie des adultes ou de taux vital de reproduction qui y sont associés le plus avec le taux de croissance de la population de moules unionidés. On peut prévoir lesquels de ces taux sont les plus susceptibles de changer lorsqu’on a des connaissances sur les taux vitaux précis de la population; les prévisions sont le plus exactes lorsqu’on connaît la fécondité et l’âge à la maturité. Il faudrait minimiser les dommages aux étapes fragiles du cycle de vie des moules afin d’éviter de mettre en péril la survie et le rétablissement futur de ces populations au Canada.

INTRODUCTION

The Mapleleaf (*Quadrula quadrula*), Eastern Pondmussel (*Ligumia nasuta*), Rainbow (*Villosa iris*) and Fawnsfoot (*Truncilla donaciformis*) are freshwater mussels belonging to the family Unionidae. Mature females of these species brood glochidia that, once expelled into the water, must attach to an appropriate fish host to complete metamorphosis. Some species in this family have evolved a "lure", which is waved to attract potential fish hosts before the glochidia are released. The Manitoba population of Mapleleaf was designated Endangered, and the Ontario population as Threatened in 2006. Eastern Pondmussel, Rainbow, and Fawnsfoot were all designated Endangered in 2007, 2006, and 2008 respectively.

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 (DFO) 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. Species and population specific information on vital rates for these four species is not sufficient to parameterize species-specific population models. Instead, we use general knowledge of the life cycle and vital rates of unionid mussels to predict which vital rates we might expect to most influence population growth. These results will help to identify the most important gaps in species specific knowledge, and contribute to the planning of more effective recovery strategies.

METHODS

Our analysis consisted of four parts: (i) information on vital rates of freshwater mussels from the family Unionidae was compiled, and representative estimates of “low” and “high” values were chosen for each vital rate. These estimates were combined in all possible permutations to build stage-structured projection matrices, each representing a different life history pattern; (ii) the sensitivity of the population growth rate to changes in each vital rate was determined for all matrices (Caswell 2001); (iii) using cluster analysis, the matrices were sorted into groups with distinct elasticity patterns; (iv) classification trees were built and used to predict the elasticity patterns of these four mussel species, given what is known of their life history and vital rates.

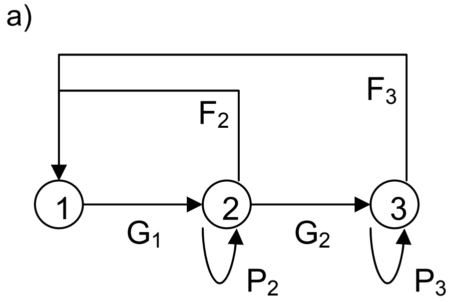
MATRICES

Using a matrix approach, the life cycle of a generic freshwater mussel was represented with annual projection intervals and by a pre-breeding stage-structured projection matrix (Caswell 2001). The life cycle of freshwater mussels 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 (s_i); $P_i = s_i\,(1\text{-}\gamma_i)$ and $G_i = s_{i+1}\,\gamma_i$. The term γ_i is calculated as:

$$\gamma_i = \frac{(s_i/\lambda)^{T_i} - (s_i/\lambda)^{T_i-1}}{(s_i/\lambda)^{T_i} - 1} \qquad (1)$$

where T_i is the duration in years of stage i , λ is the largest eigenvalue of the matrix and the age distribution within stages is assumed to be stable (Caswell 2001). 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 (s_1) incorporates the probabilities of successful attachment, metamorphosis, settling in suitable substrate, and surviving the first winter as a juvenile.



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

c)
$$M_{low} = \begin{pmatrix} 0 & 550 & 19303 \\ 1.8e^{-5} & 0.53 & 0 \\ 0 & 0.02 & 0.67 \end{pmatrix} \qquad M_{high} = \begin{pmatrix} 0 & 32934 & 212426 \\ 2.4e^{-5} & 0.79 & 0 \\ 0 & 0.15 & 0.95 \end{pmatrix}$$

Figure 1. *Generalized life cycle (a), and corresponding stage-structured projection matrix (b) used to model the population dynamics of freshwater mussels. Matrices produced using low and high vital rates (c), which give the highest and lowest population growth rate.* F_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).*

