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Recovery Potential Modelling of Lake Chubsucker (*Erimyzon sucetta*) in Canada

Modélisation du potentiel de rétablissement du sucet de lac (*Erimyzon sucetta*) au Canada

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ABSTRACT

The Committee on the Status of Endangered Wildlife in Canada (COSEWIC) had assessed the Lake Chubsucker (*Erimyzon sucetta*) as Endangered in Canada (2008). 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 Lake Chubsucker populations are particularly sensitive to perturbations that affect survival of immature individuals (from hatch to age 2), and are more sensitive to survival and fecundity of new spawners than of older adults. 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 2700 adult Lake Chubsucker, requiring 1 km^2 of suitable habitat. In the absence of mitigating efforts, additional harm or habitat limitations, we estimate that a growing Lake Chubsucker population will take approximately 12 years to reach this recovery target if starting from a population of 270 adults. Recovery strategies which incorporate improvements in the most sensitive Lake Chubsucker vital rates will have the greatest effect on population growth.

RÉSUMÉ

Le Comité sur la situation des espèces en péril au Canada (COSEPAC) a évalué le sucet de lac (*Erimyzon sucetta*) comme étant une espèce en voie de disparition au Canada (2008). Dans le présent document, nous présentons la modélisation des populations 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 ont révélé que les populations de sucets de lac sont particulièrement sensibles aux perturbations qui ont des répercussions sur la survie des individus immatures (de l'éclosion à 2 ans). De plus, les populations sont plus sensibles à la survie et à la fécondité des nouveaux géniteurs comparativement à celles des adultes plus âgés. Les dommages à cette partie du cycle de vie doivent être réduits le plus possible afin d'éviter de mettre en péril la survie et le rétablissement futur des populations du Canada. En fonction d'un objectif de durabilité démographique (c.-à-d., une population autonome à long terme), nous proposons un objectif de rétablissement de l'abondance de la population d'au moins 2 700 sucets de lac adultes nécessitant 1 km^2 d'habitat adéquat. En l'absence d'efforts d'atténuation ou dans le cas de dommages supplémentaires ou de limites relatives à l'habitat, nous estimons qu'une population croissante de sucets de lac prendra environ 12 ans pour atteindre l'objectif de rétablissement si l'on commence avec une population de 270 adultes. Les programmes de rétablissement visant une amélioration des indices vitaux des sucets de lac particulièrement vulnérables auront la plus grande incidence sur la croissance de la population.

INTRODUCTION

The Lake Chubsucker (*Erimyzon sucetta*) is a small sucker that has been observed to reach lengths up to 255 mm in the Great Lakes basin where it is found (DFO, unpubl. data). Lake Chubsucker prefers clear, still waters with abundant aquatic plants, and spawn in marshes between April and June. Threats to the Lake Chubsucker include increased turbidity, siltation and wetland drainage. The Lake Chubsucker was first designated as a species of Special Concern in 1994, re-assessed as Threatened in 2001, and assessed as Endangered in 2008.

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 Lake Chubsucker. 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. 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 Lake Chubsucker were based on sampling data from Canadian populations between 2002 and 2010. Locations included: Old Ausable Channel, Long Point Bay, Lyon’s Creek, Big Creek, L Lake, Turkey Point marshes, and St. Clair National Wildlife Area (NWA) (Bouvier and Mandrak 2011). Where necessary, estimates were supplemented by the literature.

MATRIX MODEL

Using a matrix approach, the life cycle of Lake Chubsucker 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 (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* to age *j*+1, as well as the age-specific fertility upon reaching age *j*+1 (f_{j+1}) such that

$$(1) \qquad F_j = G_j f_j$$

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).

Parameter Estimates

To estimate parameters for the matrix model (summarized in Table 1) we first established a mean size for each age class. Lake Chubsucker were collected from Old Ausable Channel after a winterkill in 2010, and aged using otoliths (n = 68). A von Bertalanffy growth curve was fitted to these data. The von Bertalanffy growth curve relates size and age with the formula $L_t = L_\infty(1 - e^{-k(t-t_0)})$, where L_t is size at time *t*, t_0 is the size at hatch, L_∞ is the asymptotic size, and *k* is a growth parameter. A small sample size of older individuals, however, resulted in a large over-estimation of asymptotic length (424 mm), while the largest individual captured in Ontario was only 255 mm. We instead estimated the asymptotic length as 268 mm, using an empirical relationship between maximum and asymptotic lengths (Froese and Binohlan 2000), and the growth curve was re-fitted (Figure 2). This yielded estimates of k = 0.185 and t_0 = -1.07. Size at hatch is traditionally overestimated by the von Bertalanffy growth curve, and was assumed instead to be 6 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 size by performing log-linear regression on fecundity-at-size data from Lake Chubsucker sampled in Nebraska (Winter 1984; Figure 2; $\ln(f)=2.6\cdot\ln(TL) - 4.1$; R^2=0.97). The size-at-age of these samples corresponded with aged data from Ontario individuals. 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 of 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

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

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:

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

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).

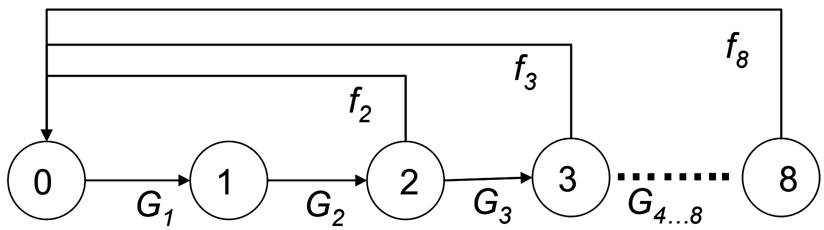
(4) $$\ln L_t + kt$$

(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. 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 3.6 years for the Lake Chubsucker (assuming an age at maturity of 2 years).

