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Recovery Potential Modelling of Carmine Shiner (Notropis percobromus) 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) had assessed the Carmine Shiner (Notropis percobromus) as Threatened in Canada (2006). Here we present population modelling 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 Carmine Shiner populations are very sensitive to perturbations that affect fecundity, and survival of young of the year. Harm to these portions of the 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), and assuming catastrophic decline events take place with 10% probability per generation (~8% annually), we propose abundance recovery targets of at least 8 880 000 adult Carmine Shiner (aged 1+), requiring ~3300 ha of suitable habitat. In the absence of mitigating efforts, additional harm or habitat limitations, we estimate that a growing Carmine Shiner population will take approximately 12 years to reach this recovery target if starting from a population of 20 000 adults. Recovery or preservation strategies which incorporate improvements in the most sensitive Carmine Shiner vital rates will have the greatest effect on population growth.

Modélisation du potentiel de rétablissement de la tête carminée (Notropis percobromus) au Canada

RÉSUMÉ

Le Comité sur la situation des espèces en péril au Canada (COSEPAC) a évalué la tête carminée (Notropis percobromus) comme étant une espèce menacée au Canada (2006). Ce document présente la modélisation de la population afin d'évaluer les dommages admissibles. 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'appuver l'évaluation du potentiel de rétablissement (ÉPR). Nos analyses ont révélé que la dynamique des populations de têtes carminées est très sensible aux perturbations qui affectent la fécondité et la survie des jeunes de l'année. On doit réduire au minimum les dommages sur ces étapes du cycle biologique afin d'éviter de mettre en péril la survie et le rétablissement futur des populations au Canada. En nous basant sur un objectif de durabilité démographique (c.-à-d. une population autonome à long terme) et une probabilité de 10 % de déclin catastrophique par génération (environ 8 % par année), nous proposons des cibles de rétablissement de l'abondance d'au moins 8 880 000 têtes carminées adultes (âgées d'un an ou plus), ce qui nécessite environ 3 300 hectares d'habitat convenable. En l'absence d'efforts d'atténuation ou de dommages supplémentaires ou de limites relatives à l'habitat, nous estimons qu'une population croissante de têtes carminées prendra environ 12 ans pour atteindre l'objectif de rétablissement si l'on commence avec une population de 20 000 adultes. Ce sont les programmes de rétablissement et les stratégies de conservation visant une amélioration des indices vitaux des têtes carminées particulièrement vulnérables qui auront la plus grande incidence sur la croissance de la population.

INTRODUCTION

The Carmine Shiner (*Notropis percobromus*), previously thought to be Rosyface Shiner (*N. rubellus*), is a member of the Minnow family, Cyprinidae, and is now recognized as a different species within the rosyface shiner species complex. In Canada, the Carmine Shiner has been found only in the Winnipeg River system. Its summer habitat includes clear, fast flowing streams and small rivers, and threats include activities that alter turbidity, flow, and/or substrate. Designated as Special Concern in 1994, Carmine Shiner has since been re-assessed as Threatened in both 2001 and 2006.

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 Carmine Shiner. 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. The effects of habitat limitations and associated density dependence were explored.

SOURCES

Where possible, life history estimates for the Carmine Shiner were based on sampling data from the Canadian population in the Whitemouth and Birch rivers in Manitoba (D. Watkinson, unpublished data). Where necessary, estimates were supplemented by life-history based allometries using the Life-History Tool in Fishbase (Froese and Pauly 2010)

MATRIX MODEL

Using a matrix approach, the life cycle of Carmine Shiner was represented with annual projection intervals and by a post-breeding age-structured projection matrix (Caswell 2001; Figure 1). Individuals were assumed to first mature at age 1, and reach a maximum age of 2

years (D. Watkinson, DFO, unpublished data). We therefore model three age classes; age-0 juveniles (young of the year), and age one and two adults.

Elements of the age-structured matrix included the fecundity coefficient of age class j (F_j), and the age specific annual survival probability from age j-1 to age j (G_j). Fecundity coefficients (F_j) represent the contribution of an adult in age class j to the next census of age-0 individuals. Since a post-breeding model is assumed, the coefficient F_j includes the annual survival probability of adults from age j-1 to age j, as well as the age-specific fertility upon reaching age j (f_j) such that

$$(1) F_i = G_i f_i$$

where f_j is the product of a stage's average number of eggs (m_j) , the proportion of females (assumed to be 50%), and the inverse of the average annual spawning periodicity (assumed to be 1).

