Fisheries and Oceans Canada Pêches et Océans Canada

Science Sciences

Canadian Science Advisory Secretariat (CSAS)

Research Document 2013/061

Central and Arctic Region

Recovery potential modelling of Rocky Mountain Sculpin (*Cottus sp.*), Eastslope populations, in Alberta

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September 2013

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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Published by:

Fisheries and Oceans Canada
Canadian Science Advisory Secretariat
200 Kent Street
Ottawa ON K1A 0E6

http://www.dfo-mpo.gc.ca/csas-sccs/
csas-sccs@dfo-mpo.gc.ca

ISSN 1919-5044

Correct citation for this publication:

Young, J.A.M. and Koops, M.A. 2013. Recovery potential modelling of Rocky Mountain Sculpin (*Cottus* sp.), Eastslope populations, in Alberta. DFO Can. Sci. Advis. Sec. Res. Doc. 2013/061. v + 16 p.

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ABSTRACT

The Committee on the Status of Endangered Wildlife in Canada (COSEWIC) had assessed the Rocky Mountain Sculpin (*Cottus sp.*) as Threatened in Canada (COSEWIC 2005). 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 Rocky Mountain Sculpin populations are particularly sensitive to perturbations that affect survival of immature individuals (from hatch to age 2), and to the collective survival of adults (ages 2-8). 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), we propose a population abundance recovery target of at least 1480 adult Rocky Mountain Sculpin, requiring 0.12 ha of suitable habitat. Current vital rate and abundance estimates suggest that the population may be in decline, with an expected time to extinction of ~75 years. Recovery strategies which incorporate improvements in the most sensitive vital rates of the Rocky Mountain Sculpin are most likely to improve the population growth rate; improvements of 10% in survival of all life stages significantly delayed extinction risks, and improvements of 20% had a stabilizing effect on the population.

Modélisation du potentiel de rétablissement du chabot des montagnes Rocheuses (*Cottus* sp.) (populations du versant est) en Alberta

RÉSUMÉ

Le Comité sur la situation des espèces en péril au Canada (COSEPAC) a déterminé que le chabot des montagnes Rocheuses (*Cottus* sp.) est une espèce menacée au Canada (COSEPAC 2005). 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'appuyer l'évaluation du potentiel de rétablissement (EPR). Nos analyses prouvent que la dynamique des populations de chabot des montagnes Rocheuses est particulièrement sensible aux perturbations qui affectent la survie des individus immatures (de l'éclosion à l'âge 2) et la survie collective des adultes (âges 2 à 8). Il faut réduire au minimum les dommages sur ces étapes du cycle de vie 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), nous proposons une cible de rétablissement de l'abondance d'au moins 1 480 chabots des montagnes Rocheuses adultes, ce qui nécessite 0,12 ha d'habitat convenable. Selon les estimations actuelles de l'abondance et de l'indice vital, la population serait peut-être en déclin et devrait disparaître d'ici environ 75 ans. Les programmes de rétablissement qui prévoient des améliorations des indices vitaux les plus sensibles des chabots des montagnes Rocheuses provoqueront une augmentation presque certaine du taux de croissance des populations; des améliorations du taux de survie de 10 % pour tous les stades biologiques ont permis de retarder considérablement le risque d'extinction; l'amélioration du taux de survie des juvéniles et des adultes de 20 % a eu pour effet de stabiliser la population.

INTRODUCTION

The Rocky Mountain Sculpin (*Cottus* sp.), recently designated as a new species, is found (in Canada) only in the Milk and St. Mary river systems in Alberta, and the Flathead River in British Columbia. Rocky Mountain Sculpin is typically found in cool, clear streams. The greatest threat to the Alberta populations is habitat alteration or loss due to the reduction of flowing waters. The Committee on the Status of Endangered Wildlife in Canada (COSEWIC) first assessed the Rocky Mountain Sculpin as Threatened in 2005 (COSEWIC 2005).

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. 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 Rocky Mountain Sculpin. 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 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 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 a typical population.

SOURCES

Where possible, life history estimates for the Rocky Mountain Sculpin were based on sampling data from Canadian populations in the St. Mary and Milk rivers, Alberta, between 2006 and 2009 (DFO unpubl. data).

MATRIX MODEL

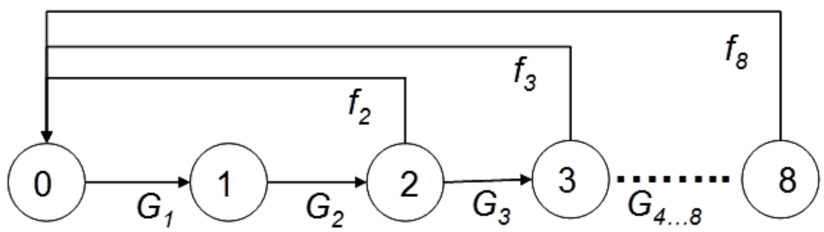
Using a matrix approach, the life cycle of Rocky Mountain Sculpin was represented with annual projection intervals and by a post-breeding age-structured projection matrix (Caswell 2001; Figure 1). Individuals were assumed to first mature at age 2, and reach a maximum age of 8 years (see following section). The model therefore represents nine age classes: young-of-the-year (YOY or age 0), juveniles (age 1) and 7 adult age classes.