Age at maturity of Lake Chubsucker has been reported as 3 years (Coker et al. 2001). This estimate was based on a propagation experiment in Highland Michigan, where a population of Lake Chubsucker was raised in a trout-rearing pond (Cooper 1936). However, the author rather ambiguously stated that “both sexes reach maturity in their third summer of life”, which could be interpreted as either age 2 or age 3. In addition, Winter (1984) found that Lake Chubsucker in Nebraska matured at age 1, and Eberts et al. (1998) found that Lake Chubsucker in Illinois matured between ages 1 and 3. We therefore assumed an age-at-maturity of 2 years and assessed the sensitivity of results to this assumption. The oldest observed Lake Chubsucker was 8 years (Coker et al. 2001), and we use this as maximum age in the model.

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)

$$M = \begin{pmatrix} 0 & 648 & 1405 & 2326 & 3317 & 4312 & 5262 & 6144 & 0 \\ 0.0014 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0.32 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0.41 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0.47 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0.51 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0.54 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0.57 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0.58 & 0 \end{pmatrix}$$

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 Lake Chubsucker. 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).*

Table 1*. Mean and standard deviation of vital rates for Lake Chubsucker. G_i = annual survival probability from age j-1 to age j, f = annual number of female offspring (multiply by 2 for total). *Used for calculating minimum viable population (MVP).*

		Survival (G_j)		Fecundity (*f*)	
age	Length(mm)	mean	sd	mean	sd
1	85	0.0014	0.0010	0	NA
2	116	0.320	0.041	2025	276
3	142	0.412	0.041	3414	513
4	163	0.472	0.039	4925	817
5	181	0.514	0.038	6451	1135
6	196	0.545	0.037	7917	1443
7	208	0.567	0.036	9280	1720
8	218	0.584	0.035	10516	1971
1 (adjusted)*	NA	0.0005	0.0010	NA	NA

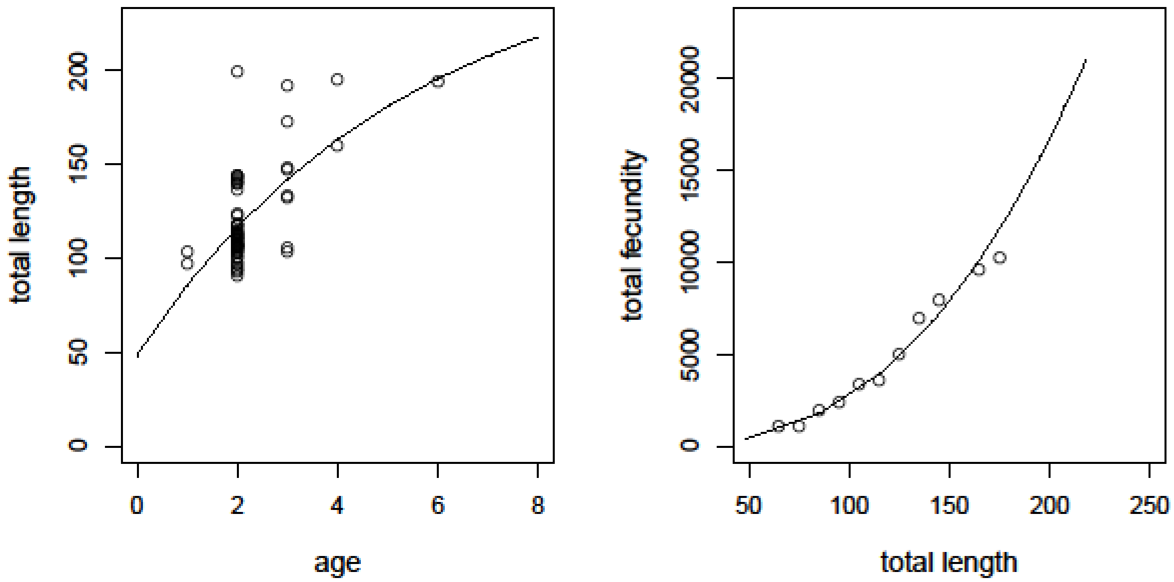


Figure 2: *Left: Von Bertalanffy growth curve, fitted to size-at-age data of Lake Chubsucker sampled from Old Ausable Channel. Right: size-specific fecundity (total number of eggs) of Lake Chubsucker in Nebraska (Winter 1984), and fitted exponential curve, used to estimate fecundity of Ontario Lake Chubsucker.*

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 (τ_v) and maximum allowable harm ($\tau_{v,\ max}$) were estimated analytically as:

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

where ε_v is the elasticity of vital rate *v*, and Λ is population growth rate in the absence of additional harm (see below). Elasticities are a measure of the sensitivity of population growth rate to perturbations in vital rate *v*, and are given by the 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 mean, maximum (upper 95% CI), and minimum (lower 95% CI) values that were based on a mean Λ of 1.4.

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

$$\Psi \approx \left(\frac{1-\Lambda}{\Lambda}\right) \Big/ \sum_{v=1}^{n} \varepsilon_v \qquad (8)$$

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

RECOVERY TARGETS

We used demographic sustainability as a criterion to set recovery targets for Lake Chubsucker. 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 28 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) 0.10, 0.15, or 0.44 per generation. The highest rate of catastrophe was simulated to explore the possibility of frequent winterkill scenarios. Winterkills are known to have occurred in Old Ausable Channel in 2003 and in 2010, which gives an annual frequency of 0.15, or a generational frequency of 0.44. 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:

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

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 lake environments from Randall *et al*. (1995) for freshwater fishes:

$$(10) \quad API = e^{-10.37} \cdot TL^{2.58}$$

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. Size of emergent fry was assumed to be 6mm (Scott and Crossman 1973), and all remaining sizes were as predicted by the fitted von Bertalanffy growth curve (Table 1). 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.

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_j) exceeds the total required habitat (a_j) 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_j) is multiplied by

$$(11) \quad h_j = \begin{cases} A_j / a_j & if\ A_j < a_j \\ 1 & if\ A_j \geq a_j \end{cases}.$$

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

RECOVERY STRATEGIES AND TIMES

We used recovery targets to determine recovery timeframes of individual populations under three hypothetical recovery strategies. 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.