Parameter Estimates

Mean and variance for fecundity and survival were estimated as follows (see Table 1). 175 Carmine Shiner sampled from both Whitemouth and Birch rivers in 2006 were aged using fin rays, and the fecundity of 21 mature females was measured (D. Watkinson, unpublished data). The log-relationship between egg number and fish length was not strong (R^2 =0.11), and the mean length of aged 1 and aged 2 adults (58mm and 59mm respectively) did not differ. We therefore assumed that fecundity does not differ by age in Carmine Shiner. The mean fecundity of the 21 mature females (mean length 60 mm) was estimated as 1229 ± 109 (± SE, range 694-2806), or 614 ± 55 when only female offspring are considered.

Adult mortality of Carmine Shiner was estimated using a life-history tool (fishbase.org), which estimates instantaneous mortality using Pauly's (1980) empirical equation based on the parameters of the von Bertalanffy growth function and on the mean annual water temperature. Values entered for the calculation were: a maximum observed fork length of 67 mm (n =316) converted to total length using the ratio TL:FL=1.07, the age at maturity (1 year), and the average annual water temperature (estimated as 8°C; D. Watkinson, unpublished data). This yielded an instantaneous mortality of 1.5 (range 0.99-2.27), or an annual survival probability of 0.22 (range 0.10-0.37). Generation time was estimated, also using the life history tool, to be 1.3 years.

Survival during the first year was estimated by combining a size-dependent mortality model (Lorenzen 2000) with the von Bertalanffy growth parameters estimated by the Fishbase tool. Mortality was assumed to decline proportionally with increases in size (Lorenzen 2000) such that

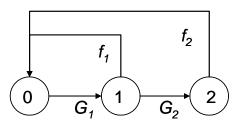
$$(2) M_t = \frac{m_0}{L_t},$$

where M_t and L_t are the instantaneous mortality and mean length at time t, and m_0 is the mortality at unit size (i.e., at $L_t = 1$). If L_t is described by the von Bertallanffy growth curve equation, survival from age j to age j+1 can be calculated by integrating equation (2) and evaluating between j and j+1:

$$s_{j\dots j+1} = \left[\frac{L_j e^{-k}}{L_{j+1}}\right]^{m_0/kL\infty}$$
(3)

k and L_{∞} are parameters of the von Bertalanffy growth equation as evaluated above. The parameter m_0 was estimated from equation (2) using the mean adult size and the instantaneous mortality calculated using the Fishbase tool, and survival from hatch to age 1 was calculated using equation (3). Variance for each survival rate was approximated by first translating the range in instantaneous mortality to a range in m_0 and then a range in first year survival using equation (3). This range was assumed to be a 99% confidence interval, and therefore contained 6 standard deviations of the mean. Variation in both survival and fecundity for stochastic simulations was generated by drawing rates from a lognormal distribution with means and variances as above

a)



b)
$$\begin{pmatrix} F_1 & F_2 & 0 \\ G_1 & 0 & 0 \\ 0 & G_2 & 0 \end{pmatrix}$$
 c)
$$M = \begin{pmatrix} 2 & 137 & 0 \\ 0.0034 & 0 & 0 \\ 0 & 0.22 & 0 \end{pmatrix}$$

Figure 1. Generalized life cycle (a), corresponding age-structured projection matrices (b), and mean values of matrix elements (c) used to model the population dynamics of Carmine Shiner. F_i represents fecundities, and G_i the transition probabilities from age j-1 to age j. Note that fertility is positive for the juvenile class since individuals who are juveniles at census t will mature upon their first birthday (if they survive) and produce offspring that will be counted at census t+1 (Caswell 2001).

Table 1. Mean and standard deviation of vital rates for Carmine Shiner. s_i = annual survival probability from age j-1 to age j; f = fecundity of mature Carmine Shiner. *Used for calculating allowable harm, and for conducting recovery projections. **Used for calculating minimum viable population (MVP).

	Vital rates			adjusted s₁	
	S ₁	S ₂	f	λ=2.3*	λ =1**
mean	0.028	0.223	614	0.0034	0.0013
standard deviation	0.014	0.048	54.5	0.0017	0.0007

ALLOWABLE HARM

We assessed allowable harm 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 ($\tau_{\nu, max}$) were estimated analytically as:

$$\tau_{_{\boldsymbol{\mathcal{V}}}} < \left(\frac{1}{\varepsilon_{_{\boldsymbol{\mathcal{V}}}}}\right) \left(\frac{1-\Lambda}{\Lambda}\right) \text{ and } \tau_{_{\boldsymbol{\mathcal{V}},\max}} = \left(\frac{1}{\varepsilon_{_{\boldsymbol{\mathcal{V}}}}}\right) \left(\frac{1-\Lambda}{\Lambda}\right)$$

where ε_{ν} is the elasticity of vital rate ν , 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 ν , and are given by the scaled partial derivatives of λ with respect to the vital rate:

(5)
$$\varepsilon_{v} = \frac{v}{\lambda} \sum_{i,j} \frac{\partial \lambda}{\partial a_{ij}} \frac{\partial a_{ij}}{\partial v}.$$

Here, a_{ii} are the matrix elements.

