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# Recovery Potential Modelling of Spotted Gar (Lepisosteus oculatus) in Canada 

# Modélisation du potential de rétablissement du lépisosté tacheté (Lepisosteus oculatus) au Canada 

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#### Abstract

The Committee on the Status of Endangered Wildlife in Canada (COSEWIC) had assessed the Spotted Gar (Lepisosteus oculatus) as Threatened in Canada (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 Spotted Gar populations are particularly sensitive to perturbations that affect survival of immature individuals. Harm to this portion 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 abundance recovery targets of at least 1400 adult Spotted Gar. In the absence of mitigating efforts or additional harm, we estimate that a growing Spotted Gar population will take approximately 65 years to reach this recovery target if starting from a population of 140 adults. However, affecting at least a 10\% increase in the survival of immature individuals can reduce the recovery time of a population by more than half.


## RÉSUMÉ

Le Comité sur la situation des espèces en péril au Canada (COSEPAC) a déterminé que le lépisosté tacheté (Lepisosteus oculatus) est une espèce « menacée » au Canada (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 ont révélé que les populations de lépisosté tacheté sont particulièrement sensibles aux perturbations qui affectent la survie des individus immatures. 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 nous basant sur un objectif de durabilité démographique (c.-à-d., une population autonome à long terme), nous proposons des cibles de rétablissement de l'abondance d'au moins 1400 lépisostés tachetés adultes. En absence d'efforts d'atténuation ou en cas de dommages supplémentaires, nous estimons que la population de lépisostés tachetés prendra environ 65 ans pour atteindre le niveau de rétablissement visé si l'on commence avec une population de 140 adultes. Toutefois, une augmentation d'au moins $10 \%$ de la survie des individus immatures peut réduire de moitié le temps nécessaire au rétablissement d'une population.

## INTRODUCTION

The Spotted Gar (Lepisosteus oculatus) is characterized by its long, beaklike mouth, long, cylindrical body, and distinctive spotting on its head, body and fins. The Spotted Gar is one of two native gar species found in Canada (Scott and Crossman 1973). It can be distinguished from the longnose gar (Lepisosteus osseus) by its shorter, wider snout, although both species are spotted. Canadian populations of the Spotted Gar are found in the Great Lakes basin, and have been verified in: Lake St. Clair, Long Point Bay, Point Pelee National Park, Rondeau Bay (Lake Erie), and Bay of Quinte (Lake Ontario). Adult Spotted Gar prefer quiet, vegetated, shallow, clear waters of lakes and rivers. Spawning occurs in the top meter of water over sand, silt, or clay substrate, preferably in areas of dense submergent and emergent vegetation (COSEWIC 2005). The spotted gar was first designated as a species of Special Concern in 1983 and re-listed as Threatened in 2000.

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 Spotted Gar. This work is based on a demographic approach developed by Vélez-Espino and Koops (2007, 2009a, 2009b), which uses a population-based recovery target, and provides long-term projections of population recovery under a variety of feasible recovery strategies.

## METHODS

Our analysis consisted of four parts: (i) information on vital rates was compiled and used to build stage-structured projection matrices, using uncertainty in life history to represent variation in the life cycle for stochastic simulations; (ii) we used these matrices in a stochastic perturbation to determine the sensitivity of the population growth rate to changes in each vital rate, as well as to determine allowable harm. This analysis was conducted following VélezEspino 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.

## SOURCES

Where possible, life history estimates for the Spotted Gar were based on sampling data from the Canadian population in Rondeau Bay, Lake Erie (Glass et al.). These data were supplemented with findings from Love (2004), who investigated a population of Spotted Gar in South-Eastern Louisiana.

## MATRICES

Using a matrix approach, the life cycle of Spotted Gar was represented with annual projection intervals and by a post-breeding stage-structured projection matrix (Caswell 2001) with four life stages: age-0, juvenile, early adult, and late adult (Figure 1). Individuals were assumed to first mature at age 4 (COSEWIC 2005), and so the juvenile stage consisted of ages 1, 2 and 3. Early adult was defined as ages 4-6, and late adult as ages 7 to maximum recorded age (18, COSEWIC 2005). The adult midpoint was chosen based on catch-at-age data suggesting that Spotted Gar are fully recruited to gear at age 6 (W. Glass, unpublished data)