The currently available information on population densities of Lake Chubsucker have a very large margin of error, and did not allow for an accurate estimate of initial population size. For stochastic simulations we assumed an initial size of 10% of MVP, and results should therefore be considered comparative. 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 1.4 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 mean vital rates of the Lake Chubsucker as described above, we estimate the population growth rate of this species to be $\lambda = 1.35$. When stochastic variation was incorporated, the geometric mean population growth rate was $\lambda = 1.4$. Elasticity analysis showed that the growth rate is most sensitive to perturbations of early life survival ($s_{1,2}$, Figure 3). In addition, the population is more sensitive to changes in survival and fecundity of newly mature adults, while changes in older adult rates are less important. The means of deterministically and stochastically determined elasticities are nearly identical, but certain elasticities are very sensitive to stochastic variation; the importance of survival of juveniles and fecundity of newly mature adults can vary widely with environmental changes (see error bars in Figure 3). 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 almost 90% of the variation in the population growth rate.

Estimates of the maximum allowable harm to 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 33% to juvenile survival (simultaneous harm to ages 0 and 1), 54% to adult survival (ages 2-8) or 49% to fecundity of all ages. If human activities are such that harm exceeds just one of these thresholds, the future survival and recovery of individual populations is likely to be compromised; simulations suggest that recovery time can be severely delayed by levels of harm *below* the maximum allowable harm suggested in Table 2 (Figure 6).

If Lake Chubsucker do not mature until age 3, the elasticity patterns were similar to results with maturity at age 2, but the estimated population growth rate was lower ($\lambda = 1.2$). Consequently, allowable harms under this scenario should also be smaller; 15%, 32% and 33% reductions in juvenile survival, adult survival and fecundity, respectively.

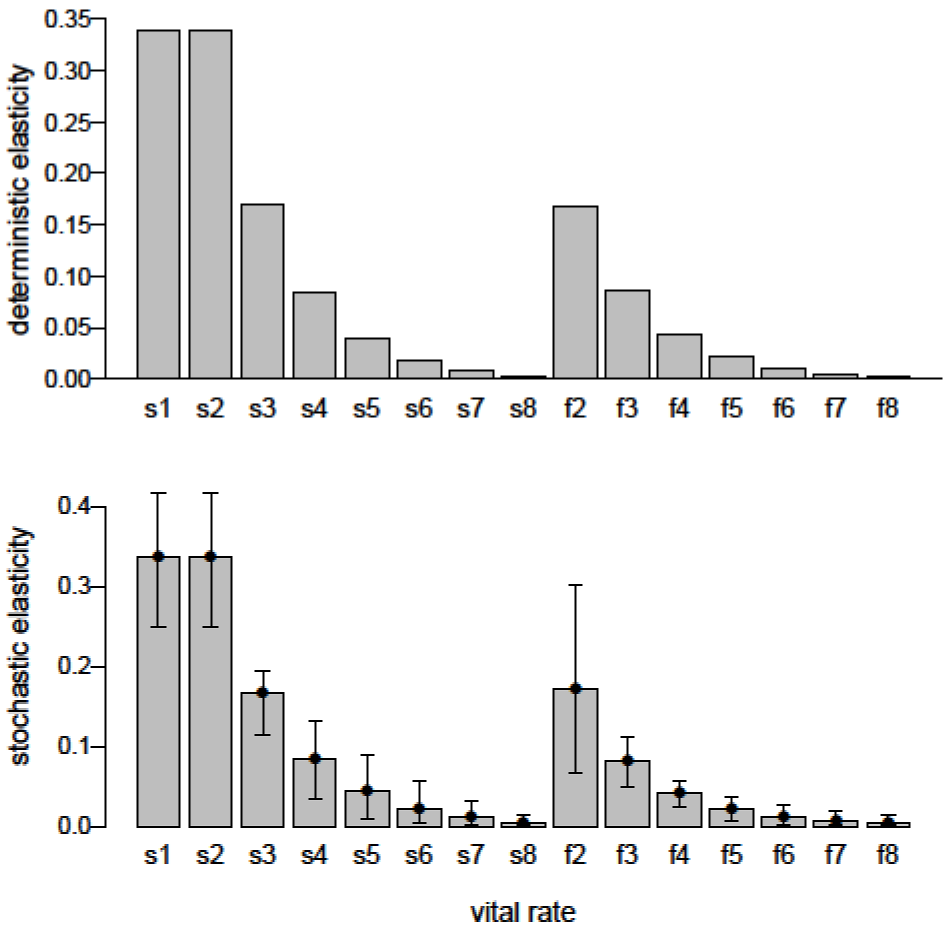


Figure 3. *Results of the deterministic and stochastic perturbation analysis showing elasticities (ε_v) of the vital rates: annual survival probability of age j-1 to age j (s_j) and fertility (f). Stochastic results include associated bootstrapped 95% confidence interval.*

Table 2. *Summary of maximum allowable harm ($\tau_{v,max}$) estimates for combined vital rates of Lake Chubsucker, based on a stochastic perturbation analysis and a population growth rate (Λ) of 1.4. Juvenile survival includes ages 0 and 1. Adult survival and fecundity includes mature adults aged 2-8. Consistent with the precautionary approach, bold values indicate the maximum allowable harm recommended for management decisions.*

Stochastic element	Maturity: 2 years			Maturity: 3 years		
	Juvenile Survival	Adult Survival	Fecundity	Juvenile Survival	Adult Survival	Fecundity
Deterministic mean	-0.38	-0.80	-0.77	-0.17	-0.43	-0.51
Stochastic mean	-0.41	-0.86	-0.83	-0.18	-0.45	-0.54
+ 95% CI	**-0.33**	**-0.54**	**-0.49**	**-0.15**	**-0.32**	**-0.33**
- 95% CI	-0.56	-1.75	-1.94	-0.21	-0.76	-1.02

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.