Since survival was calculated using an equation that assumes ideal growth conditions, and was based on an allometry rather than population data, the original survival estimates resulted in an eigenvalue (population growth rate) that was likely unrealistically high (λ = 17.6). To adjust this value, we assumed that density dependence (crowding) would result in a lower realized survival for age-0. The adjustment factor was calculated as the total habitat available divided by the total habitat required by the minimum viable population size (see results). Λ was therefore estimated as 2.3. The lognormal variance of s_1 was not changed for the adjusted s_1 value.

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 Vélez-Espino and Koops 2007); (ii) calculate λ for each matrix; (iii) calculate the ϵ_{ν} of s_i and f_i for each matrix; and (iv) estimate mean stochastic elasticities and their parametric, bootstrapped 95% confidence intervals. For each vital rate, we then calculated maximum allowable harm for mean,

maximum (upper 95% CI), and minimum (lower 95% CI) values that were based on a mean Λ of 2.3.

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 was estimated as

(6)
$$\Psi \approx \left(\frac{1-\Lambda}{\Lambda}\right) / \sum_{\nu=1}^{n} \varepsilon_{\nu}$$

where n is the number of vital rates that are simultaneously harmed, εv 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

We used demographic sustainability as a criterion to set recovery targets for Carmine Shiner. 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 100 years (approximately 77 generations). We estimated MVP for individual populations, not the species in total. To estimate MVP, we assumed discrete populations that function as demographically independent units (i.e., little or no immigration or emigration).

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; (ii) projection matrices were drawn at random from these to generate 5000 realizations of population size per time step (i.e., over 100 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, defined as a 50% reduction in abundance, was incorporated into these simulations, and occurred at a probability (P_k) 0.05 or 0.10 per generation. We used these simulations to determine the number of adults necessary for the desired probability of persistence (see Results) over 100 years. Mean age-0 survival was adjusted with constant lognormal variance such that the population was at equilibrium (geometric mean growth rate of λ =1). This was done to simulate the probability of persistence of a stable population over the long term, since population growth is not sustainable over time.

MINIMUM AREA FOR POPULATION VIABILITY

Following Vélez-Espino *et al.* (2010), we estimate the minimum area for population viability (MAPV) as a first order quantification of the amount of habitat required to support a viable population. We calculate MAPV for each age-class in the population as:

(7)
$$MAPV_i = MVP_i \cdot API_i$$
.

MVP_j is the minimum number of individuals per age-class required to achieve the desired probability of persistence over 100 years, as estimated for the recovery target. Individuals were distributed among age classes according to the stable age distribution, which is represented by the dominant right eigenvector (w) of the mean projection matrix based on the growth rate $\lambda = 2.3$ (**M** $w = \lambda \cdot w$) (De Kroon *et al.* 1986). The recovery target, MVP, is expressed in terms of

adult numbers only, so that $MVP_2+MVP_3 = MVP$. API_j is the area required per adult individual (the inverse of density). We estimate API based on an allometry for river environments from Randall *et al.* (1995) for freshwater fishes:

(8) API =
$$e^{-13.28} \cdot TL^{2.904}$$

where TL is the average total length of an adult measured in mm.

The mean API for age-0 and for adults was estimated from equation (8) in two different ways: i) using the geometric mean of lengths at the endpoints of each stage (Minns 2003), or ii) using the mean size-at-age of the youngest individuals in each stage. Based on assumptions in the models used to estimate individual growth and mortality, the more numerous fish at the beginning of the age class should require more space than the larger but fewer remaining individuals at the end of an age class. The latter API calculation may therefore be more appropriate. Size of emergent fry was assumed to be 5 mm (Scott and Crossman 1973; size at hatch of the related Rosyface Shiner), and adults were assumed to range from 53 mm to 73 mm based on sampling data (D. Watkinson). An MAPV for each stage was estimated from equation (7), and the MAPV (method i) and MAPV₂ (method ii) for the entire population was estimated by summing across all life stages.

To explore the effects of limited habitat availability on extinction probabilities and recovery times we incorporated habitat loss parameters into the matrix model and simulations. This model (Minns 2003) assumes that if the area of available habitat (A_i) exceeds the total required habitat (a_i) then survival is independent of the habitat supply. If, however, required habitat is greater than the habitat available, the survival of each age-class is reduced linearly in proportion to the ratio between habitat supply and required habitat. Specifically, survival (s_i) is multiplied by

(9)
$$h_j = \begin{cases} A_j/a_j & \text{if } A_j < a_j \\ 1 & \text{if } A_j \ge a_j \end{cases}.$$

In the simulations, habitat required (a_j) was calculated at each time step as the sum of number of individuals in each stage (N_i) times API_i .