PARAMETER ESTIMATES

Parameter values are largely unknown for Canadian populations of these four mussel species, but all estimates used here are from studies on mussels also belonging to the family Unionidae. High and low values for each vital rate were estimated as follows (see Table 1 for summary). Jansen et al. (2001) reported a survival of 0.000018 from glochidia to age 2 for *Pygonodon grandis*. *Pygonodon grandis* is a non-lure species, and since the presence of a lure is likely to increase glochidial survival (Jansen et al. 2001) we use 0.000018 as a low estimate of survival from released glochidium to juveniles having survived one winter (s_1). For a high value of s_1 we combine estimates of glochidial and first winter survival of the Wavyrayed Lampmussel (*Lampsilis fasciola*; Young and Koops 2010). A large range of survival for juvenile mussels has been reported. *Pygonodon grandis* was reported to have a survival as high as 0.82-0.91 from age 2 to 5 (or 0.93-0.97 annually), and mortality of juvenile *Fusconaia ebena* was reported as "negligible" (Jansen et al. 2001). We use the lower bound (0.93) as a conservative high estimate of annual juvenile survival (s_j). A mark-recapture study of *Elliptio fisheriana*, *E. complanata*, and *Lampsilis cariosa* found much lower survival rates (0.43-0.69) for smaller mussels (< 55 mm; Villella et al. 2004). We use the geometric mean of this range as a lower estimate of juvenile survival. The same study found that larger mussels of all species had survival rates >90% and up to 99%. We therefore use 95% as an upper estimate of adult survival (s_a). Four populations of Northern Riffleshell (*Epioblasma torulosa rangiana*) in Northeastern US were found to have a geometric mean annual survival of 67% (Crabtree and Smith 2009). This species is considered endangered in the US, and so this is an appropriate lower bound on adult survival given that all four of the Canadian species addressed here are considered Endangered or Threatened.

Haag and Staton (2003) counted numbers of glochidia for 8 species of freshwater mussels. Mean fecundities for these species ranged from 9647 to 325 709, and we use the geometric mean of the 8 values, multiplied by 0.5, as our lower estimate of fecundity (f). As an upper bound, we use the geometric mean of the range 200 000 – 1 million as an upper estimate for fecundity. McMahon (1991) reports the age of maturity of Unionid freshwater mussels to be 6-12 years, while COSEWIC (2010) found that the Wavy-rayed Lampmussel matured at 3 years. We therefore use 3 years as a low estimate and 9 years as a high estimate of age at maturity (T_{mat}). Of the four species addressed here, *Q. quadrula* is likely the longest lived at 64 years (COSEWIC 2006). The maximum ages of the other three species are unknown, but Haag and Rypel (2010) report maximum ages of other Unionids as low as 4 years in the Southern US. We use 55 years as an upper estimate of average maximum age for Unionids (T_{max}), and 13 years as a lower estimate.

Table 1. *Low and high estimates of vital rates pertaining to the life cycle of freshwater mussels of the family Unionidae.*

Vital Rate	Symbol	Estimates (low, high)	Source
Glochidial survival	s_1	1.8 E-5	Jansen et al. 2001 (table 11.3)
		2.4 E-5	Young and Koops 2010
Juvenile survival	s_j	0.54	Villella et al. 2004
		0.93	Jansen et al. 2001 (table 11.3)
Adult survival	s_a	0.67	Crabtree and Smith 2009
		0.95	Villella et al. 2004
Fecundity	f	28879	Haag and Staton 2003
		223607	
Age at maturity	T_{mat}	3	COSEWIC 2010
		9	McMahon 1991
Maximum age	T_{max}	13	Haag and Rypel 2010
		55	COSEWIC 2006 (*Q. quadrula*)

ANALYSES

All permutations of high and low vital rates were combined to build 64 matrices representing different life history patterns. A life history with late maturity (age 9) and short maximum lifespan (age 13) was considered unlikely, and all matrices containing this combination were removed for a total of 48 different life histories. Annual population growth rate was calculated from each matrix as the dominant eigen value (λ), and the sensitivity of the growth rate to perturbations in each vital rate (its elasticity) was measured. Elasticities are a measure of the relative effects of proportional changes in vital rates, and are given by the partial derivatives of λ with respect to e_{kl}, the individual elements of the matrix ($\varepsilon_{kl} = \partial \log \lambda / \partial \log e_{kl}$, Caswell 2001).