Elements of the stage-structured matrix included the fecundity coefficient of stage class $j\left(F_{j}\right)$, the probability of surviving stage $j$ and remaining in stage $j\left(P_{j}\right)$, and the transition probability of surviving one stage and moving to the next $\left(G_{j}\right) . P_{j}$ and $G_{j}$ are subdivided into annual survival probability of an individual in stage $j\left(\sigma_{j}\right)$ and the probability of moving from $j$ to $j+1$ given $\sigma ; P_{j}=\sigma_{j}$ $\left(1-\gamma_{j}\right)$ and $G_{j}=\sigma_{j} Y_{j}$, where the term $\gamma_{j}$ is calculated from a geometric distribution with mean $1 / T_{j}$ in which $\mathrm{T}_{j}$ is the duration of stage $j$ in years. Fecundity coefficients $\left(F_{j}\right)$ depend on adult survival through the previous year as well as the stage-specific fertility $f_{j}$ such that

$$
\begin{equation*}
F_{j}=f_{j} P_{j}+f_{j+1} G_{j} \tag{1}
\end{equation*}
$$

where $f_{j}$ is the product of a stage's average number of eggs $\left(m_{j}\right)$, the proportion of females (assumed to be $50 \%$ ), and the inverse of the average spawning periodicity (assumed to be 1 ).

Estimates of mortality and egg-number-at-age were obtained as follows (see Table 1 for summary). For adult annual instantaneous natural mortality rate we performed a catch curve analysis (Hilborn and Walters 1992) on length at age data (W. Glass, unpublished data). This yielded the annual instantaneous mortality rate of 0.7968 , or an annual survival of 0.4508 . Variation in adult mortality was generated by drawing mortality rates from a normal distribution around the instantaneous mortality rate, using the standard error of the catch curve regression as an estimate of variance. Random mortality rates were converted back to annual survival rates. Mean and variance of juvenile survival was estimated as in Vélez-Espino and Koops (2009b), with stochastic values drawn from a beta distribution. Age-0 survival was estimated after all other vital rates by solving the projection matrix at equilibrium using an optimization tool (i.e., solving for age-0 survival so that the eigenvalue of the projection matrix equals 1 ).

Stochastic age-0 survival values were taken from a uniform distribution with minimum of 0.5• $\sigma_{1}$. The maximum value was iteratively adjusted so that the geometric mean stochastic growth rate equalled 1.

To estimate fecundity ( $f$ ), we first calculated a weighted (by survival) mean length for each adult class using a female length at age relationship derived by Glass et al. (Equation 2). We then converted length to mass (Glass et al.), and mass to fecundity (Love 2004; Equation 3):

$$
\begin{align*}
& \ln L=0.041(\text { age })+6.25  \tag{2}\\
& f=8052(\ln \text { mass })-46820 \tag{3}
\end{align*}
$$

where $L$ is length in mm and mass is measured in grams. Variance for these estimates was estimated as the variance in the annual fecundities for each age in the class (Vélez-Espino and Koops 2009b), and stochastic values were drawn from a lognormal distribution.
a)


1. YOY
2. Juveniles
3. Young adults
4. Older adults
b) $\quad M=\left(\begin{array}{cccc}0 & F_{2} & F_{3} & F_{4} \\ G_{1} & P_{2} & 0 & 0 \\ 0 & G_{2} & P_{3} & 0 \\ 0 & 0 & G_{3} & P_{4}\end{array}\right)$
c) $\quad M=\left(\begin{array}{cccc}0 & 331 & 2213 & 2444 \\ 0.0017 & 0.15 & 0 & 0 \\ 0 & 0.07 & 0.30 & 0 \\ 0 & 0 & 0.15 & 0.41\end{array}\right)$

Figure 1. Generalized life cycle (a), corresponding stage-structured projection matrices (b), and mean values of matrix elements (c) used to model the population dynamics of the Spotted Gar. Fir represents fecundities, $P_{j}$ is survival in stage $j$, and $G_{i}$ is transition from stage $j$ to stage $j+1$. Note that fertility is positive for the juvenile stage since some juveniles may mature during the interval from to $t+1$ and produce offspring at $t+1$ (Caswell 2001).