RECOVERY STRATEGIES AND TIMES

We used recovery targets to determine recovery timeframes of individual populations under three hypothetical recovery strategies. We focused on positive changes in annual survival probability of juveniles (s_1) , of adults (s_2) , or in fertility (f_2) that might result from specific recovery actions (e.g., the rehabilitation or enhancement of habitat). Specifically, each strategy consisted of improving the associated vital rates by either 10% or 20% to demonstrate the relative performance of investing in different recovery actions.

The initial population size of adults was estimated to be 10 000 adult females (20 000 adults total), based on the estimated abundance of a Plains Minnow (*Hybognathus placitus*) population (20 000 fish per 35 km of river), the length of river occupied by Carmine Shiner (170 km), supposing 1/3 of captured fish are mature, and ½ of those female (D Watkinson, pers. Comm.), and finally rounding down to the nearest order of magnitude. As above, the initial population was distributed among age classes according to the stable age distribution. For each recovery strategy, we calculated the probability of recovery in a similar manner to the recovery targets, drawing projection matrices based on a geometric mean growth rate of 2.3 for simulations of the status quo (recovery in the absence of improvement or harm). For each strategy the means 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 100 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. Simulations both with and without habitat restrictions imposed are compared. When a 95% probability of recovery could not be achieved due to insufficient habitat, the long term probability of a population being at a recovered level is reported.

RESULTS

ALLOWABLE HARM

Based on the elasticities of the mean vital rates of the Carmine Shiner life cycle, population growth rate is very sensitive to perturbations of both fecundity (f) and survival in the first year (s_1). Elasticites for these rates are just under 1, and so a proportional change in either rate will affect the growth rate in nearly the same proportion. Carmine Shiner are relatively insensitive to changes in adult survival (s_2 ; Figure 2). Means of stochastic elasticities do not differ in ranking from the deterministic elasticities, and confidence intervals associated with the stochastic estimates are not wide, suggesting that elasticities are not overly sensitive to variation in vital rates. Comparing correlations among vital rates and elasticities shows that uncertainty that is present in elasticities is driven primarily by uncertainty in the estimate of juvenile survival.

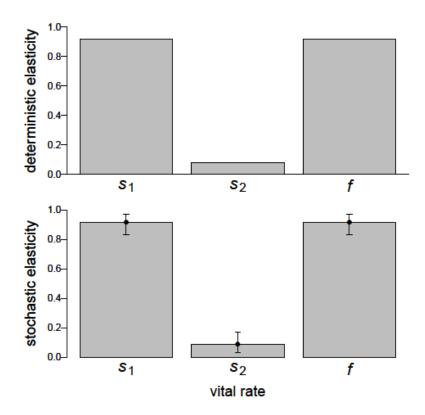


Figure 2. Results of the deterministic and stochastic perturbation analysis showing elasticities (ϵ_{ν}) of the vital rates: annual survival probability of age j-1 to age j (s_i) and fertility (f). Stochastic results include associated bootstrapped 95% confidence interval.

Estimates of the maximum allowable harm to individual vital rates depended on the stochastic element (e.g., mean or upper or lower 95% CI; Table 2). From a precautionary perspective (i.e., assuming an upper 95% CL), our results suggest a maximum allowable reduction of 59% to either survival of age-0 individuals or fecundity. Harms that simultaneously impact all aspects of the Carmine Shiner life cycle (ψ in equation 4) should not exceed 27% per vital rate. Notice that the allowable harm for adult survival is greater than 100%. The estimates of fecundity and age-0 survival are sufficiently high that the population would continue to grow (λ >1) even if adults do not survive to reproduce on their second birthday. If human activities are such that harm exceeds just one of these thresholds, however, the future survival and recovery of individual populations is likely to be compromised; our simulations suggest that recovery time can be severely delayed by levels of harm below the maximum allowable harm suggested in Table 2 (see recovery results below).

Table 2. Summary of maximum allowable harm ($\tau_{v,max}$) estimates for individual and combined vital rates of Carmine Shiner, based on a stochastic perturbation analysis and a population growth rate (Λ) of 2.3. s_i = annual survival probability from age j-1 to age j and f = fertility. Consistent with the precautionary approach, bold values indicate the maximum allowable harm recommended for management decisions.

Stochastic Element	S ₁	S_2	f	All rates
Deterministic mean	-0.62	-7.01	-0.62	-0.30
Stochastic mean	-0.62	-6.54	-0.62	-0.30
+ 95% CI	-0.59	-3.30	-0.59	-0.27
- 95% CI	-0.69	-17.93	-0.69	-0.34

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 to the simulated extinction probabilities for each catastrophe scenario (Equations 10 and 11 below).