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 800 adults aged 2-8 (range: 600 – 1000 adults) when the probability of catastrophic decline (50%) was assumed to be 10% per generation. If catastrophes occurred at 15% per generation (~4% annually), MVP was 2730 adults (range: 1936 – 3764). In both scenarios, the probability of extinction for the respective MVPs were approximately 0.01 over 100 years (Figure 4). Extinction risk, P(ext.), for the 15% per generation catastrophe scenario can be defined as a function of initial population, N adults, as:

(12) $$P(ext.) = 41 \cdot N^{-1.047}$$

If a given Lake Chubsucker population experiences significant winterkill more frequently than 4% annually, the MVP will be much higher. The frequent winterkill scenario (15% annually or 44% per generation) resulted in an MVP of over 10 million adults. Additionally, MVP simulations assumed an extinction threshold of 2 adults (or 1 female). We observed that assuming a higher, quasi-extinction threshold (i.e., if the population is considered effectively extinct before it declines to 2 adults) results in a linear increase in MVP. If the quasi-extinction threshold is defined as 20 adults, and the chance of catastrophe is 15% per generation, MVP increases from 2730 to ~16800 adults. Thus, if the true extinction threshold is greater than 2 adults, larger recovery targets should be considered. The relationship between MVP and extinction threshold (ET), for a catastrophe probability of 15% per generation, can be approximated as

(13) $$MVP = 911 \cdot ET - 574$$

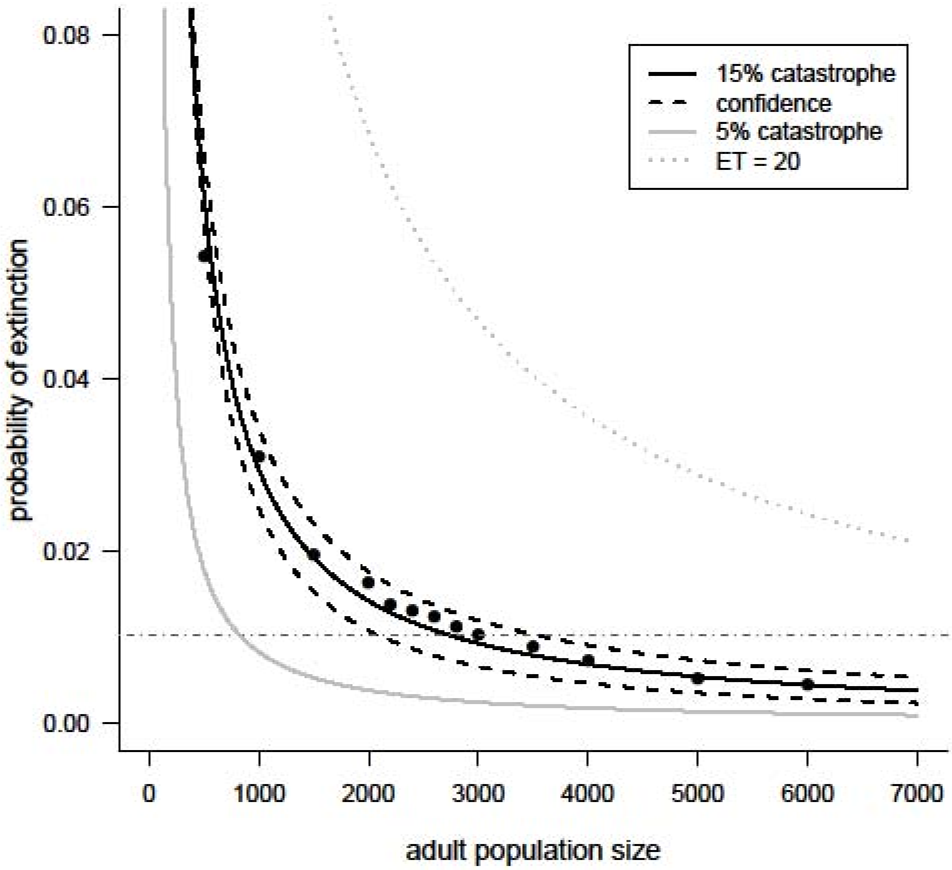


Figure 4. *Probability of extinction within 100 years of 10 simulated Lake Chubsucker populations, at equilibrium, as a function of adult population size. Black curves assume a 15% probability of catastrophic decline (solid = mean, dotted = max and min of 10 runs), and an extinction threshold of 2 adults. Grey curves represent 10% probability of catastrophe 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 3)*

RECOVERY TIMES

Under current estimated conditions (i.e. assuming a population growth rate of 1.4), and in the absence of recovery efforts or additional harm, a Lake Chubsucker population was predicted to increase from ~270 adults to the MVP target of 2730 adults in approximately 12 years (assuming a 15% 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 ($s_{1,2}$). Conversely, the time to recovery increased exponentially as harm was added to vital rates (Figure 6).