Table 1. Mean, variance and range of vital rates for Spotted Gar, used to estimate deterministic and stochastic elasticity of each vital rate. $s_{i}=$ annual survival probability at stage $i$ and $f_{i}=$ fertility at stage $i$.

|  | Vital rate |  |  |  |  |  |  |
| :--- | :--- | ---: | :---: | :---: | :---: | :---: | ---: |
| Statistic | $s_{1}(\lambda=1)$ | $s_{1}(\lambda=1.078)$ | $s_{2}$ | $s_{3}$ | $s_{4}$ | $f_{3}$ | $f_{4}$ |
| mean | $1.33610^{-3}$ | $1.67110^{-3}$ | 0.2254 | 0.4508 | 0.4508 | 4406 | 5915 |
| variance |  |  | 0.0127 | 0.1398 | 0.1398 | 245538 | 1413324 |
| maximum | $2.25110^{-3}$ | $3.09110^{-3}$ |  |  |  |  |  |
| minimum | $8.35710^{-4}$ | $8.35710^{-4}$ |  |  |  |  |  |

## 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 $(\lambda)$ as determined by the largest eigenvalue of the projection matrix (Caswell 2001). Setting equilibrium (i.e., $\lambda=1$ ) as the minimum acceptable population growth rate, allowable harm ( $\mathrm{T}_{\mathrm{v}}$ ) and maximum allowable harm ( $\mathrm{T}_{\mathrm{v}, \max }$ ) were estimated analytically as:

$$
\begin{equation*}
\mathrm{T}_{v}<\left(\frac{1}{\varepsilon_{v}}\right)\left(\frac{1-\Lambda}{\Lambda}\right) \text { and } \mathrm{T}_{v, \max }=\left(\frac{1}{\varepsilon_{v}}\right)\left(\frac{1-\Lambda}{\Lambda}\right) \tag{4}
\end{equation*}
$$

where $\varepsilon_{v}$ is the elasticity of vital rate $v$, and $\Lambda$ 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 partial derivatives of $\lambda$ with respect to $e_{k l}$, the individual elements of the matrix $\left(\varepsilon_{k l}=\partial \log \lambda / \partial \log e_{k l}\right)$.

We estimated $\Lambda$ as the geometric mean of three $\lambda$ values: (i) Designation population growth rate ( $\lambda_{\text {designation }}$ ), as determined by COSEWIC's criterion "A" for the status assessment of species
based on observed or inferred rates of population decline. Under this criterion, a species is listed as threatened if there is evidence of a $50 \%$ decline over the last 10 years or three generations (3s) (i.e., $\lambda=0.5^{1 / 10}$ or $\lambda=0.5^{1 / 3 s}$ ), whichever is greatest. By incorporating age-atmaturity, egg number-at-age, maximum age, and natural mortality into a life table analysis, we estimated that Spotted Gar have a generation time of $\sim 5$ years, which gives a $\lambda_{\text {designation }}$ of 0.955. (ii) Maximum population growth rate at low densities ( $\lambda_{\max }$ ), as estimated by an allometric relationship between production per unit biomass and weight at maturity for freshwater fishes (Randall and Minns 2000). Assuming that length-at-maturity was 555.7 mm (Glass et al., overall relationship for male and female), mass-at-maturity was 661.5 g , giving $\lambda_{\max }=1.312$. (iii) The population growth rate at equilibrium ( $1 ; \lambda_{\text {equilibrium }}$ ), which is an important dynamic attractor (Turchin 1995). The geometric mean of $\lambda_{\text {designation }}, \lambda_{\max }$, and $\lambda_{\text {equilibrium (i.e., }} \Lambda$ ) was 1.078.

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 VélezEspino and Koops 2007); (ii) calculate $\lambda$ for each matrix; (iii) calculate the $\varepsilon_{v}$ of $s_{i}$ and $f_{i}$ for each matrix; and (iv) estimate mean stochastic elasticities and their parametric, bootstrapped 95\% confidence intervals. For each vital rate, we then calculated maximum allowable harm for mean, maximum (upper $95 \% \mathrm{Cl}$ ), and minimum (lower $95 \% \mathrm{Cl}$ ) values that were based on a geometric mean $\wedge$ of 1.078 (age-0 survival was adjusted to achieve this mean value).

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

$$
\begin{equation*}
\Psi \approx\left(\frac{1-\Lambda}{\Lambda}\right) / \sum_{v=1}^{n} \varepsilon_{v} \tag{5}
\end{equation*}
$$

where $n$ is the number of vital rates that are simultaneously harmed, $\varepsilon_{v}$ is the elasticity of vital rate $v$, and $\psi$ 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 the Spotted Gar. 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 20 generations).