While choosing a larger recovery target will result in a lower risk of extinction, there are also costs associated with an increased target (increased effort, time, etc.). When determining MVP from the fitted power curves, we attempted to balance the benefit of reduced extinction risk and the cost of increased 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 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) 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). This represents the point between the upper and lower boundaries where the reduction in extinction risk per investment in recovery is maximized. Calculated in this way, MVP was ~516 000 adults (ages 1 and 2), with a range of 346 000 - 817 000 adults, when the probability of catastrophic decline (50%) was assumed to be 5% per generation (~4% annually). If catastrophes occurred at 10% per generation (~8% annually), MVP was 8 884 000 adults (range: 6 137 000 -480 000 adults). In both scenarios, the probability of extinction for the respective MVPs were approximately 0.03 over 100 years (Figure 3).

Extinction risk, P(ext.), for the 5% or 10% per generation catastrophe scenarios can be defined as a function of population size, N,

(10)
$$P(ext)_{5\%} = 51 \cdot N^{-0.573}$$

(11)
$$P(ext)_{10\%} = 412 \cdot N^{-0.600}$$

If a higher risk of extinction is deemed acceptable, equations (10) and (11) can be used to calculate the appropriate MVP. For instance, to achieve an extinction risk of 10% over 100 years, the MVP for a population experiencing catastrophes at a probability of 10% per generation would be 1.06 million adults (Table 3).

Given that Carmine Shiner is very sensitive to the most uncertain parameter (age-0 survival), and the large MVP targets suggested above, we explored the sensitivity of the MVP target to the variance in age-0 survival. MVP decreased dramatically when variance in age-0 survival was reduced. A 10% reduction in the standard deviation reduced MVP to 3.1 million adults, and a 50% reduction resulted in an MVP of 396 000 (Figure 4).

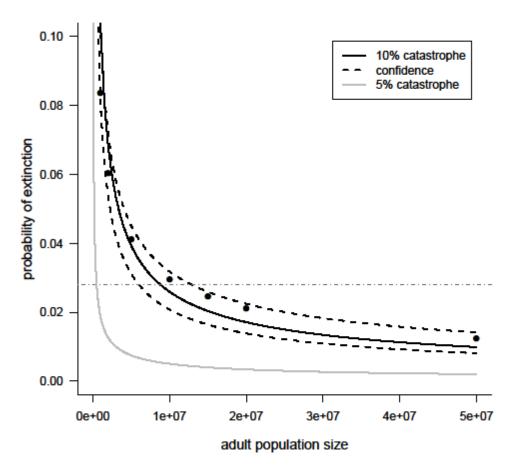


Figure 3. Probability of extinction within 100 years of 10 simulated Carmine Shiner populations at equilibrium, as a function of population size. Bold curves assume a 10% probability of catastrophic decline per generation (solid = mean, dotted = max and min of 10 runs). Solid grey line represents 5% probability of catastrophe. Dashed horizontal reference line is at 0.028 and intersects curves at the associated MVPs.

RECOVERY TIMES

Assuming a population growth rate of 2.3, and in the absence of recovery efforts, additional harm, or habitat restrictions, a Carmine Shiner population was predicted to increase from 20 000 adults to the MVP target of 8.9 million adults in approximately 12 years (assuming a 10% per generation probability of catastrophe). Simulated recovery strategies decreased recovery times as much as 3 years (Figure 5). The most effective simulated strategy was an improvement to survival of immature individuals ($s_{1,2}$). The time to recovery increased exponentially as harm was added to vital rates (Figure 6). Consistent with the sensitivity and allowable harm results, recovery time was more severely delayed when rates with higher elasticity were harmed. These results suggest that lower allowable harms should be considered to reduce delays in recovery time, especially in the case of early life survival and fecundity.

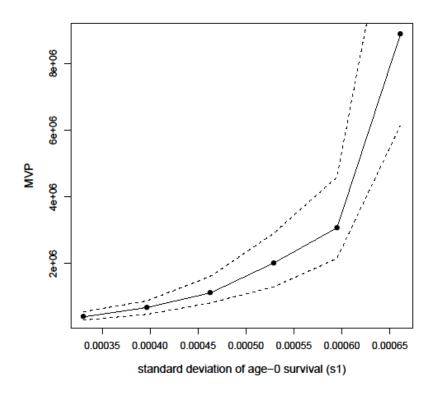


Figure 4. Minimum Viable Population (MVP) targets (solid) and confidence bounds (dashed) for Carmine Shiner as a function of the standard deviation around first year survival. A 10% per generation probability of catastrophic decline was assumed.