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) $$F_j = G_j f_j$$

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 spawning periodicity (assumed to be 1).

a)



b) $$M = \begin{pmatrix} 0 & F_2 & F_3 & ..... & F_8 & 0 \\ G_1 & 0 & .... & & & \\ 0 & G_2 & 0 & & & \\ & 0 & G_3 & & & \\ & & ... & ... & & \\ 0 & & & 0 & G_8 & 0 \end{pmatrix}$$

c) $$M = \begin{pmatrix} 0 & 12 & 27 & 47 & 72 & 100 & 130 & 160 & 0 \\ 0.014 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0.39 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0.46 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0.52 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0.55 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0.58 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0.60 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0.62 & 0 \end{pmatrix}$$

Figure 1. Generalized life cycle (a), corresponding the age-structured projection matrix (b), and mean values of matrix elements (c) used to model the population dynamics of Rocky Mountain Sculpin. F_i represents fecundities, and G_i the survival probabilities from age j-1 to age j. Note that fertility is positive for the age 1 class (F_2) since individuals recorded as age 1 in census t will mature upon their second birthday (if they survive) and produce offspring that will be counted at census t+1 (Caswell 2001).

Parameter Estimates

To estimate parameters for the matrix model (summarized in Table 1) we first established a mean size for each age class. Rocky Mountain Sculpin collected from both populations were aged using otoliths (N=134). Age-0 fish averaged 32 mm in length. Since fish were collected in late summer and had grown considerably since hatch, the ages were adjusted based on sampling date and assuming a hatch date of May 1st. A von Bertalanffy growth curve was fitted to the adjusted data to relate size and age using the formula: $L_t = L_\infty(1-e^{-k(t-t_0)})$, where L_t is size at time t, t_0 is the hypothetical age at which the fish would have had length *0*, L_∞ is the asymptotic size, and k is a growth parameter. The estimated parameter values were: L_∞ = 131.8 k =0.145 and t_0 = -1.69. The lengths-at-age predicted by this curve were used for all subsequent calculations, except for size-at-hatch, which was overestimated by the curve and assumed instead to be 5 mm (Scott and Crossman 1973). Uncertainty in mean size-at-age was incorporated by calculating bootstrapped confidence intervals on the fitted growth curve (Baty and Delignette-Muller 2009).

Fecundity was described as a function of fork length (FL) by performing log-linear regression ($\ln(f)=3.52\cdot\ln(\mathrm{FL}) - 9.94$; R^2=0.92, N=14). Mean fecundity for each age-class was calculated using mean size-at-age, and multiplied by the sex ratio (0.5). Uncertainty in fecundity incorporated both uncertainty in size-at-age (using confidence intervals on the von Bertalanffy growth curve), and uncertainty in fecundity-at-size (using confidence intervals from the log-linear fecundity regression). The combined uncertainty bounds were assumed to contain all possible fecundity values within 4 standard deviations of the mean (i.e., variance was calculated assuming that the range of uncertainty was a 95% confidence interval).

Size-dependent mortality was estimated by combining a size-dependent mortality model (Lorenzen 2000) with von Bertalanffy growth parameters and a catch curve analysis of age-frequency data (Hilborn and Walters 1992). The ages of un-aged fish were calculated based on their lengths, using the fitted von Bertalanffy growth curve above. 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 Bertalanffy 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:

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

k and L_∞ are parameters of the von Bertalanffy growth equation as evaluated above. The parameter m_0 can be estimated by performing a modified catch curve analysis where logged frequencies are binned based on equation (4), so that m_0 can be described by the slope of the catch curve regression (β), scaled by the von Bertalanffy parameters (equation 5).

(4) $$\ln L_t + kt$$

(5) $$m_0 = -kL_\infty\beta$$

Weighted catch curve regressions were performed to decrease the bias from rarer, older fish (Maceina and Bettoli 1998, Freund and Littell 1991). Survival from stage j to stage j+1 was calculated using equation (3). Variance for each survival rate was approximated by first translating the standard error of β from the catch curve regression into a standard error for m_0, then applying the delta method (Oehlert 1992) to equation (3) to estimate the variance of the transformed parameter. This process was repeated separately for each year of sampling (2006-2009) and for each population (St. Mary and Milk rivers). Sample sizes from the Milk River were sufficient for catch curve analysis only in 2006. Therefore, the averaged means and variances from the St. Mary population were used for model simulations, and Milk River parameter estimates are reported. Survival and fecundity rates for stochastic simulations were drawn from lognormal distributions with mean and variances as described above. Generation time was calculated from the age-specific survival and fecundity estimates as per Caswell (2001), and yielded a generation time of 4.1 years for the Rocky Mountain Sculpin. Sampled Rocky Mountain Sculpin were observed to be mature at 2 years, and live a maximum of 8 years.