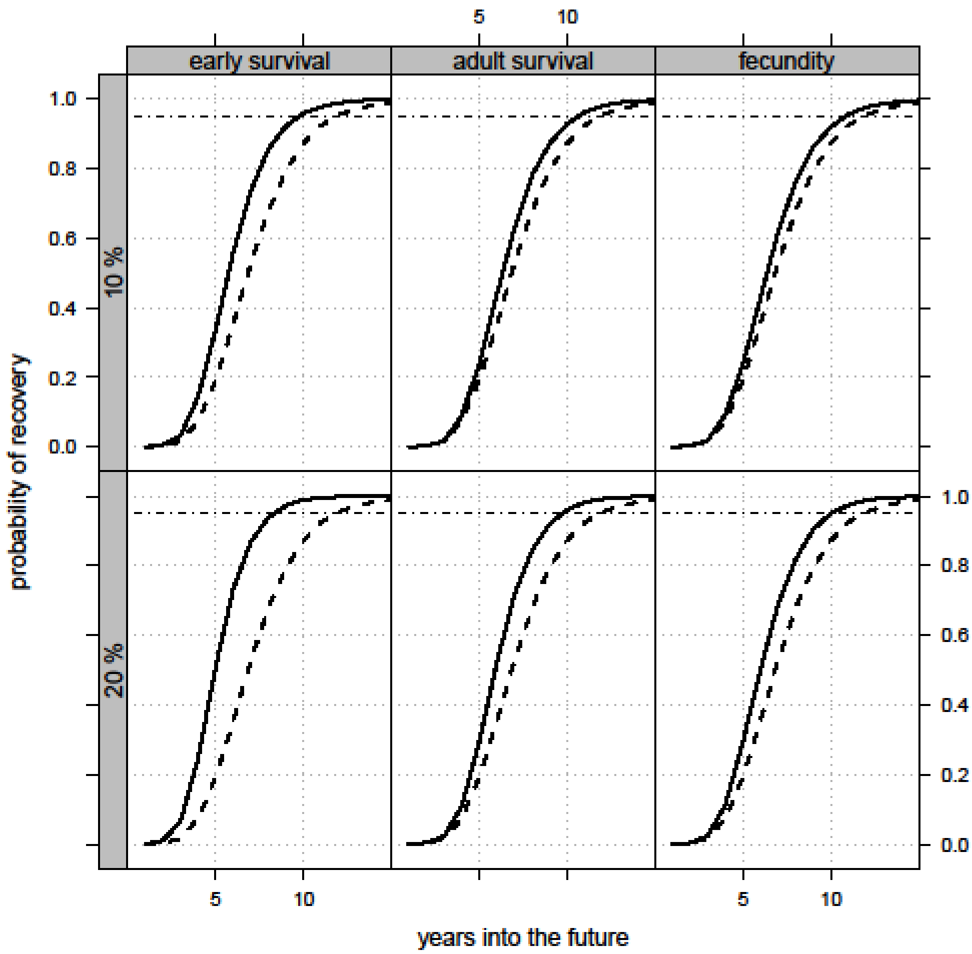


Figure 5. *The probability of recovery of 10 simulated Lake Chubsucker populations under 3 hypothetical recovery strategies and 2 degrees of improvement, based on an initial adult population size that was 10% of the recovery target (273 adults). Dashed lines show recovery under status quo conditions, assuming no harm, a population growth rate of 1.4, and a probability of catastrophe of 15% per generation. Solid lines represent improvement of 10% or 20%, to early survival ($s_{1,2}$), adult survival ($s_{3..8}$), or fecundity ($f_{2..8}$).*

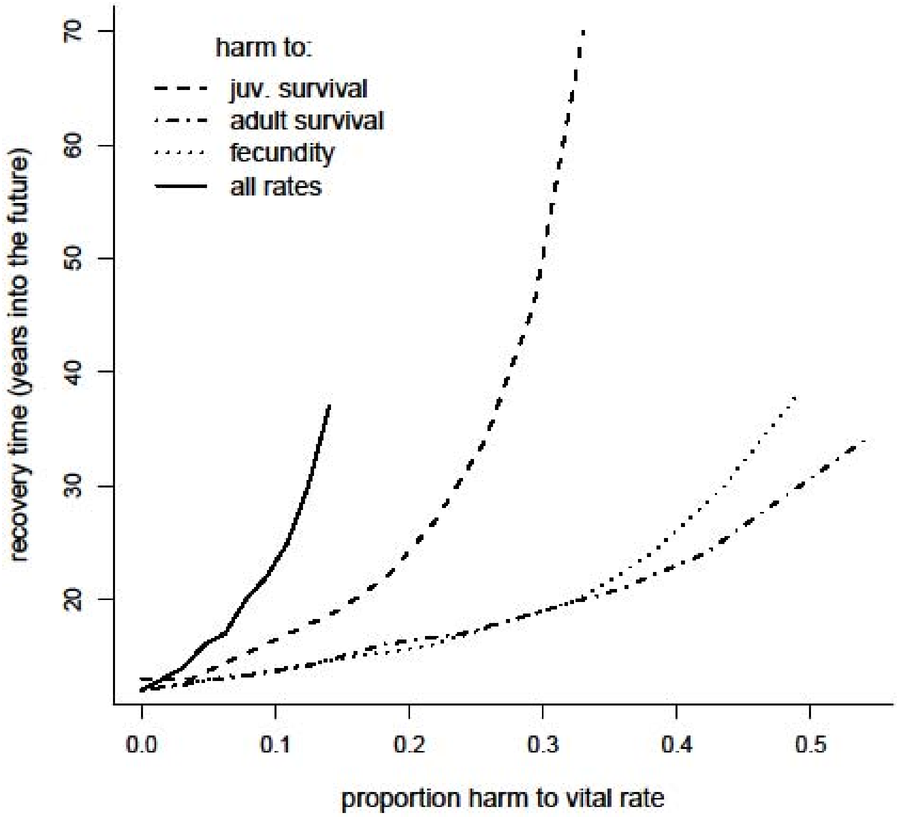


Figure 6. *Predicted change in the time to 95% chance of recovery of a Lake Chubsucker population as a function of increased harm (by proportion of vital rate) to: fecundity (f_n), early survival ($s_{1,2}$), adult survival ($s_{2..8}$), or all rates. Zero harm indicates status quo conditions. 15% per generation probability of catastrophe assumed.*

MINIMUM AREA FOR POPULATION VIABILITY

The stable stage distribution for Lake Chubsucker is 99.92% YOY, 0.05% age 1, and 0.03% adult individuals (ages 2-8). With a target MVP of 2730 adults, under a 0.15 probability of catastrophe per generation, a population of this size was predicted to require 1 km^2 of suitable habitat (Table 3). This area assumes that each individual requires the areas listed in Table 3, and 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 (2730 adults), experiencing 15% chance of catastrophe per generation, and having available 1 km^2 of suitable habitat (MAVP), had a 98% probability of persistence over 100 years. This was only very slightly lower than the 99% 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).

Habitat restrictions also reduced the ability of the 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 15000 simulations) of population size over time assuming 1 km^2 of available 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. At MAPV, the median population abundance over all simulations was 3900 adults (~40% larger than MVP; Figure 8), but there was approximately 22% chance of the population abundance being below MVP at any given time (Figure 9). Decreasing habitat caused the probability of a population being "recovered" to decrease exponentially, but increasing the available habitat by 50% reduced the probability of being below MVP to < 5% (Figure 9).