MINIMUM AREA FOR POPULATION VIABILITY

The stable stage distribution for Carmine Shiner is 99.84% YOY, 0.13% age 1, and 0.03% age 2 individuals (Table 4). With a target MVP of 516 000 adults under a 5% probability of catastrophe per generation, MAPV was 193.6 ha and MAPV₂ was 14.8 ha. With a target MVP of 8.9 million adults, under a 10% probability of catastrophe per generation, MAPV was 3 335 ha, and MAPV₂ was 254 ha (Table 3). The estimated available Carmine Shiner habitat in the Birch and Whitemouth rivers is 402 ha, which is sufficient area for a recovered population if Carmine Shiner experience catastrophic decline at a frequency of 0.05 per generation. If catastrophes occur at 0.10 per generation and API is as in method (i), however, the available habitat will support only 12% of the population. This ratio was used to reduce the survival of age-0 individuals for calculations of allowable harm. Note that these area estimates assume the required habitat per individual listed in Table 3, which does not account for any overlapping of individual habitats (sharing) that may occur.

Recovery and Extinction with Habitat Limitations

When habitat restrictions and associated density dependence were incorporated into population projections, both probabilities of persistence and times to recovery were affected. A population at MVP (8.9 million adults), experiencing 10% chance of catastrophe per generation, and having available 3 300 ha of suitable habitat (MAVP), had a 95.6% probability of persistence over 100 years. This was only slightly lower than the 97% probability of persistence observed in simulations that did not include habitat restrictions or density dependence. If habitat was reduced below the MAPV level, however, extinction risk increased exponentially (Figure 7).

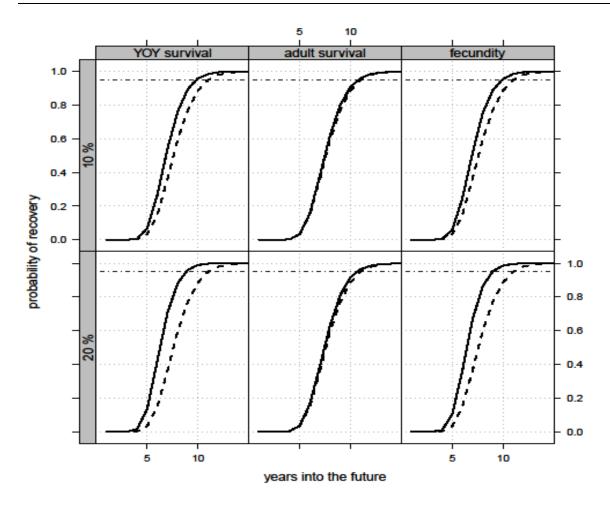


Figure 5. The probability of recovery of 10 simulated Carmine Shiner populations under 3 hypothetical recovery strategies and 2 degrees of improvement, based on an initial adult population size of 10 000 adult females. Dashed lines show recovery under status quo conditions, assuming no harm, a population growth rate of 2.3, and a probability of catastrophe of 10% per generation. Solid lines represent improvement of 10% or 20%, to young of the year (YOY) survival (s_1) , adult survival (s_2) or fecundity (t).

Habitat restrictions reduce the ability of a population to recover. If the habitat required for a recovered population exceeded the available habitat, simulated populations reached "recovery" abundance occasionally, but did not remain at that abundance due to density dependence (Figure 8). Figure 8 shows the median and 95% confidence intervals (based on 15 000 simulations) of population size over time assuming a) the estimated available habitat, or b) the required habitat (MAPV). Also shown is a sample population and its 100 year trajectory. The proportion of simulated populations which were larger than the recovery target (on average over the long term) is shown in Figure 9. Given the current habitat area, the population rarely, if ever, exceeded the recovery target, and had a median population size of ~2.3 million adults. At MAPV, the median population size was 9.4 million (larger than MVP) with only a 7% chance of the population abundance being below MVP at any given time (Figure 9).

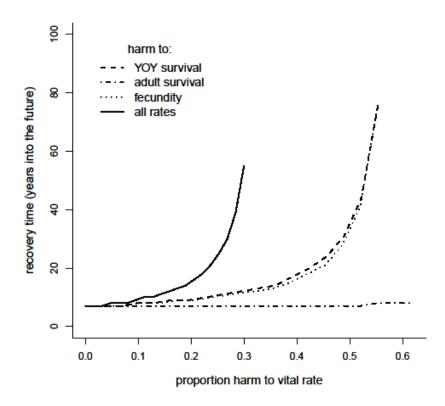


Figure 6. Predicted change in the time to 95% chance of recovery of a Carmine Shiner population that is experiencing increased harm to young of the year survival (s_1) , adult survival (s_2) , fecundity (f), or all vital rates simultaneously. Recovery times are shown as a function of the proportion reduction to each vital rate(s). See Table 2 for maximum allowable harm values.