Elasticities were calculated for each vital rate and for all 48 matrices. Using the elasticity value as the dependent variable, the matrices were sorted by a K-means clustering analysis into three groups with distinct elasticity patterns (Hartigan and Wong 1979). A classification tree was built using the assigned groupings as a response variable, and the vital rates (high/late or low/early) as predictors (Breiman et al. 1984). Wherever possible, known vital rates for the four mussel species in question were used to predict their expected elasticity pattern. All analyses were performed using the programming language R, version 2.11.1 (R Development Core Team, 2010; elasticity code modified from Morris and Doak 2002).

RESULTS

SENSITIVITY PATTERNS

Overall, juvenile and adult survival had the highest elasticity values (0.48 and 0.56 respectively, averaged over all 48 sets). Cluster analysis revealed 3 distinct groupings of elasticities (Figure 1) with the following distinguishable characteristics:

Group 1: Reproduction dominant

> Age at maturity, fecundity and glochidial survival are significantly more sensitive in this group than in the others; juvenile survival, adult survival and age at maturity all rank similarly in importance.

Group 2: Adult survival dominant

> Adult survival is on average 1.8 times as important as juvenile survival; this group is the only group in which maximum age is at all relevant.

Group 3: Juvenile survival dominant

> Juvenile survival is very important, and is more than twice as sensitive as both adult survival and age at maturity.

Of the 48 matrices considered, 16 belonged to group 1, 24 to group 2, and 8 to group 3. The mean and range of elasticities for each group are summarized in Table 2. Note that the elasticity of age at maturity is negative. This means that increasing the age at maturity will decrease the population growth rate.

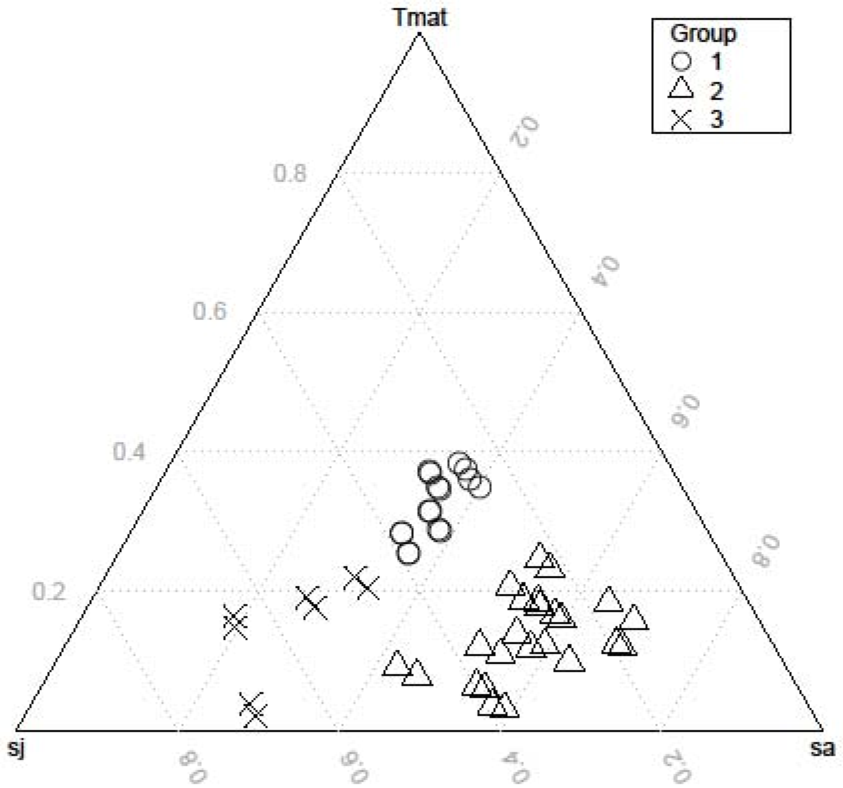


Figure 1. *Triangular plot depicting elasticities of age at maturity (Tmat), adult survival (sa), and juvenile survival (sj) for freshwater unionid mussels. Each point represents a different life history matrix. Elasticities are scaled so that the three values are plotted as proportions. Symbols represent the assigned elasticity pattern group: 1. Reproduction dominant; 2. Adult survival dominant; 3. Juvenile survival dominant.*

