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Recovery Potential Modelling of Silver Shiner (*Notropis photogenis*) in Canada

Modélisation du potentiel de rétablissement du méné miroir (*Notropis photogenis*) au Canada

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ABSTRACT

The Committee on the Status of Endangered Wildlife in Canada (COSEWIC) has assessed the Silver Shiner as *Threatened* in Canada (COSEWIC 2010). Here we present population modelling to assess population sensitivity, determine population-based recovery targets, and conduct long-term projections to estimate risk of extirpation in support of a recovery potential assessment (RPA). Models represent four Canadian populations: Grand River, Thames River, Bronte Creek, and Sixteen Mile Creek. Two model variations, representing competing hypotheses regarding the lifespan of Silver Shiner: short-lived (3 years) and long-lived (>10 years) were compared. Our analyses demonstrated that the dynamics of Silver Shiner populations are very sensitive to perturbations that affect the survival of immature individuals or the fertility of first time spawners, especially for the short-lived model. Harm to these portions of the life cycle should be minimized to avoid jeopardizing the survival and future recovery of Canada's populations. Based on an objective of demographic sustainability (i.e., a self-sustaining population over the long term), we propose population abundance recovery targets of ~780,000 adult Silver Shiner (ages 1-3) in the case of the short-lived model, or ~700 adults (ages 3-10+) in the case of the long-lived model. These abundances require, at minimum, 0.87 km^2 or 0.07 km^2 for the short- or long-lived model respectively. Current estimated population abundances for all four Canadian populations exceed the long-lived targets, but only the Grand River population exceeds the short-lived target. At current densities and given current estimated available habitat, a short-lived Bronte Creek population is at greatest risk of extirpation in the next 100 years, with risk ranging from 5%-100% risk depending on frequency of catastrophic events. Risk to the Sixteen Mile Creek and Thames River populations ranges from 0%-33%. Both long- and short-lived models estimate that Silver Shiner populations are currently growing, but these estimated growth rates are very uncertain.

RÉSUMÉ

Le Comité sur la situation des espèces en péril au Canada (COSEPAC) a évalué la situation du méné-miroir et l'espèce a été désignée *menacée* au Canada (COSEPAC 2010). Ce document présente la modélisation de la population afin d'évaluer la sensibilité de la population, d'établir les objectifs de rétablissement en fonction de la population, et d'effectuer des projections à long terme dans le but d'estimer le risque de disparition à l'appui d'une évaluation du potentiel de rétablissement (EPR). Les modèles représentent quatre populations au Canada : celles des rivières Grand et Thames et des ruisseaux Bronte et Sixteen Mile. Deux variations de modèle représentent les deux hypothèses concurrentes concernant la durée de vie du méné-miroir, postulant une durée de vie courte (3 ans) ou longue (>10 ans). Nos analyses ont montré que la dynamique des populations de méné-miroir est très sensible aux perturbations qui affectent la survie des individus immatures et la fertilité des géniteurs de premier frai, en particulier pour le modèle postulant une courte durée de vie. On doit réduire au minimum les ravages sur ces étapes du cycle de vie afin d'éviter de mettre en péril la survie et le rétablissement futur des populations du Canada. En nous fondant 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'environ 780 000 ménés-miroirs adultes (âgés de 1 à 3 ans) pour le modèle postulant une courte durée de vie, et d'environ 700 adultes (âgés de 3 à 10 ans ou plus) pour le modèle postulant une longue durée de vie. Ces abondances exigent, au minimum, 0,87 km^2 ou 0,07 km^2 respectivement pour les modèles de courte et de longue durées de vie. Les estimations de l'abondance actuelle des quatre populations du Canada dépassent les cibles pour une longue durée de vie, mais seule la population de la rivière Grand dépasse la cible pour une courte durée de vie. Étant donné les densités actuelles et les estimations actuelles d'habitat disponible, une population de courte durée de vie de la rivière Bronte court le risque de disparition le plus élevé au cours des 100 prochaines années, les risques se situent entre 5 % et 100 % en fonction de la fréquence des événements catastrophiques. Les risques pour les populations du ruisseau Sixteen Mile et la rivière Thames se situent entre 0 % et 33 %. Les modèles pour une courte ou une longue durée de vie estiment tous les deux que les populations de méné-miroir augmentent à l'heure actuelle, mais ces estimations du taux de croissance sont très incertaines.

INTRODUCTION

Silver Shiner (*Notropis photogenis*) was assessed in May 2011 as *Threatened* by the Committee on the Status of Endangered Wildlife in Canada (COSEWIC 2011). There are four separate populations (little to no mixing of individuals) of Silver Shiner in Canada. These will be referred to as the Grand River population, the Thames River population, the Bronte Creek population, and the Sixteen Mile Creek population. 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 2007a; 2007b) 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 2007a). Here, we contribute to components two and three by identifying population sensitivity, and quantifying recovery targets, required habitat, current abundance, and risk of extinction, with associated uncertainty, for Canadian populations of Silver Shiner. This work is based on a demographic approach developed by Vélez-Espino and Koops (2007; 2009a; 2009b), which determines a population-based recovery target based on long term population projections.