Table 3. *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). 15% per generation probability of catastrophe assumed.*

			ET = 2		ET = 50	
Age	Distribution (%)	API (m^2)	MVP	MAPV (km^2)	MVP	MAPV (km^2)
0	99.92	0.1	9.08×10^6	0.94	150×10^6	15.49
1	0.05	4.7	4556	0.02	75,047	0.35
2-8	0.03	8.5-45.9	2730	0.04	44,976	0.60
				1.00		16.44

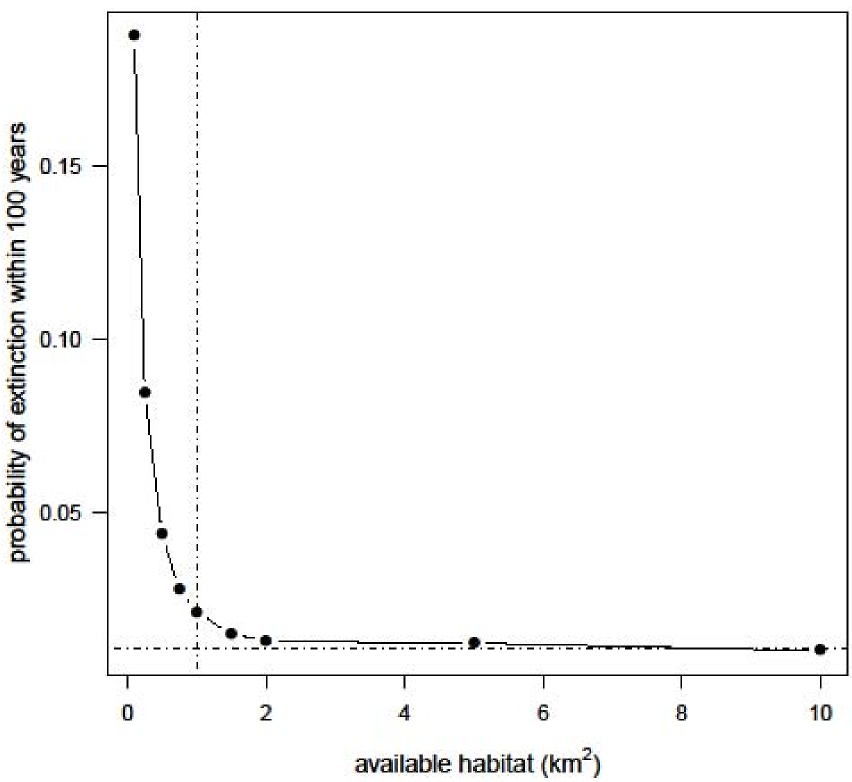


Figure 7. *Probability of extinction within 100 years of 10 simulated Lake Chubsucker populations at minimum viable population (MVP) size, and experiencing habitat based density dependence, as a function of available habitat area. Simulations assume a 15% chance of catastrophe. Dashed reference lines show Minimum Area for Population Viability (MAPV, vertical) and the probability of extinction in the absence of habitat restrictions (0.011, horizontal).*

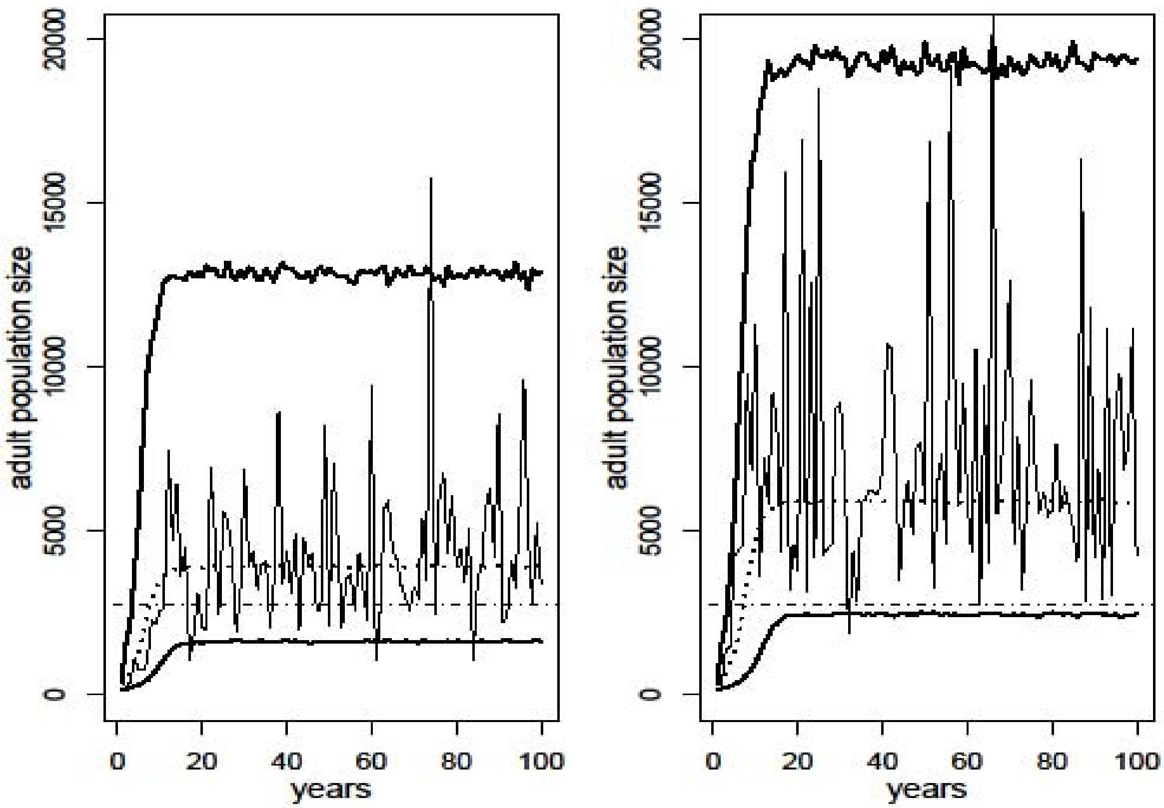


***Figure 8**: Adult population size over time of Lake Chubsucker populations experiencing density dependence, and 15% per generation catastrophic decline. An example population (narrow solid line), and mean (dotted line) and 95% confidence interval (solid thick lines) of 15 000 simulated populations are shown. Horizontal reference line is at the minimum viable population size (MVP). Simulation assumed that habitat area was at the Minimum Area for Population Viability (MAPV) (left panel), or at 1.5 times MAPV (right panel).*