Table 2. *Mean and range of elasticities for freshwater mussel vital rates by elasticity pattern group.* s_1*=glochidial survival;* s_j*=juvenile survival;* s_a*=adult survival; f=fecundity;* T_{mat}*=age at maturity;* T_{max}*=maximum age. Bold: group distinguishing rates. * value is significantly higher in this group compared to other groups (pairwise wilcoxon test, p<0.05).*

Group	s_1	s_j	s_a	***f***	T_{mat}	T_{max}
1: Reproduction dominant	0.25* (0.21, 0.27)	0.49 (0.42, 0.53)	0.56 (0.47, 0.67)	0.25* (0.21, 0.27)	**- 0.52*** (-0.33, -0.67)	0.004 (0, 0.03)
2: Adult survival dominant	0.11 (0.01, 0.18)	0.32 (0.07, 0.66)	**0.59** (0.26, 0.83)	0.11 (0.01, 0.18)	- 0.14 (-0.03, -0.26)	0.01 (0, 0.10)
3: Juvenile survival dominant	0.12 (0.09, 0.15)	**0.98*** (0.70, 1.21)	0.46 (0.29, 0.66)	0.12 (0.09, 0.15)	- 0.28 (-0.02, -0.46)	0.00004 (0, 0.0002)

CLASSIFYINIG ELASTICITY BASED ON LIFE HISTORY

Mean sensitivities for all vital rates (except glochidial and adult survival) differed significantly depending on whether the low or high value was considered (Mann-Whitney *U* test, all *p*-values < 0.05 except for s_1, p=0.44 and s_a, p=0.15). Higher juvenile survival or fecundity resulted in a higher sensitivity to changes in these values. Conversely, species with earlier maturation or shorter lifespan were more sensitive to age at maturity and maximum age than were late-maturing or long-lived species.

While sensitivities were significantly influenced by the values of nearly all vital rates, only two vital rates (fecundity and age at maturity) were required to predict the elasticity pattern with approximately 92% confidence; only 4/48 matrices were classed incorrectly using these two predictors in a classification tree. Adding knowledge of adult and juvenile survival increased the accuracy to 100% (Figure 2). Matrices in the Reproduction dominant elasticity group (group 1) were all characterized by early maturity and high fecundity. High fecundity and late maturity tended to result in an emphasis on juvenile survival (group 3) with two exceptions, both having high adult survival, low juvenile survival, and belonging to group 2 (Adult survival dominant). Matrices with lower fecundity were all classified as Adult survival dominant (group 2) with two exceptions. Both exceptions had low adult survival, high juvenile survival, matured late, and belonged to group 3 (Juvenile survival dominant). If either age at maturity or fecundity are unknown, predicting the elasticity pattern from this model becomes much less accurate (21% and 42% misclassification rate respectively)