We estimated recovery targets as follows. (i) 50000 projection matrices were generated using the means, variances, and distributions as in the allowable harm analysis, and based on a growth rate of $\lambda=1$; (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 $\left(\mathrm{P}_{\mathrm{k}}\right)$ of $0,0.05,0.10$, or 0.15 per generation. We used
these simulations to determine the number of adults necessary for the desired probability of persistence (see Results) over 100 years.

## 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 ( $s_{3,4}$ ), or in fertility ( $f_{3,4}$ ) 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.

Since population dynamics were stochastic, we based recovery timeframes on the number of years to achieve a 0.95 probability of reaching the recovery target. The initial size of the adult population ranged from 2 to $20 \%$ of the recovery target, and was distributed among age classes according to the stable age distribution. This stable age distribution was represented by the dominant right eigenvector ( $w$ ) of the mean projection matrix based on the growth rate $\lambda=1.078$ $(\mathbf{M} w=\lambda \cdot w)$ (De Kroon et al. 1986). For each initial population size and 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 1.078 for simulations of the status quo (recovery in the absence of improvement or harm). For each strategy the mean (and $\mathrm{min} / \mathrm{max}$ ) of the associated vital rates were increased by $10 \%$ (or $20 \%$ ) before randomly generating projection matrices. We then used 3000 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 $t$.

## MINIMUM AREA FOR POPULATION VIABILITY

Following Vélez-Espino et al. (2010), we estimate the minimum area for population viability (MAPV) as a first order quantification of the amount of habitat required to support a viable population. We calculate MAPV for the adult portion of the population as:
(6) $\quad M A P V_{a}=M V P_{a} \cdot A P I_{a}$,
where $\mathrm{MVP}_{\mathrm{a}}$ is the minimum adult population size that results in the desired probability of persistence over 100 years, as estimated for the recovery target, and $\mathrm{APl}_{a}$ is the area required per adult individual (the inverse of density). We estimate API based on an allometry for lake environments from Randall et al. (1995) for freshwater fishes:

$$
\begin{equation*}
\mathrm{API}=\mathrm{e}^{-10.37} \cdot \mathrm{TL}^{2.58} \tag{7}
\end{equation*}
$$

where TL is the average total length of an adult measured in mm .
To extend the estimate of required habitat to the entire population, we used the stable stage distribution calculated from the model population projection matrix. The API for each stage was estimated from equation 7 using the geometric mean of lengths at the endpoints of each stage (API for emergent fry = 0.001). Suitable spawning habitat for the Spotted Gar in Rondeau Bay is defined separately from adult habitat, and so we define a separate MAVP spawner. API for spawning adults was estimated as the mean diameter of Spotted Gar eggs ( 3.02 mm ; Love
2004), multiplied by 2 times the mean fecundity of older adults to account for both male and female eggs (Table 1). An MAPV for each stage was estimated from equation 6, and the MAPV for the entire population was estimated by summing across all life stages.

To explore the effects of limited habitat availability on extinction probabilities and recovery times we incorporated habitat loss parameters into the matrix model and simulations. This model (Minns 2003) assumes that if the area of available habitat $\left(A_{j}\right)$ exceeds the required habitat $\left(\mathrm{a}_{\mathrm{j}}\right)$ for a given stage then the stage-specific survival is independent of the habitat supply. If, however, required habitat is greater than the habitat available, the stage-specific survival is reduced linearly in proportion to the ratio between habitat supply and required habitat. Specifically, survival $\left(s_{j}\right)$ is multiplied by

$$
h_{j}=\left\{\begin{array}{cl}
A_{j} / a_{j} & \text { if } A_{j}<a_{j}  \tag{8}\\
1 & \text { if } A_{j} \geq a_{j}
\end{array} .\right.
$$

In the simulation, habitat required $\left(a_{j}\right)$ is calculated at each time step as the number of individuals in each stage $\left(N_{j}\right)$ times $A P I_{j}$. In cases where habitat is shared by more than one life stage, $a_{j}$ was calculated as the sum of $N_{j} \cdot A P I_{j}$ for those stages. In these instances, the survival reduction $\left(h_{j}\right)$ was applied to all relevant stages. Habitat for reproduction (spawning habitat) is considered separately since it comprises a small portion of the entire adult habitat. Changes in spawning area were assumed to affect YOY survival (Velez-Espino et al. 2008).