*Table 1. Mean and standard deviation of vital rates for Rocky Mountain Sculpin and associated annual deterministic growth rate (λ). G_i = annual survival probability from age j-1 to age j. Maximum (St. Mary River, 2006) and minimum (Milk River, 2006) annual survival also shown. f = annual number of female offspring (multiply by 2 for total). sd = standard deviation. *Used for calculating minimum viable population (MVP).*

		Survival (G_j)				Fecundity (f)	
age	Length(mm)	mean	sd	minimum	maximum	mean	sd
1	42	0.010	0.008	0.0002	0.028	0	NA
2	54	0.39	0.049	0.23	0.54	32	1.9
3	65	0.46	0.047	0.31	0.61	58	2.4
4	74	0.52	0.045	0.36	0.65	92	4.5
5	82	0.55	0.043	0.40	0.68	130	7.9
6	88	0.58	0.041	0.44	0.70	172	12.9
7	94	0.60	0.040	0.46	0.72	216	19.7
8	99	0.62	0.039	0.48	0.73	259	28.4
1 (adjusted)*	NA	0.017	NA	NA	NA	NA	NA
growth rate (λ)		0.86		0.32	1.32		

ALLOWABLE HARM AND REQUIRED RECOVERY EFFORTS

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

(6a) $$\tau_v < \left(\frac{1}{\varepsilon_v}\right)\left(\frac{1-\lambda}{\lambda}\right) \quad \text{and} \quad \tau_{v,\max} = \left(\frac{1}{\varepsilon_v}\right)\left(\frac{1-\lambda}{\lambda}\right)$$

where ε_v is the elasticity of vital rate v, and λ is population growth rate in the absence of additional harm (see below). Similarly, for populations in decline, the minimum recovery efforts (minimum increase in vital rates necessary to stabilize or stimulate population growth) were estimated as

(6b) $$\psi_v < \left(\frac{1}{\varepsilon_v}\right)\left(\frac{\lambda_{target} - \lambda}{\lambda}\right) \quad \text{and} \quad \psi_{v,\min} = \left(\frac{1}{\varepsilon_v}\right)\left(\frac{\lambda_{target} - \lambda}{\lambda}\right).$$

Elasticities 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:

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

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 (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_v of G_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 the mean, maximum (upper 95% CI), and minimum (lower 95% CI) values that were based on the mean λ as calculated in these stochastic simulations.

Because human activities often impact multiple vital rates simultaneously, we also used elasticities to approximate allowable simultaneous harm or recovery efforts to survival or fertility rates. Cumulative harm or recovery efforts were estimated, respectively, as

(8) $$\mathrm{T} \approx \left(\frac{1-\lambda}{\lambda}\right)\Big/\sum_{v=1}^{n}\varepsilon_v \quad \text{or} \quad \Psi \approx \left(\frac{\lambda_{target} - \lambda}{\lambda}\right)\Big/\sum_{v=1}^{n}\varepsilon_v$$

where n is the number of vital rates that are simultaneously harmed, ε_v is the elasticity of vital rate *v*, and T (ψ) is allowable harm (recovery effort) 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 Rocky Mountain Sculpin. 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 24 generations).

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) 0.10, or 0.15 per generation (0.025 or 0.038 annually). We used these simulations to determine the number of adults necessary for the desired probability of persistence (see Results) over 100 years. For these simulations, mean age-0 survival was adjusted, with constant variance, so that the population growth rate was at equilibrium (geometric mean 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 estimated the minimum area for population viability (MAPV) as a first order quantification of the amount of habitat required to support a viable population. We calculated MAPV for each age-class in the population as

$$(9) \qquad MAPV_j = MVP_j \cdot API_j.$$

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 ($\mathbf{M}\, w = \lambda \cdot w$) (De Kroon *et al*. 1986). The recovery target, MVP, is expressed in terms of adult numbers only (ages 2-8). API_j is the age-specific area required per individual (the inverse of density). We estimate API based on an allometry for river environments from Randall *et al*. (1995) for freshwater fishes:

$$(10) \qquad API = e^{-13.28} \cdot TL^{2.904}$$

where TL is the average total length in mm.

The API for each age class was estimated from equation (10) using the geometric mean of lengths at the endpoints of each class as predicted by the fitted von Bertalanffy growth curve. An MAPV for each stage was estimated from equation (9), and the MAPV for the entire population was estimated by summing across all age classes.

RECOVERY STRATEGIES AND TIMES

The effects of three hypothetical recovery strategies are compared. Since it is likely not possible to direct efforts toward individual vital rates, we focused on positive changes in annual survival probability in early life (i.e., $s_{1,2}$), in adults ($s_{3..8}$), or in fertility ($f_{2..8}$) 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.

Recovery was simulated in a similar manner to the recovery targets. Projection matrices were drawn, using the same vital rates as for allowable harm calculations, to determine status quo dynamics (i.e., in the absence of harm or recovery). 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 i) a cumulative distribution function for the time to reach the recovery target, for growing populations, or ii) a median time to extinction for declining populations. Results were averaged over 5 runs. The probability of recovery (or extinction) at time t was equal to the proportion of realizations of population size that met or exceeded the recovery target (or fell below the extinction threshold) at time t.

RESULTS

ALLOWABLE HARM AND MINIMUM RECOVERY EFFORTS

Based on the mean vital rates of the Rocky Mountain Sculpin as described above, we estimate that populations are, on average, in decline ($\lambda = 0.87$). Growth rates calculated from the four separate years of data ranged from severe decline ($\lambda = 0.31$; St. Mary River 2007) to substantial growth ($\lambda = 1.32$; St. Mary River 2006). The single growth rate calculated for the Milk River (2006) also suggested severe decline ($\lambda = 0.32$). Given the uncertainty around these estimates, the trajectory of Rocky Mountain Sculpin cannot be confirmed as either increasing or decreasing.