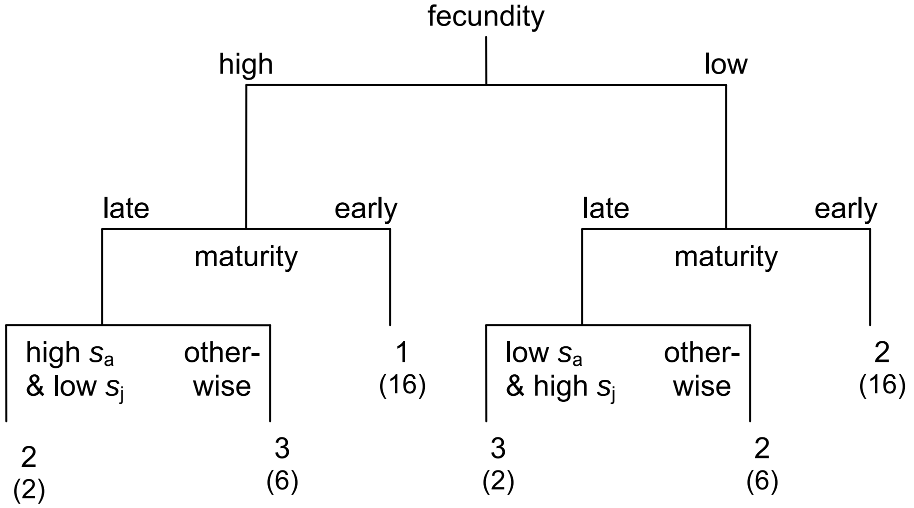


Figure 2. *Decision tree for predicting the elasticity pattern of a species based on its life history and vital rates (See Table 1 for vital rate values and Table 2 for summary of elasticity groups). Elasticity pattern groups: 1 – Reproduction dominant; 2 – Adult survival dominant; 3 – Juvenile survival dominant. In brackets are the numbers of matrices (out of 48) classified into each branch.*

Ligumia nasuta

Unreleased glochidia from female Eastern Pondmussel were counted, giving an average fecundity of ~27000 (N=3; Kelly McNichols, unpubl. data). Additional vital rates for Eastern Pondmussel are currently unknown. Given its low fecundity, this species most likely belongs to elasticity group 2 (Adult survival dominant, 22/24 matrices; Figure 2, Table 3), but possibly to group 3 (Juvenile survival dominant, 2/24 matrices).

Truncilla donaciformis

Fawnsfoot in Canada have been recorded to reach up to 52 mm (COSEWIC 2008). Of three aged individuals, the larges was 45.6 mm, and 11 years old. This suggests that Fawnsfoot can be categorized as short-lived and early maturing. Fawnsfoot will therefore fall into either group 1, if fecundity is high (8/16 matrices), or group 2, if fecundity is low (8/16 matrices). If group 1, population growth rate will be most sensitive to age at maturity, equally sensitive to juvenile and adult survival, and more sensitive to fecundity and glochidial survival than the other two groups. In the latter case, adult survival will be most important.

Quadrula quadrula

Mapleleaf in Manitoba have been found to live as long as 64 years, and so we classify Mapleleaf as long-lived. Age at maturity of Mapleleaf in Mississippi was estimated at ~8 years (Whitney et al. 1997). Given the cooler Canadian climate we assume that this is the minimum age of maturity for the Canadian population (COSEWIC 2006), and categorize Mapleleaf as late-maturing. In addition, fecundity values for Canadian populations are likely lower than the 30 000 and 50 000 ova reported for southern populations of congener species, *Quadrula asperata* and *Quadrula pustulosa*, respectively (COSEWIC 2006, Haag and Staton 2003). If so, Mapleleaf have "low" fecundity. As seen in Figure 2, low fecundity and late maturity suggest Mapleleaf will most likely exhibit group 2 elasticity patterns (Adult survival dominant, 6/8 matrices) with a possibility of Juvenile survival dominant elasticities (group 3, 2/8 matrices) if juvenile survival itself is high, and adult survival low.

Villosa iris

180 individuals from Ontario rivers were aged in 2010 (T. Morris, unpubl. data). The oldest individual was 48 years old, making Rainbow a long-lived species ("high" maximum age"). While not all individuals could be sexed, the youngest identified female was 9 years. Since juveniles cannot be sexed, we conclude that Rainbow mature by 9 years at the latest (the estimate for "late" age at maturity). Applying catch curve analysis to the catch-at-age frequency yields an adult survival of 0.927, which falls into the range of "high" adult survival. A classification tree with these three predictors (age at maturity, maximum age, and adult survival) suggests that Rainbow will belong either to group 2 (Adult survival dominant, 6/8 matrices) or group 3 (juvenile survival dominant, 2/8 matrices).