## RESULTS

## ALLOWABLE HARM

Based on the elasticities of the mean vital rates of the Spotted Gar life cycle, population growth rate is most sensitive to perturbations of annual survival in early life ( $s_{i}$ ), and is also sensitive to survival and fertility ( $f_{i}$ ) of early adults (Figure 2). Although the means of stochastic elasticities do not differ in ranking from the deterministic elasticities, wide confidence intervals associated with the stochastic estimates suggest that elasticities are sensitive to variation in vital rates. Comparing correlations among vital rates and elasticities shows that uncertainty in elasticities is driven primarily by uncertainty in the estimate of juvenile survival.

Estimates of the maximum allowable harm to individual vital rates depended on the stochastic element (e.g., mean or upper or lower $95 \%$ CL; Table 2 ). From a precautionary perspective (i.e., assuming an upper $95 \% \mathrm{CL}$ ), our results suggest a maximum allowable reduction of $15 \%$ and $19 \%$ to survival of juveniles or age-0 individuals respectively, and $21 \%$ or $22 \%$ for early adult fertility and survival, respectively (Table 2). Simultaneous impacts on overall survival or fertility ( $\psi$ in equation 4 ) should not exceed $5 \%$ or $16 \%$, respectively (Table 2 ). For a population containing $N$ adults, a $5 \%$ reduction in adult survival is equivalent to an additional loss of $0.05 \cdot s_{3} \cdot N$ adults annually. Given a population of 1400 adults, for instance, 32 fewer adults would survive each year. 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; our simulations suggest that recovery time can be severely delayed by levels of harm below the maximum allowable harm suggested in Table 2 (see recovery results below).


Figure 2. Results of the deterministic and stochastic perturbation analysis showing elasticities ( $\varepsilon_{v}$ ) of the vital rates: annual survival probability of stage $i\left(s_{i}\right)$ and fertility of stage $i\left(f_{i}\right)$. Stochastic results include associated bootstrapped $95 \%$ confidence interval.

Table 2. Summary of maximum allowable harm ( $T_{v, \text { max }}$ ) estimates for individual and combined vital rates of Spotted Gar, based on a stochastic perturbation analysis and a population growth rate ( 1 ) of 1.078. $s_{i}$ and $f_{i}=$ annual survival probability of stage $i$ and fertility at stage $I$, respectively. $s_{n}$ and $f_{n}=$ annual survival probability and fertility, respectively, across all ages. Consistent with the precautionary approach, bold values indicate the maximum allowable harm recommended for management decisions.

| Stochastic <br> element | $\boldsymbol{s}_{1}$ | $\boldsymbol{s}_{2}$ | $\boldsymbol{s}_{1,2}$ | $\boldsymbol{s}_{3}$ | $\boldsymbol{s}_{4}$ | $\boldsymbol{s}_{3,4}$ | $\boldsymbol{s}_{\boldsymbol{n}}$ | $f_{3}$ | $\boldsymbol{f}_{4}$ | $\boldsymbol{f}_{\boldsymbol{n}}$ |
| :--- | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| Deterministic |  |  |  |  |  |  |  |  |  |  |
| Mean | -0.21 | -0.18 | -0.10 | -0.34 | -1.46 | -0.28 | -0.07 | -0.28 | -0.91 | -0.21 |
| Mean | -0.22 | -0.19 | -0.10 | -0.33 | -1.10 | -0.26 | -0.07 | -0.29 | -0.90 | -0.22 |
| $+95 \%$ CL | -0.19 | -0.15 | -0.08 | -0.22 | -0.35 | -0.14 | -0.05 | -0.21 | -0.62 | -0.16 |
| $-95 \%$ CL | -0.31 | -0.29 | -0.15 | -0.57 | -4.97 | -0.51 | -0.11 | -0.59 | -1.62 | -0.43 |

## RECOVERY TARGETS

Probability of extinction decreases as a power function of population size (Figure 3). Functions of the form $y=a \cdot x^{-b}$ were fitted using least squares to the simulated extinction probabilities for each catastrophe scenario (Table 3).

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 $82,196,528$ or 1424 adults when the probability of a catastrophic ( $50 \%$ ) decline was $0,0.05,0.1$, or 0.15 respectively. These MVPs all result in probabilities of extinction of approximately 0.01 over 100 years (Figure 3).

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 an slightly exponential 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 1424 to 13840 adults. Thus, if the true extinction threshold is greater than 1 adult female, larger recovery targets should be considered. The relationship between MVP and extinction threshold can be approximated as
(9) $\quad M V P=681 \cdot E T^{1.03}$,
where $E T$ is the extinction threshold.