It is likely impossible to isolate harm or recovery to individual age classes, but the additive nature of elasticities allows us to consider the collective effects of perturbations on different life stages. When rates affecting juvenile and adult life stages were collected and examined separately, elasticity analysis showed that the population growth rate is most sensitive to perturbations of adult survival ($s_{3..8}$) but also very sensitive to changes in survival of YOY and juveniles (Figure 2, panel 1). Although the means of deterministically and stochastically determined elasticities are nearly identical, elasticities are still sensitive to stochastic variation (Figure 2, panel 2). Comparing correlations among vital rates and elasticities shows that the uncertainty in these elasticities can be largely attributed to uncertainty in the estimate of age-0 survival. Variation in age-0 survival also explains 86% of the variation in the population growth rate. The pattern of elasticities is also sensitive to whether the population is growing or in decline (Figure 2, panel 3). When there is population growth, the population is very sensitive to juvenile survival, and the importance of reproduction decreases with age. If the population is in decline, the importance of survival varies less with age, but the fecundity of older fish is more important than that of younger fish.

The minimum recovery efforts for each vital rate depended on the stochastic element (e.g., mean or upper or lower 95% CI; Table 2). The results of manual perturbations of the vital rates are also presented. Two target growth rates are compared: i) the proportional improvements required to achieve stabilization ($\lambda = 1$), and ii) the improvements required to achieve the inverse of the rate of decline ($\lambda = 1.14$). From a precautionary perspective (i.e., assuming the highest effort of all methods), our results suggest a minimum improvement of 40% to juvenile survival (both ages 0 and 1), 37% to survival of adults, or 20% to survival of all ages. A fecundity rate that is 138% higher than the current estimate would be required to achieve stabilization. When choosing a recovery strategy, the scope for improvement should also be considered. Table 2 presents the absolute maximum scope for improvement (i.e., supposing survival could potentially be 100%, and no bounds for fecundity), and a plausible scope for improvement. The plausible scope compares the mean survival rates with those estimated from the “best” of the four years. Scope for improvement in fecundity assumes that all ages could produce the maximum number of eggs observed in one female (690; COSEWIC 2005). While the target growth rate of 1.14 is possible within the maximum scope, only stabilization is within the plausible scope. If recovery efforts do not meet at least one of these thresholds, the future survival and recovery of individual populations is likely to be compromised.

The minimum recovery efforts required are very sensitive to the assumed population growth rate of 0.87. If new evidence suggests that the growth rate was underestimated, the required efforts could decrease considerably. It is possible, for instance, that the frequency of poor survival was overrepresented in the four years sampled. Three of the estimated growth rates were very low, one was near equilibrium, and only one sample suggested growth. Figure 3 shows how the growth rate changes as a function of the frequency of poor years. Here, a poor year was assumed to be the mean of the three poor years (λ = 0.39), and a good year was the mean of the years of growth and equilibrium (λ = 1.14). Also shown is the improvement to survival (s_n) that would be required to achieve stability. As the frequency of poor years decreases, the growth rate increases quickly, and the required recovery effort decreases. In this case, the population would be stable if years of low survival occurred only once every 8 years.