Table 3. *Known vital rate estimates (Est.) and classification (H/L) of each rate as high/low, early/late (maturity) or short/long (lifespan), for four freshwater mussel species. Possible elasticity pattern groups are given with a confidence level based on a cluster analysis of matrices representing 48 different life histories (see text): 1 – Reproduction dominant, 2 – Adult survival dominant, 3 – Juvenile survival dominant.*

	Ligumia nasuta		*Truncilla Donaciformis*		*Quadrula quadrula*		*Vilosa iris*	
Parameter	Est.	H/L	Est.	H/L	Est.	H/L	Est.	H/L
s_1 (glochidial survival)	-	-	-	-	-	-	-	-
s_j (juvenile survival)	-	-	-	-	-	-	-	-
s_a (adult survival)		-	-	-	-	-	0.93	high
f (fecundity)	27000	low	-	-	< 50000	low	-	-
T_{mat} (age maturity)	-	-	-	early	$\geq$ 8	late	$\leq$ 9	late
T_{max} (maximum age)	-	-	$\geq$ 11	short	64	long	48	long
Group (Confidence)	2 (92%) 3 (8%)		1 (50%) 2 (50%)		2 (75%) 3 (25%)		2 (75%) 3 (25%)	

DISCUSSION

Our results show that the vital rates and life history of a freshwater mussel population can be used to categorize the sensitivity of population growth rate to changes in vital rates. Three distinct elasticity pattern groups were identified: 1. Reproduction dominant; 2. Adult survival dominant; 3. Juvenile survival dominant. Elasticity patterns were most accurately predicted when fecundity (high or low) and age at maturity (early or late) were known. Based on available estimates, Rainbow, Mapleleaf and Eastern Pondmussel most likely fall into group 2, where population growth is most sensitive to adult survival and somewhat sensitive to juvenile survival. These species also have a smaller probability of being very sensitive to juvenile survival and somewhat sensitive to adult survival (group 3). Both groupings are only slightly sensitive to glochidial survival, fecundity, and age at maturity. Fawnsfoot, however, is equally likely to belong to group 2 (adult survival dominant) or group 1 (reproduction dominant) depending on whether it has high or low fecundity. In the latter case, the growth rate of Fawnsfoot will be more sensitive than the other three species to age at maturity, fecundity and glochidial survival.

ALLOWABLE HARM AND RECOVERY TIMES

Without complete vital rate information, current population growth rates cannot be estimated. We therefore cannot determine whether the populations in question are increasing or in decline, nor can we give accurate estimates of allowable harm or recovery times. Using the elasticity groupings and vital rate decision tree, however, we can predict which vital rates are likely to be most sensitive to harm and most receptive to recovery. Harms to those vital rates with the highest elasticities are expected to be most detrimental to population growth rate. Conversely, recovery strategies which increase those same rates are expected to have the most positive impact on population growth. For example, if adult survival has an elasticity of 0.6, then a 10% change (increase or decrease) will result in a 0.1*0.6=6% change in the population growth rate. In general, harm to adult or juvenile survival should be minimized.

In the planning of recovery strategies, the scope for improvement of any given vital rate should be considered in addition to its sensitivity (e.g., Vélez-Espino and Koops 2009). For instance, glochidial survival was one of the least sensitive vital rates for freshwater mussels, but the scope for improvement in this rate may exceed that of a more sensitive rate like adult or juvenile survival. This could be the case if there is existing harm to glochidial survival, such as a physical barrier between mussel and host fish, or if adult or juvenile survival is already very high. Given the small order of magnitude of glochidial survival, changes that are similar proportionally to changes in adult or juvenile survival will be much smaller biologically, and may even fall within the range of uncertainty in glochidial survival.

KNOWLEDGE GAPS

Our analysis shows that when some vital rate information is absent, a species' sensitivity to perturbation (elasticity) is most accurately determined when age at maturity and fecundity are known. Understanding the most likely elasticity pattern can then provide guidance for recovery strategies and additional research. In the case where population growth is most sensitive to age at maturity, this rate becomes doubly important; while it cannot necessarily be manipulated, estimates of age at maturity will largely affect the accuracy of any projection simulations (under-estimating age at maturity will result in a large overestimate of population growth rate).

Decision trees based on two vital rates can provide guidance, but complete vital rate information allows for much stronger conclusions, and also for projection simulations. To that end, the most understudied vital rates are juvenile and glochidial survival. Early life survival of the species in question and of freshwater mussels in general, requires further attention. For instance, little is known about the relationship between the host population density and the frequency of host-mussel encounters. In particular, the magnitude of difference in glochidial survival between lure and non-lure species should be explored. If, instead, the population growth rate were measured it could be used to infer a survival rate for glochidia (if all other vital rates are known). Population growth rate is not known for any of the four species considered here.

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