Figure 3. Probability of extinction within 100 years of 10 simulated Spotted Gar populations at equilibrium, as a function of population size. Bold curves assume a $15 \%$ probability of catastrophic decline (solid = mean, dotted = max and min of 10 runs). Solid grey lines represent 10\%,5\% and 0\% probabilities of catastrophe. Dashed horizontal reference line is at 0.01 and intersects curves at the associated MVPs (Table 3)

Table 3. Coefficients of fitted power curves for probability of extinction within 100 years as a function of population size (Figure 3). Also shown are associated minimum viable population sizes (MVP) and the associated probability of extinction for that population size; values are calculated as the point where benefit of reduced extinction risk per recovery cost is maximized.

| Prob. Catastrophe | a | b | MVP | Prob. Extinction |
| :---: | :---: | :---: | :---: | :---: |
| 0 | 3.706 | -1.362 | 82 | 0.0121 |
| 0.05 | 4.340 | -1.153 | 196 | 0.0120 |
| 0.10 | 6.466 | -1.033 | 528 | 0.0102 |
| 0.15 | 10.002 | -0.952 | 1424 | 0.0097 |

## RECOVERY TIMES

Under current conditions, and in the absence of recovery efforts, a Spotted Gar population that was at $10 \%$ of the above MVPs is predicted to take $45,51,57$ or 66 years to reach a $95 \%$ probability of recovery, when probability of catastrophe was $0.0,0.05,0.1$, or 0.15 respectively (Figure 4). For a probability of catastrophe of 0.15 , the simulated recovery strategies improved recovery times from 66 years to between 18 and 46 years. Recovery times associated with each strategy varied with initial population size (Figure 5); between 27 and 68 years if starting from $2 \%$ (improved from a status quo time of 96 years), and between 14 and 35 years if starting from 20\% (improved from 51 years). The most effective simulated strategy was an improvement to survival during early life (age-0 to maturity, $s_{1,2}$ ). Improving these vital rates by $10 \%$ was more effective than improving either adult survival or fecundity by $20 \%$. Conversely, the time to recovery increased exponentially as harm was added to vital rates (Figure 6). Consistent with the sensitivity and allowable harm results, recovery time was more severely delayed when rates with higher elasticity were harmed. For example, reducing early survival ( $s_{1,2}$ ) by a proportion equal to just half of the recommended allowable harm (Table 2) doubled the recovery time. These results suggest that lower allowable harms should be considered to reduce delays in recovery time, especially in the case of early life survival.


Figure 4. The probability of recovery of 10 simulated Spotted Gar populations under 3 hypothetical recovery strategies and 4 probabilities of catastrophe, based on an initial adult population size that was $10 \%$ of a recovery target ( $84,196,528$ and 1424 adults for catastrophic probabilities of $0,0.05,0.1$ and 0.15 respectively). Grey line shows recovery under status quo (SQ) conditions, assuming no harm and a population growth rate of 1.078 . Solid and dashed lines represent improvement of $10 \%$ and $20 \%$, respectively, to early survival ( $s_{1,2}$ ), adult survival $\left(s_{3,4}\right)$, or fecundity $\left(f_{3,4}\right)$.


Figure 5. Stochastic projections of mean Spotted Gar recovery times over a range of initial population sizes (number of adults) for 3 hypothetical recovery strategies ( 6 sub-strategies). Assumes 15\% probability of catastrophe, and a recovery target of 1424 adults (initial populations range from 2-20\% of this target). Grey line shows recovery times in the absence of mitigation or additional harm (status quo: SQ), and numbered lines correspond to strategies influencing early survival (1), adult survival (2), and fecundity (3).


Figure 6. Predicted change in the time to $95 \%$ chance of recovery of a Spotted Gar population that is experiencing increased harm to multiple vital rates: fecundity ( $f_{n}$ ), early survival ( $s_{1,2}$ ), adult survival ( $s_{3,4}$ ), or all survival $\left(s_{n}\right)$. Left panel: recovery times as a function of the proportion reduction to each set of vital rates. Right panel: recovery times as a function of scaled harm which ranges from status quo (0 harm) to maximum allowable harm (1; see Table 2 for allowable harm values)