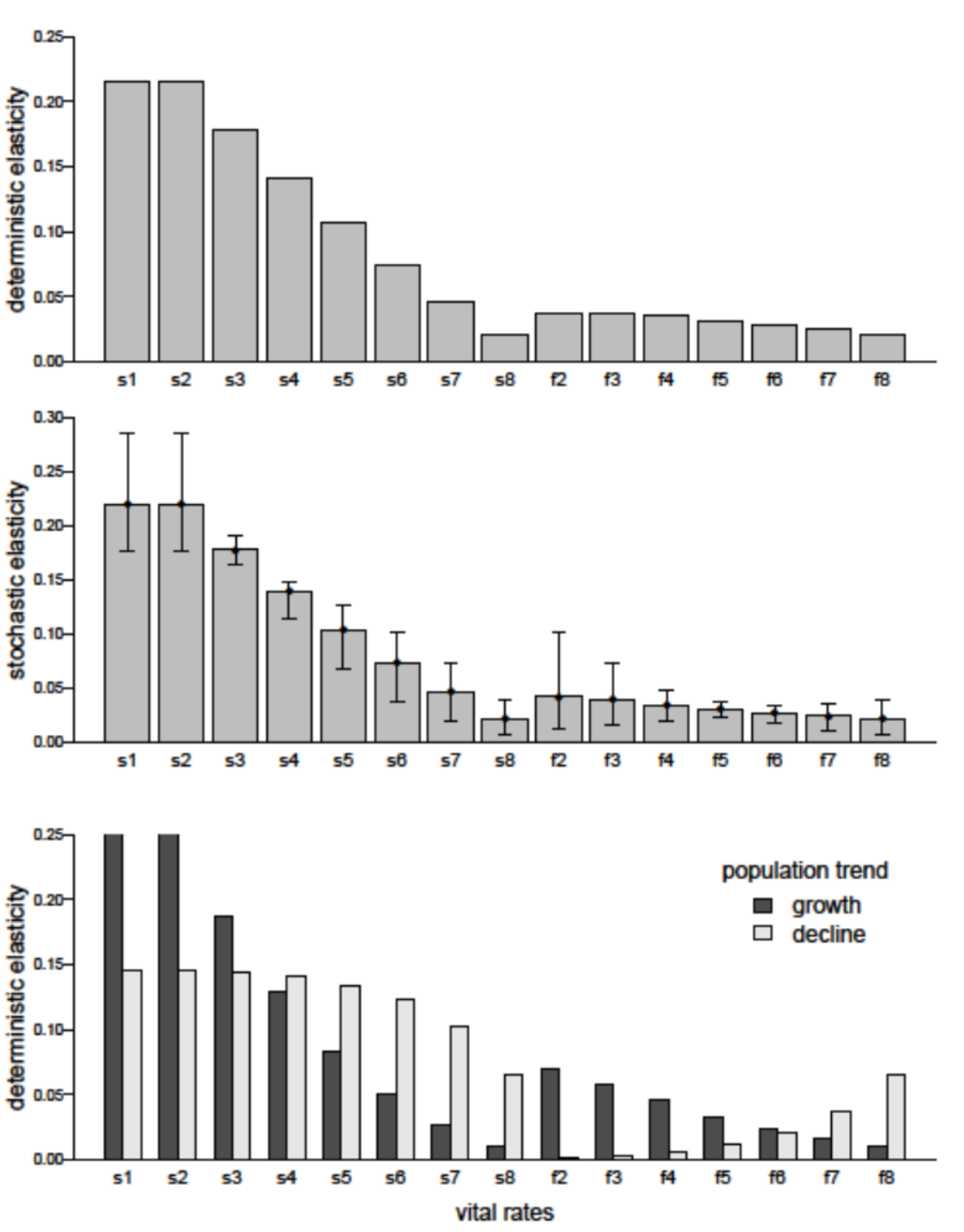


Figure 2. Results of the deterministic (panel 1) and stochastic (panel 2) perturbation analysis showing elasticities (ε_v) of the vital rates: annual survival probability of age j-1 to age j (s_j) and fertility (f). Stochastic results include associated bootstrapped 95% confidence interval. Panel 3: Deterministic elasticity of a growing (St. Mary River, 2006) and a declining (Milk River, 2006) population.

Table 2. *Summary of minimum recovery effort ($\psi_{v,min}$) estimates for combined vital rates of Rocky Mountain Sculpin, based on a stochastic perturbation analysis and a population growth rate (λ) of 0.87, and a target growth rate (λ_{target}) of 1 (stabilize population) or 1.14 (stimulate growth). s_j = juvenile survival (age 0 to maturity); s_a=adult survival (maturity to age 8); s_n=survival of all ages; f=fecundity, All = all survival and fecundity rates. Manual = Recovery effort calculated using manual perturbations. Max. scope = maximum proportion improvement (100% survival). Plausible scope = proportion improvement to reach survival rates from "best" year (St. Mary River, 2006). Consistent with the precautionary approach, bold values indicate the recommended minimum recovery effort.*

	target =1					target=1.14				
	s_j	s_a	s_n	*f*	All	s_j	s_a	s_n	f	All
Deterministic	0.37	0.28	0.16	0.74	0.12	0.75	0.57	0.32	1.50	0.25
Stochastic	0.34	0.26	0.15	0.67	0.12	0.70	0.55	0.31	1.40	0.25
+ 95% CI	0.26	0.22	0.12	0.40	0.09	0.53	0.45	0.25	0.83	0.19
- 95% CI	**0.42**	**0.37**	**0.20**	**1.38**	**0.17**	**0.88**	**0.77**	**0.41**	**2.87**	**0.36**
Manual	0.39	0.29	0.17	0.92	0.14	0.79	0.60	0.33	2.20	0.26
Max. Scope	1.55	0.62	0.62	NA	0.25	1.55	0.62	0.62	NA	0.25
Plausible scope	0.30	0.20	0.20	0.25	0.20	0.30	0.20	0.20	0.25	0.20