Table 3. Number of individuals for each life stage to support a minimum viable population (MVP) and the resulting estimate of required habitat, for each stage and for the entire population, based on i) geometric mean size of stage (MAPV), or lower size bound of stage (MAPV₂). Results for two probabilities of catastrophe (Equation 10 and 11) and three levels of acceptable extinction risk are shown.

		5% catastrophe			10% catastrophe		
Extinction Risk	stage	MVP	MAPV	$MAPV_2$	MVP	MAPV	MAPV ₂
10%	YOY	3.3 x10 ⁷	18.4	0.6	6.5 x10 ⁸	368.3	11.9
	Adult	53 000	1.5	0.9	1 059 000	29.3	18.4
	Total		19.9	1.5		397.6	30.3
5%	YOY	1.1 x10 ⁸	61.9	2.0	2.1 x10 ⁹	1 169.2	37.8
	Adult	178 000	4.9	3.1	3 362 000	93.0	58.4
	Total		66.8	5.1		1 262.2	96.2
3%	YOY	3.2 x 10 ⁸	179.4	5.8	5.4 x10 ⁹	3 089.5	99.9
	Adult	516 000	14.3	9.0	8 884 000	245.7	154.3
	Total		193.7	14.8		3 335.2	254.2

Table 4. Stable stage distribution (percentage of the population in each stage), and area per individual (API) by stage.

Age	Distribution (%)	API (m²)
0	99.84	0.005
adult	0.13	0.277

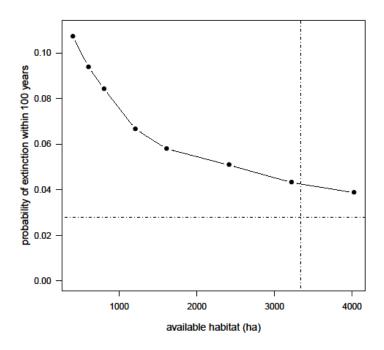


Figure 7: Probability of extinction within 100 years of 10 simulated Carmine Shiner populations at minimum viable population (MVP) size of 8.9 million adults, and experiencing habitat based density dependence, as a function of available habitat area. Simulations assume a 10% chance of catastrophe. Left endpoint represents estimated available habitat. Dashed reference lines show Minimum Area for Population Viability (MAPV, vertical) and the probability of extinction in the absence of habitat restrictions (0.028, horizontal).

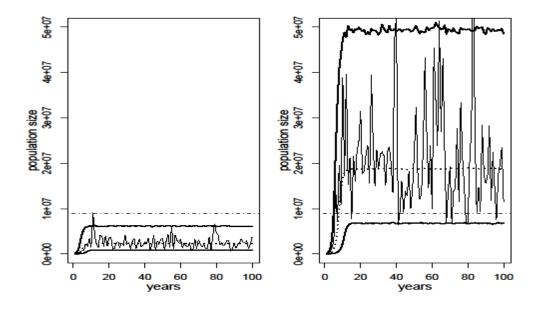


Figure 8. Population size over time of Carmine Shiner populations experiencing density dependence, and 10% per generation catastrophic decline. An example population (narrow solid line), and mean (dotted line) and 95% confidence interval (solid thick lines) of 15 000 simulated populations are shown. Horizontal reference line is at the minimum viable population size (MVP). Simulation assumed that habitat area was at the estimated available habitat (~402ha; left panel), or the Minimum Area for Population Viability (MAPV, ~3300ha; right panel).

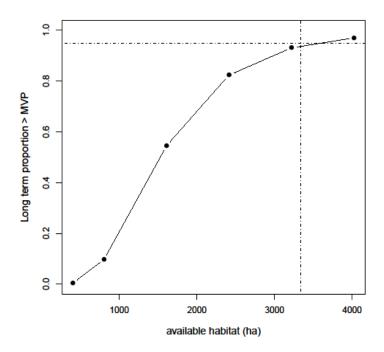


Figure 9. The mean long term probability (over 15 000 100-year projections) of population abundance being above MVP (8.9 million adults), as a function of available habitat. 10% per generation probability of catastrophe was assumed. Left endpoint represents estimated available habitat. Reference lines are at the minimum area for population viability (vertical) and at 95% probability of recovery (horizontal).

DISCUSSION

Our results show that to avoid jeopardizing the survival and future recovery of Carmine Shiner, human-induced harm to reproduction and first year survival of the species should be minimal. Specifically, our modelling suggests that (i) neither rate should be reduced by more than 59%, and (ii) harms that simultaneously affect both rates should not exceed a 27% reduction in either rate. Any harm beyond just one of these thresholds is expected to compromise the future survival and recovery of a population. Furthermore, recovery time is expected to be delayed exponentially as harm approaches these thresholds. It is important to note that these estimates of allowable harm assume that population growth rate before harm (λ) is 2.3. If new information reveals that any of our parameters were overestimated, allowable harm recommendations should be revisited, as the lower population growth rate will both reduce the scope for harm and produce longer times to recovery.