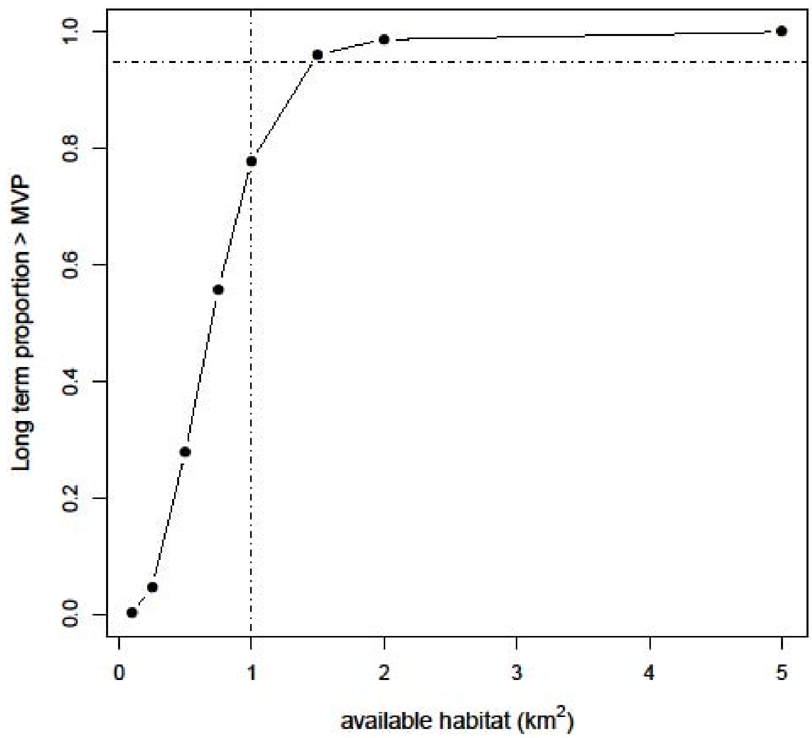


Figure 9: *The mean long term probability (over 15 000 100-year projections) of population abundance being above MVP (2730 adults), as a function of available habitat. 15% per generation probability of catastrophe was assumed. Reference lines are at the minimum area for population viability (vertical) and at 95% probability of recovery (horizontal).*

DISCUSSION

Our results show that to avoid jeopardizing the survival and future recovery of Lake Chubsucker, human-induced harm should be minimal during early life of the species. This is especially true if Canadian populations of Lake Chubsucker do not mature until age 3. Specifically, our modelling suggests that (i) annual survival rate cannot be reduced by more than 33% for YOY and age 1 individuals, or 54% for adults, and (ii) fertility cannot be reduced by more than 49% over all life stages. If maturity does not occur until age 3, these percentages are 15%, 32%, and 33% respectively. 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 1.4. If research indicates that any of our parameters are overestimated, 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 800 or 2730 adults when the probability of a catastrophic (50%) decline (P_k) was 0.10 or 0.15 per generation respectively. If a population is frequently affected by catastrophic levels of winterkill, much larger populations (e.g., greater than 10 million adults) are required. Or connectivity may be required among populations creating a meta-population with the potential for migration and rescue effects. 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. However, winterkill events in Boreal lakes in Alberta were observed to occur as frequently as 1 in every 4 years (Danylchuk and Tonn 2003). We therefore recommend recovery targets based on at least a 15% probability of catastrophe, but suggest that data be collected to confirm the frequency of winterkill events experienced in Ontario's fish habitats. Recovery targets based on MVP can be easily misinterpreted (Beissinger and McCullough 2002) as a reference point for exploitation or allowable harm. A recovery target is neither of these things because it pertains exclusively to a minimum abundance level for which the probability of long-term persistence within a recovery framework is high. Therefore, abundance-based recovery targets are particularly applicable to populations that are below this threshold, and are useful for optimizing efforts and resources by selecting those populations that are in the greatest need of recovery.

Our analyses show that, in the absence of recovery efforts or harm, and assuming a 15% probability of catastrophe per generation, a population with an abundance at 10% of the recovery target has a 95% probability of reaching that target in 12 years, provided there is ample suitable habitat available (Figure 7). 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 the annual survival rate of immature Lake Chubsucker; efforts to improve adult survival or fecundity by a similar proportion are expected to be much less effective.

Model results suggest that a recovered population of Lake Chubsucker requires 1 km^2 of suitable habitat. Insufficient habitat increases the extinction risk exponentially, and delays recovery indefinitely. For populations where habitat is below MAPV, we recommend that recovery efforts focus on improving the amount of suitable habitat available. Simulations also showed that if populations are experiencing density dependence due to habitat restrictions, then an area of 1.5 km^2 is required to ensure that the population remains above the MVP target. Note that these estimates do not account for habitat that is shared by different life stages.

Vélez-Espino et al. (2010) estimated the MVP and MAPV for Lake Chubsucker to be 8127 adults and 6.39 km^2 respectively. The model used for these estimates was built for the purpose of comparison with other species, and was consequently less detailed than the model presented above. The considerably higher estimates from Vélez-Espino et al. may be explained by two factors: (i) adults were assumed to be 346mm, which is likely larger than mean adult size in Canada, and would results in a larger required area per adult individual (API), (ii) MVP was estimated based on an allometry of required population size as a function of population growth rate, and growth rate in turn was estimated based on body size. These allometries result in larger MVP's for larger bodied fish, and so the larger mean adult size used for the previous model would result in a larger MVP.