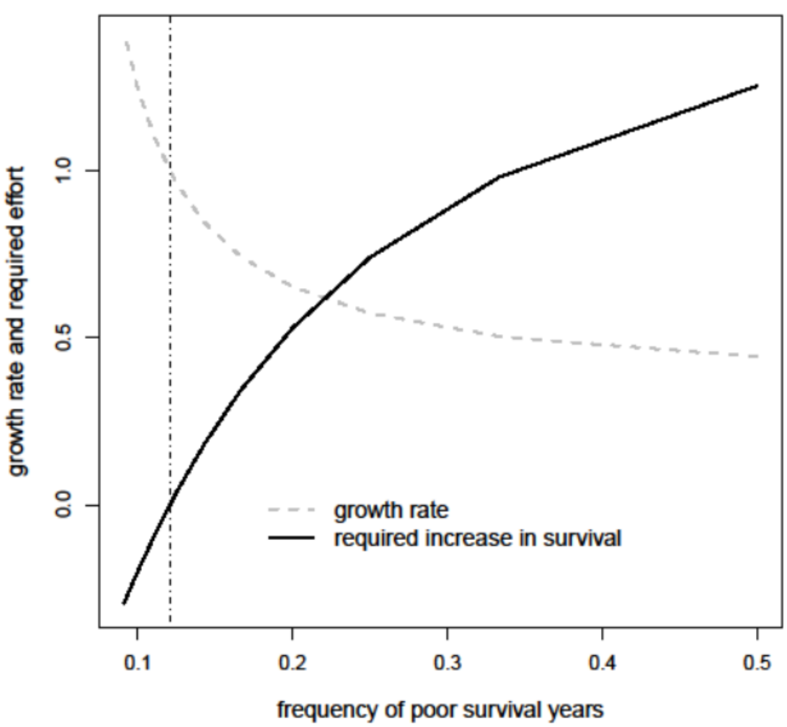


Figure 3. Relationship between the frequency of years experiencing population decline (low survival) and the population growth rate (dashed line), and the proportional increase in survival rates required to achieve stability (λ=1; solid line). Vertical reference line shows the frequency at which the population is at equilibrium, and no recovery efforts are required (frequency = 0.12). If the frequency is less than this value, harm (negative recovery effort) may be allowable.

RECOVERY TARGETS

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

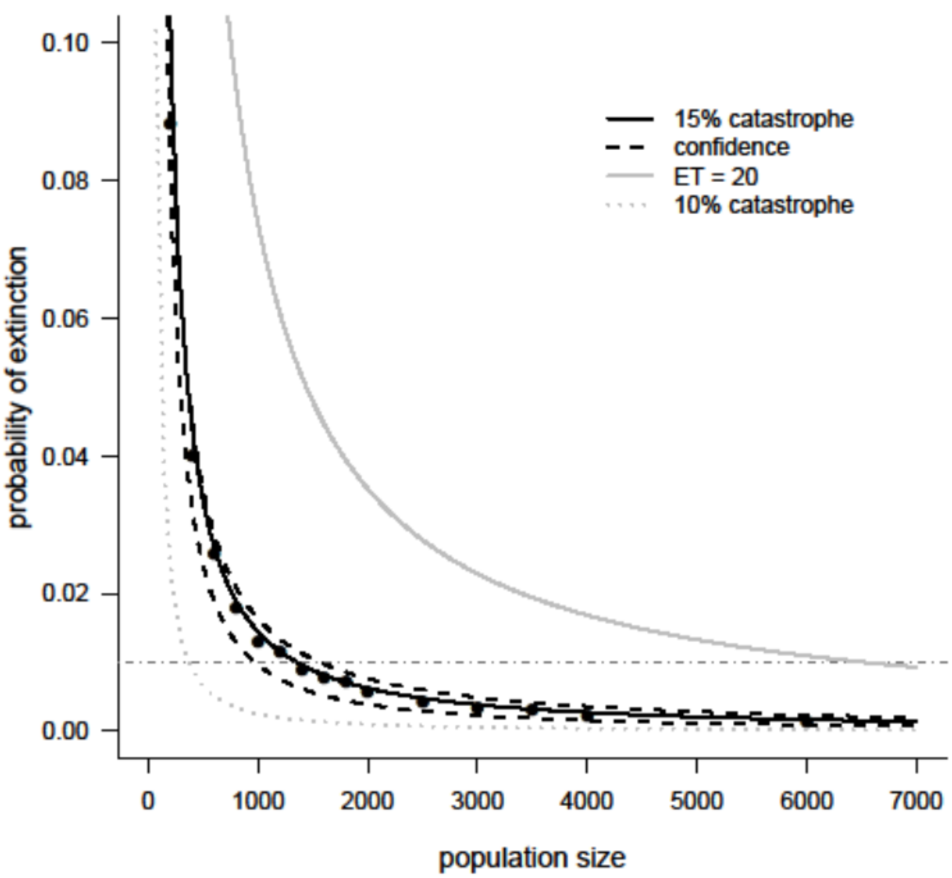


Figure 4. Probability of extinction within 100 years of 10 simulated Rocky Mountain Sculpin populations, at equilibrium, as a function of adult population size. Black curves assume a 15% probability of catastrophic decline (solid = mean, dotted = max and min of 10 runs), and an extinction threshold of 2 adults. Grey curves represent 10% probability of catastrophe (dotted), or 15% probability of catastrophe and an extinction threshold of 20 adults. Dashed horizontal reference line is at 0.01 and intersects curves at the associated MVPs (Table 4).

While choosing a larger recovery target will result in a lower risk of extinction, there are also costs associated with an increased target (increased 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 0.1% probability of extinction, as this is the most stringent criteria in the literature; (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 320 adults aged 2-8 (range: 230 – 400 adults) when the probability of catastrophic decline (50%) was assumed to be 10% per generation (2.5% annually). If catastrophes occurred at 15% per generation (3.8% annually), MVP was 1100 adults (range: 850 – 1480). Given the possible decline of the Rocky Mountain Sculpin populations, all simulations were conducted assuming the highest of these targets (1480). In both scenarios, the probability of extinction for the respective MVPs was approximately 0.01 over 100 years (Figure 3). The upper confidence bound of extinction risk, P(ext.), for the 15% per generation catastrophe scenario can be defined as a function of initial adult population, N, as

(12) $P(ext.) = 32.5 \cdot N^{-1.1}$.