## MINIMUM AREA FOR POPULATION VIABILITY

The stable stage distribution for Spotted Gar is $99.82 \%$ YOY, $0.16 \%$ juvenile, and $0.02 \%$ adult individuals. With a target MVP of 196 adults under a 0.05 probability of catastrophe per generation, the MAPV is 47.8 ha. With a target MVP of 1424 adults, under a 0.15 probability of catastrophe per generation, the MAPV is 360.8 hectares (Table 4). The estimated available habitat in Rondeau Bay is sufficient to sustain a Spotted Gar population of this size. If, however, a larger, more realistic extinction threshold is assumed, YOY/Juvenile habitat becomes limiting. For example, if the extinction threshold is assumed to be 20 adults, the MVP increases to nearly 14000 adults requiring $\sim 3500$ ha, which is larger than both Rondeau Bay and Point Pelee habitats (Table 5). Note, however, that exact habitat preferences of juvenile Spotted Gar are unknown, and older juveniles may utilize adult habitat

When habitat restrictions and associated density dependence are incorporated into population projections, both probabilities of persistence and times to recovery are affected. A population at MVP (1424 adults), experiencing 15\% chance catastrophe per generation, and having available the 360 ha of suitable habitat (MAVP) had a $97 \%$ probability of persistence over 100 years. This is slightly lower than the $99 \%$ probability of persistence observed in simulations that did not include habitat restrictions or density dependence. If habitat is reduced below the MAPV level, as may be the case for YOY/Juvenile habitat in Rondeau Bay, the probability of extinction over 100 years increases exponentially (Figure 7). Reductions in stage-specific habitat are nearly as detrimental as reductions in habitat of all life stages. Conversely, increasing available habitat above MAPV can reduce the probability of extinction, but only if habitat for all life stages is
simultaneously improved. These results suggest that the true critical habitat should be greater than the MAPV listed above to maintain the persistence criteria. Reductions to habitat also delay recovery exponentially, and this is especially true for YOY and juvenile habitat (Figure 8). Conversely, increasing habitat has little to no affect on time to recovery; populations that were at or below carrying capacity required the same time to recover with or without habitat restrictions.

Table 4. Area per individual (API), number of individuals for each stage to support a minimum viable population (MVP) and the resulting estimate of required habitat for each stage and for the entire population (MAPV), under two probabilities of catastrophe per generation $\left(P_{k}\right)$ and two extinction thresholds (ET)

| Stage | API ( $\mathrm{m}^{2}$ ) | $\mathrm{P}_{\mathrm{k}}=0.05, \mathrm{ET}=1$ |  | $\mathrm{P}_{\mathrm{k}}=0.15, \mathrm{ET}=1$ |  | $\mathrm{P}_{\mathrm{k}}=0.15, \mathrm{ET}=20$ |  |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
|  |  | MVP | MAPV (ha) | MVP | MAPV (ha) | MVP | MAPV (ha) |
|  |  | 92387 |  | 671224 |  | 6522759 |  |
| YOY | 0.220 | 6 | 20.3 | 8 | 147.4 | 2 | 1432.0 |
| Juveniles | 139.2 | 1452 | 20.2 | 10554 | 146.9 | 102561 | 1427.6 |
| Young adults | 452.8 | 156 | 7.1 | 1134 | 51.4 | 11017 | 498.9 |
| Older adults | 522.2 | 40 | 2.1 | 290 | 15.1 | 2821 | 147.3 |
| Spawners | 0.036 | 196 | 0.0007 | 1424 | 0.005 | 13838 | 0.05 |
| Total |  |  | $\begin{array}{r} 49.648782 \\ 2 \\ \hline \end{array}$ |  | 360.8 |  | 3505.9 |

Table 5. Available habitat ( $A_{j}$ ) versus required habitat (MAPV) for Rondeau Bay and Point Pelee. Extinction threshold is the adult population size below which the population is considered extinct. $A_{j} / M A P V$ shows the ratio of available to required habitat. Values below 1 indicated insufficient space. *Some habitat in Rondeau bay is shared between stages; spawning habitat is nested within YOY/Juvenile habitat, which is nested within adult habitat.