In addition to providing estimates of allowable harm, this work also provides recovery targets based on the concept of MVP. These targets were estimated at approximately 500 000 or 8.9 million adults when the probability of a catastrophic (50%) decline (P_k) was 0.05 or 0.10 per generation respectively. According to Reed *et al.* (2003), catastrophic events (a one-time decline in abundance of 50% or more) occur at a probability of 0.14 per generation in vertebrates. Given the short generation time of Carmine Shiner, however, the annual probability generated by a 15% per generation probability is likely too frequent. We therefore recommend recovery targets based on a 10% probability of catastrophe, but suggest that data be collected to confirm the frequency of catastrophic events for Carmine Shiner. Recovery targets based on MVP can be easily misinterpreted as a reference point for exploitation or allowable harm (Beissinger and McCullough 2002). 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.

The MVP targets for Carmine Shiner found in this work were orders of magnitude larger than previous MVP estimates for a related species, Pugnose Shiner (Notropis anogenus), of ~14 000 adults (Venturelli et al. 2010). Differing methodology and assumptions, such as simulation timeframe and level of acceptable extinction risk, do not allow for direct comparison of these numbers. However, when the same methods and assumptions were used for both species, MVP for Carmine Shiner was found to be between 5 and 15 times larger than that of Pugnose Shiner, depending on the probability of catastrophe (L.A. Vélez-Espino and M.A. Koops, unpublished data). While the age at maturity and maximum age was the same for both species, there are life-history differences that may have influenced this result. Both fecundity and adult survival of Pugnose Shiner were estimated to be nearly twice as high as for Carmine Shiner. resulting in a higher potential population growth rate. This difference could help Pugnose Shiner populations recover more quickly when they approach extinction. In addition, the generation time for Pugnose Shiner was estimated to be longer than that of Carmine Shiner, which resulted in a lower annual probability of catastrophe for Pugnose Shiner. These results suggest that MVP is very sensitive to even small differences in life history, and that species specific information is always preferable.

Our analyses show that, in the absence of recovery efforts or harm, and assuming a 10% probability of catastrophe per generation, a population with an abundance of 20 000 adults has a 95% probability of reaching the recovery target in 12 years, provided there is ample suitable habitat available (Figure 5). Additional harm will delay the recovery of a population, with the severity of the delay being related to the sensitivity of the vital rate being harmed. To reduce recovery times, we recommend recovery actions that increase either the fecundity rate, or the annual survival rate of immature Carmine Shiner; efforts to improve adult survival by a similar proportion are expected to be much less effective.

Model results suggest that a recovered population of Carmine Shiner requires 3 300 ha of suitable habitat. Insufficient habitat increases the extinction risk exponentially, and delays recovery indefinitely. Note that estimates do not account for habitat that is shared by different life stages.

UNCERTAINTIES

We emphasize the need for research on Carmine Shiner in Canada to determine (i) survival rates, especially for young of the year, and (ii) the frequency and extent of catastrophic events.

In lieu of life history data, parts of our analysis assumed that allometric relationships between maximum size and mortality were representative of Canadian Carmine Shiner populations. Ideally, recovery modelling should be based on the life history characteristics of the populations to which they are applied. This is particularly important for survival of YOY, which has a large impact on the population growth rate and consequent allowable harm recommendations, but was also the most uncertain parameter. The uncertainty around this parameter also strongly affected the MVP; small changes in the variance of age-0 survival resulted in proportionally large changes in the MVP.

The range of population growth rates achieved in stochastic simulations was very wide (0.6-13) and included λ =1. Therefore, if the actual 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 Carmine Shiner populations. In lieu of early-life survival estimates, we stress the importance of determining the population growth rate.

The choice of the recovery target is impeded by a lack of information regarding catastrophic events; targets and model predictions vary widely depending on the frequency of catastrophic decline in the population. Research that identifies the magnitude and frequency of catastrophic events will greatly reduce the uncertainty in estimates of minimum viable population size, and thus in recommendations for the recovery of Carmine Shiner in Canada.

Finally, predictions from this model assume random mating and complete mixing of the population (i.e., all individuals interact and can reproduce with one another). This assumption should be considered when applying MVP targets to populations, and larger targets should be set if the assumption does not hold. A further consideration is that MVP targets suggested above assume an extinction threshold of 1 adult female. If a higher extinction threshold is likely, we suggest that a larger target be set.

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