MVP simulations assumed an extinction threshold of 1 adult female (or 2 adults). We observed that assuming a higher, quasi-extinction threshold (i.e., if the population is considered effectively extinct before it declines to 1 female) results in a roughly linear increase in MVP. If the quasi-extinction threshold is defined as 20 adults, and the chance of catastrophe is 15% per generation, mean MVP increases from 1100 to 6260 adults. Thus, if the true extinction threshold is greater than 1 adult female, larger recovery targets should be considered. The relationship between MVP and the extinction threshold (ET; number of adults), for a catastrophe probability of 15% per generation, can be roughly approximated as

(13) MVP = 332·ET - 250.

RECOVERY TIMES

The St. Mary River population of Rocky Mountain Sculpin is currently estimated at 127 500 adults (D. Watkinson, DFO unpubl. data). Under current estimated conditions (i.e. assuming a population growth rate of 0.87), and in the absence of recovery efforts or additional harm, a population of this size is expected to go extinct in approximately 76 years (range: 52-110 years). A population of 1480 (MVP) was predicted to go extinct in 42 years (range: 25-68 years; Figure 5). Improving the survival of juveniles by 20% delayed this extinction by 67 years, and similar improvements to adult survival by 141 years (Table 3). When survival of all ages was improved by 20%, the population began to grow, and the risk of imminent extinction was eliminated. Improvements to fecundity were the least effective recovery strategy.

MINIMUM AREA FOR POPULATION VIABILITY

The stable stage distribution for Rocky Mountain Sculpin is 96.91% YOY, 1.67% age 1, and 1.43% adult individuals (ages 2-8). With a target MVP of 1480 adults, under a 0.15 probability of catastrophe per generation, a population of this size was predicted to require 0.12 ha of suitable habitat (Table 4). If an extinction threshold of 20 adults was assumed, the population of 6260 adults was predicted to require 0.52 ha of suitable habitat. These areas assume that each individual requires the areas listed in Table 4, and does not account for any overlapping of individual habitats (sharing) that may occur.

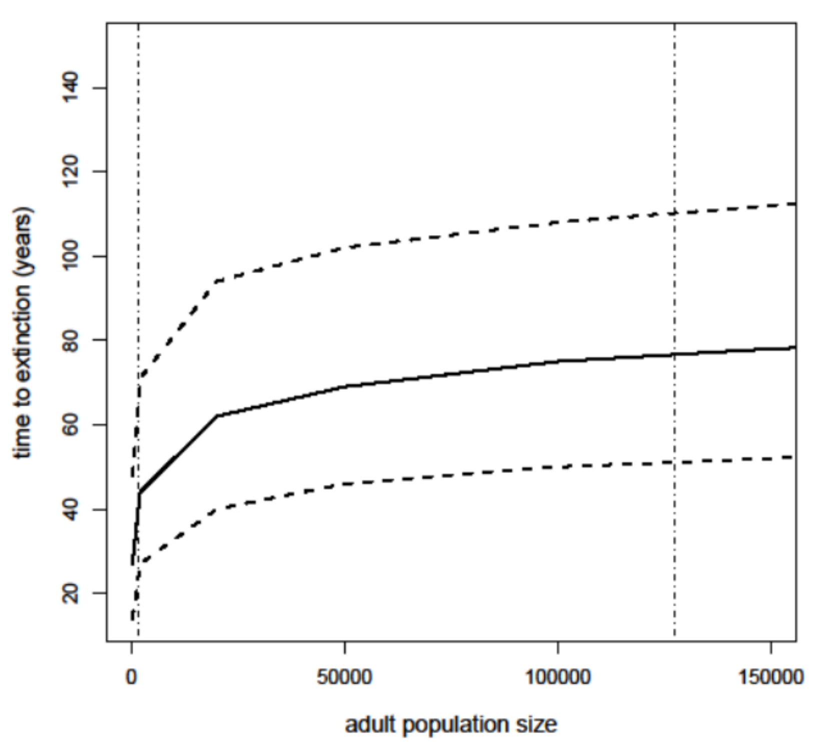


Figure 5. Time to extinction of 10 simulated Rocky Mountain Sculpin populations in decline (λ = 0.87), as a function of adult population size. Median (solid) and 95% bootstrapped confidence interval (dashed). Vertical reference lines represent the Minimum Viable Population size (MVP=1480 adults), and the estimated abundance in St. Mary River (127 500 adults).

Table 3. Effects of recovery efforts on: expected (median) time to extinction, rate of population growth/decline, and the risk of extinction within 100 years of Rocky Mountain Sculpin. Recovery strategies are s_j = juvenile survival (hatch to age 2); s_a = adult survival; s_n = survival of all age; f = fecundity of all adults; All = all survival and fecundity rates. Strategies that result in (near) stabilization or growth are highlighted.

	Strategy									
	s_j		s_a		s_n		*f*		All	
Effort	10%	20%	10%	20%	10%	20%	10%	20%	10%	20%
Time to extinction	62	109	68	183	141	>250	50	59	>250	>250
Growth rate (λ)	0.90	0.93	0.91	0.96	0.95	**1.03**	0.88	0.90	**0.97**	**1.08**
Extinction risk (100 years)	0.94	0.43	0.88	0.14	0.25	**<0.001**	1.00	0.96	**0.06**	**<0.001**

Table 4. Stable stage distribution (percentage of the population in each stage), area per individual (API), number of individuals for each age class to support a minimum viable population (MVP) and the resulting estimate of required habitat for each stage and for the entire population (MAPV) for two extinction thresholds (ET). 15% per generation probability of catastrophe assumed.