| Rondeau Bay | Aj (ha) | Extinction Threshold (adults) |  |  |  |  |  |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
|  |  | 2 |  | 20 |  | 50 |  |
|  |  | MAPV | A/JMAPV | MAPV | A/MAPV | MAPV | A/MAPV |
| Spawning | $309^{\text {a }}$ | 0.005 | 60296 | 0.050 | 6,205 | 0.128 | 2407 |
| YOY/Juveniles* | $732^{\text {a }}$ | 294 | 2.5 | 2860 | 0.3 | 7372 | 0.1 |
| Adult* | $2591{ }^{\text {a }}$ | 66 | 39 | 646 | 4.0 | 1666 | 1.6 |
| Total Rondeau Bay | $3148^{\text {a }}$ | 361 | 8.7 | 3506 | 0.9 | 9038 | 0.3 |
| Total Point Pelee | $286{ }^{\text {b }}$ | 361 | 0.8 |  |  |  |  |

a: DFO, unpublished data
b: Chantal Vis, Parks Canada Agency, unpublished data


Figure 7. Probability of extinction within 100 years of 10 simulated Spotted Gar populations at minimum viable population (MVP) size, and experiencing habitat based density dependence, as a function of habitat area. Simulations assume a $15 \%$ chance of catastrophe. $X$-axis indicates habitat size as a proportion of minimum area for population viability (MAPV; Table 4). Each curve represents a different habitat unit. Dashed reference lines show MAPV (vertical) and the probability of extinction in the absence of habitat restrictions (horizontal).


Figure 8. Time to $95 \%$ chance of recovery of 10 simulated Spotted Gar populations at minimum viable population (MVP) size, and experiencing habitat based density dependence, as a function of habitat area. Simulations assume a 15\% chance of catastrophe. X-axis indicates habitat size as a proportion of minimum area for population viability (MAPV; Table 4). Each curve represents a different habitat unit. Dashed reference lines show MAPV (vertical) and the time to recovery in the absence of habitat restrictions (horizontal).

## DISCUSSION

Our results show that human-induced harm should be minimal to avoid jeopardizing the survival and future recovery of the Spotted Gar. Specifically, our modelling suggests that (i) annual survival rate cannot be reduced by more than $19 \%$ for YOY, $15 \%$ for juveniles, or $14 \%$ for adults and (ii) fertility cannot be reduced by more than $21 \%$ for young adults. Population decline is also likely if harm reduces the survival of all ages by more than $5 \%$, survival of immature individuals by more than $8 \%$, or the fertility of all adults by more than $15 \%$. 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 $(\lambda)$ is 1.078 . Lower population growth rates 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 82, 196,528, and 1424 adults when the probability of a catastrophic ( $50 \%$ ) decline $\left(P_{k}\right)$ was $0,0.05,0.10$ and 0.15 per generation respectively. According to Reed et al. (2003), catastrophic events (a one-time decline in abundance of $50 \%$ or more) occur at a probability of 0.14 per generation in vertebrates. We therefore recommend recovery targets based on a $15 \%$ probability of catastrophe. 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 between 2 and 20\% of the recovery target has a $95 \%$ probability of reaching that target in 51-96 years (Figure 5). Additional harm will delay the recovery of a population, with the severity of the delay being related to the sensitivity of the vital rate being harmed (Figure 6). To reduce recovery times, we recommend recovery actions that increase the annual survival rate of immature Spotted Gar (first 4 years of life) by $>10 \%$; efforts to improve adult survival or fecundity by the same proportion are expected to be much less effective, and require actions that increase these rates by > 20\% to achieve similar results.

## UNCERTAINTIES

We emphasize the need for research on Spotted Gar in Canada to determine (i) life history characteristics, (ii) the size and growth rate of populations, and (iii) mechanisms of population decline. 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 Louisiana were representative. Ideally, recovery modelling should be based on the life history characteristics of the populations to which they are applied. To this end, we recommend research to determine such life-history basics as fecundity, clutch size, and especially survival in early life. Uncertainty in early life survival had the greatest effect on the uncertainty in elasticities and allowable harm. In lieu of early-life survival estimates, we stress the importance of determining the true population growth rate.

Although this assessment identifies strategies for Spotted Gar recovery (e.g., increased early survival), the extent to which survival in early life is more likely to respond to changes in habitat or predator abundance is unknown. This poses a significant impediment to the implementation of these strategies. The choice of the recovery target itself is also impeded by a lack of information regarding catastrophic events; targets and model predictions vary widely depending on the frequency of catastrophic decline in the population. Research that identifies the magnitude and frequency of catastrophic events will greatly reduce the uncertainty in estimates of minimum viable population size, and thus in recommendations for the recovery of Spotted Gar 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. Since the true extinction threshold is likely higher, we suggest that a larger target be used (equation 9 ).

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