UNCERTAINTIES

We emphasize the need for research on Lake Chubsucker in Canada to determine (i) survival rates during early life, (ii) fecundity as a function of size for Canadian populations, (iii) the age at maturity, and (iv) the frequency and extent of winterkill events for Lake Chubsucker in Ontario.

In lieu of life history data from populations in Canada (namely, fecundity rates), parts of our analysis assumed that life history data from populations in Nebraska were representative. Ideally, recovery modelling should be based on the life history characteristics of the populations to which they are applied. This is particularly important for age-at-maturity, which had a relatively large impact on the population growth rate and consequent allowable harm recommendations. Uncertainty in early life survival had the greatest effect on the uncertainty in elasticities and population growth rate, and should also be investigated in more depth. The range of population growth rates achieved in stochastic simulations was very wide (0.6-2.5) and included λ=1. Therefore, if the true values of some (or all) vital rates are in the lower ranges of their confidence intervals, then populations could be experiencing slower growth than suggested above, and may even be in decline. More accurate estimates of uncertain vital rates are needed to confirm the status of Lake Chubsucker populations. 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, such as winterkill, will greatly reduce the uncertainty in estimates of minimum viable population size, and thus in recommendations for the recovery of Lake Chubsucker 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 true extinction threshold is likely, we suggest that a larger target be set using equation (13).

REFERENCES

Baty, F. and Delignette-Muller, M.L. 2009. nlstools: tools for nonlinear regression diagnostics. R package. http://CRAN.R-project.org/package=nlstools.

Beissinger, S.R., and McCullough, D.R. 2002. Population Viability Analysis. Chicago: University of Chicago Press.

Bouvier, L.D. and Mandrak, N.E. 2011. Information in support of a Recovery Potential Assessment of Lake Chubsucker (*Erimyzon sucetta*) in Canada. DFO Can. Sci. Advis. Sec. Res. Doc. 2011/048. vi + 22 p.

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

Coker, G.A., Portt, C.B. and Minns, C.K. 2001. Morphological and ecological characteristics of Canadian freshwater fishes. Can. Manuscr. Rep. Fish. Aquat. Sci. 2554: iv+86p.

Cooper, G.P. 1936. Some results of forage fish investigations in Michigan. Trans. Am. Fish. Soc. 65: 132-142.

Danylchuk, A.J. and Tonn, W.M. 2003. Natural disturbances and fish: local and regional influences on winterkill of fathead minnows in boreal lakes. Trans. Am. Fish. Soc. 132: 289-298.

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

DFO 2007. Revised protocol for conducting recovery potential assessments. DFO Can. Sci. Advis. Sec. Sci. Advis. Rep. 2007/39.

Eberts, Jr. R.C., Santucci, Jr. V.J. and Wahl, D.H. 1998. Suitability of the lake chubsucker as prey for largemouth bass in small impoundments. N. Amer. J. Fish. Manage. 18:295-307.

Freund, R.J. and Littell, R.C. 1991. SAS System for Regression, 2nd edition. SAS Institute, Cary, North Carolina.

Froese, R. and C. Binohlan. 2000. Empirical relationships to estimate asymptotic length, length at first maturity and length at maximum yield per recruit in fishes, with a simple method to evaluate length frequency data. J. Fish Biol. 56: 758-773.

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

Lorenzen, K. 2000. Allometry of natural mortality as a basis for assessing optimal release size in fish-stocking programmes. Can. J. Fish. Aquat. Sci. 57: 2374-2381.

Maceina, M.J. and Bettoli, P.W. 1998. Variation in largemouth bass recruitment in four mainstream impoundments of the Tennessee River. N. Amer. J. Fish. Manage. 18: 998-1003.

Minns, C.K. 2003. An area-per-individual (API) model for estimating critical habitat requirements in aquatic species-at-risk. DFO Can. Sci. Advis. Sec. Sci. Res. Doc. 2003/074.

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

Oehlert, G.W. 1992. A note on the delta method. Am. Stat. 46: 27-29.

Randall, R.G., Kelso, J.R.M., and Minns, C.K. 1995. Fish production in freshwaters: are rivers more productive than lakes? Can. J. Fish. Aquat. Sci. 52: 631-643.

R Development Core Team. 2009. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0, URL http://www.R-project.org.

Reed, D.H., O'Grady, J.J, Ballou, J.D., and Frankham, R. 2003. The frequency and severity of catastrophic die-offs in vertebrates. Animal Conserv. 6: 109-114.

Scott, W.B., and Crossman, E.J. 1973. Freshwater Fishes of Canada. Bull. Fish. Res. Board Can. No. 184. Ottawa, Ontario, Canada. 966 p.

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

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

Vélez-Espino, L.A. and Koops, M.A. 2009a. Quantifying allowable harm in species at risk: application to the Laurentian black redhorse (*Moxostoma duquensnei*). Aquatic Conserv: Mar. Freshw. Ecosyst. 19: 676-688.

Vélez-Espino, L.A. and Koops, M.A. 2009b. Recovery potential assessment for lake sturgeon in Canadian designatable units. N. Amer. J. Fish. Manage. 29: 1065-1090.

Vélez-Espino, L.A., Randall, R.G., and Koops, M.A. 2010. Quantifying habitat requirements of four freshwater species at risk in Canada: Northern Madtom, Spotted Gar, Lake Chubsucker, and Pugnose Shiner. DFO Can. Sci. Advis. Sec. Sci. Res. Doc. 2009/115.

Winter, R.L. 1984. An Assessment of Lake Chubsuckers (*Erimyzon sucetta* (Girard)) as Forage for Largemouth Bass (*Micropterus salmoides* (Lacepede)) in a Small Nebraska Pond. G. Zuerlein, Eds. Nebraska Technical Series No. 16. Nebraska Game and Parks Commission.