			ET = 1		ET = 20	
Age	Distribution (%)	API (m^2)	MVP	MAPV (m^2)	MVP	MAPV (m^2)
0	96.91	0.004	99970	408	424566	1735
1	1.67	0.13	1718	225	7296	957
2-8	1.43	0.24-1.15	1480	601	6260	2542
total				1234		5234

DISCUSSION

Our results show that to avoid jeopardizing the survival and future recovery of Rocky Mountain Sculpin, human-induced harm to the survival of all life stages should be minimal. Current estimates suggest that both St Mary River and Milk River populations may be in decline. Recovery efforts that alleviate current harms or improve current conditions are required. Specifically, stabilization of the population (target growth rate of $\lambda = 1$) requires: 42% improvement in juvenile survival, 37% improvement in adult survival, or 20% improvement in survival of all ages. If there is scope for improvement in fecundity as well, a 17% improvement in all vital rates would achieve the target growth rate. These efforts will be sufficient if population abundance exceeds the Minimum Viable Population (MVP) recovery targets described below. If abundance does not exceed these targets, we recommend a target growth rate that is the inverse of the current estimated rate of decline (target $\lambda = 1.14$). This target would require improvements of 88%, 77%, 41%, or 36% for juvenile survival, adult survival, all survival, or all vital rates, respectively.

It is important to note that estimates of recovery efforts assume that the population growth rate before harm (λ) is 0.87. If research indicates that any of our parameters are underestimated, required recovery efforts will be reduced. For instance, extremely poor survival of Rocky Mountain Sculpin was observed in two out of four years in the St. Mary River. If these poor years occur only once every 8 years, as opposed to the 3 of 5 years observed in sample data, then the Rocky Mountain Sculpin populations could be stable.

In addition to providing estimates of recovery efforts, this work also provides recovery targets based on the concept of MVP. The MVP was estimated at 1480 adults when the probability of a catastrophic (50%) decline (P_k) was 0.15 per generation and an extinction threshold of 2 adults. Increasing the extinction threshold to 20 adults increases the MVP to 6260 adults. 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. We therefore recommend recovery targets based on at least a 15% probability of catastrophe, but suggest that data be collected to confirm the frequency and severity of catastrophic decline experienced by Rocky Mountain Sculpin. Recovery targets based on MVP can be easily misinterpreted (Beissinger and McCullough 2002) as a reference point for exploitation or allowable harm. A recovery target is neither of these things because it pertains exclusively to a minimum abundance level for which the probability of long-term persistence within a recovery framework is high. Therefore, abundance-based recovery targets are particularly applicable to populations that are below this threshold, and are useful for optimizing efforts and resources by selecting those populations that are in the greatest need of recovery. We stress that these MVP targets refer to adult numbers only. If juveniles are being included in abundance estimates, then the MVP should include these age classes as well (see Table 4).

Our analyses show that, in the absence of recovery efforts or additional harm, and assuming a 15% probability of catastrophic decline, a population at the currently estimated abundance of the St. Mary River population will go extinct in 75 years. A population at MVP will go extinct in 42 years. To delay this time, we recommend recovery actions that increase the annual survival rate of Rocky Mountain Sculpin. Improvements in excess of 20% were predicted to reverse the declining trend and significantly reduce the extinction risk. Efforts to improve fecundity by a similar proportion are expected to be much less effective.

Model results suggest that a recovered population of Rocky Mountain Sculpin requires 0.12 ha of suitable habitat if the extinction threshold is 2 adults, or 0.52 ha if the extinction threshold is 20 adults. Insufficient quality or quantity of habitat or other resources increases the extinction risk exponentially, and delays recovery indefinitely (Young and Koops 2010a, 2010b). Note that these estimates do not account for habitat that is shared by different life stages.

UNCERTAINTIES

We emphasize the need for research on Rocky Mountain Sculpin in Canada to determine (i) survival rates during early life, (ii) the frequency and extent of catastrophic events for these populations, and (iii) the frequency of low adult survival years.

In lieu of direct estimates of survival of immature individuals our analysis assumed that a model of size-dependent mortality was representative. Ideally, recovery modelling should be based on the life history characteristics of the populations to which they are applied. Uncertainty in age-0 survival had a relatively large impact on both the population growth rate and elasticity values, and consequently strongly influenced recommendations. The range of population growth rates achieved in stochastic simulations was very wide (0.56-1.77) and included $\lambda=1$. Therefore, if the true mean values of some (or all) vital rates are in the higher ranges of their confidence intervals, then populations could be experiencing a higher growth rate than the estimated mean above, and may not be in decline. More accurate estimates of uncertain vital rates are needed to confirm the status of the Rocky Mountain Sculpin population. In lieu of early-life survival estimates, we stress the importance of determining the true 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 conservation of Rocky Mountain Sculpin 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, and larger targets should be set if the assumption does not hold. A further consideration is that MVP targets suggested above assumed an extinction threshold of 1 adult female. If a higher true extinction threshold is likely, we suggest that a larger target be set using equation (13).

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