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 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) the minimum area of suitable habitat required to support the MVP was estimated and used to simulate the effects of density dependence on crowded populations.

SOURCES

Where possible, life history estimates for Silver Shiner (Table 1) were based on sampling data from Canadian populations collected between May 31 and July 13 2011 (DFO, unpubl. data). Fecundity estimates were extrapolated based on the literature for the closely related Emerald Shiner (*Notropis atherinoides*; Schapp 1989).

THE MODEL

Using a matrix approach, the life cycle of Silver Shiner was represented with annual projection intervals and by a post-breeding age-structured projection matrix (Caswell 2001; Figure 1).

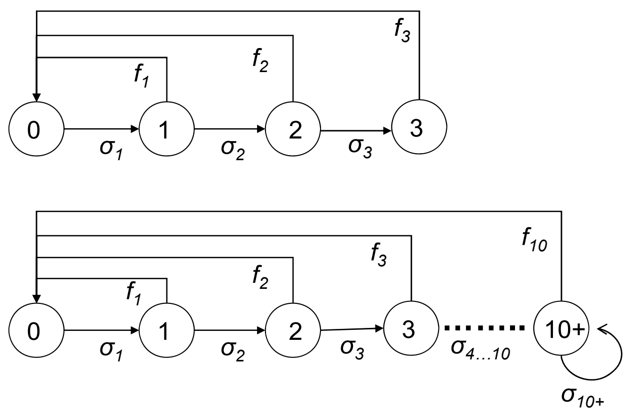
Elements of an age-structured matrix include the fecundity coefficient of age class *j* (F_j), the age-specific annual probability of surviving from age *j*-1 to age *j* (σ_j), and the probability of surviving and remaining in the same stage (P_j; Equation (1); Table 1), This last element is relevant only for the oldest age-class, which incorporates all individuals above that age. The probability of remaining in the last stage is determined by the maximum possible age (T_{max}):

(1) $$P_j = \sigma_j \left(1 - \frac{1}{T_{\max} - j - 1}\right)$$

Table 1. Values, symbols, descriptions, and sources for all parameters used to model Silver Shiner. Estimates are provided for both long- and short-lived model scenarios.

Vital Rate	Description	Symbol	Estimate Short-lived	Estimate Long-lived	Source / Reference
Growth	Asymptotic size	L_∞	88.766	151.237	Von Bertalanffy growth model fitted to Ontario size-at-age data; Table 2
	Growth coefficient	k	3.737	0.104	
	Age at 0 mm	t_0	-0.018	-3.329	
	Mean total length (mm, age *t*)	L_t	6 – 89 mm	44 – 114 mm	
Size-dependent mortality	Instantaneous mortality at age *t*	M_t	1.4 - 7.2	0.4 – 6.3	Lorenzen 2000
	Slope of length frequency catchcurve	β	NA	-2.97	Equation (8)
	Instantaneous mortality at unit size	m_0	2378	46.5	Equation (4) (short-lived); Equation (9) (long-lived)
Annual survival	YOY survival	σ_1	0.0096	0.310	Equation (7)
	Age 1+ survival	σ_{2+}	0.25	0.46-0.66	
Fecundity	Fertility (egg count at age *j*)	η_j	2,452 – 2,630	1,421 - 5,656	Extrapolated from Emerald Shiner; Schapp 1989
	Proportion female	φ	0.5	0.5	No data, assumed
	Proportion reproductive at age *j*	ρ_j	$\rho_1 = 0.88$	$\rho_3 = 0.5$	Size at maturity (McKee and Parker 1982); sampled data
	Spawning periodicity	T	1	1	Baldwin 1983
	Annual female offspring of age *j*	f_j	1226-1315	710 - 2828	Equation (3)
Matrix	Probability of remaining in final stage	Pj	NA	0.33	Equation (1), Caswell 2001
	Effective fecundity (average female offspring for class *j*)	F_j	1 - 328	180 - 930	Equation (2), Caswell 2001
	Maximum age	T_{max}	3	11	Two independent age analyses
Analysis	Annual population growth rate	λ	11.3	3.57	Caswell 2001
	Generic vital rate (survival, maturity, fertility)	v			Caswell 2001, Morris and Doak 2002
	Elasticity (proportional sensitivity of rate *v*	ε_v			Equation (10), Caswell 2001

a)



b)

$$M_{SL} = \begin{pmatrix} F_1 & F_2 & F_3 & 0 \\ \sigma_1 & 0 & 0 & 0 \\ 0 & \sigma_2 & 0 & 0 \\ 0 & 0 & \sigma_3 & 0 \end{pmatrix} \quad M_{LL} = \begin{pmatrix} 0 & 0 & 0 & F_3 & .... & F_{10} & F_{10+} \\ \sigma_1 & 0 & 0 & 0 & .... & 0 & 0 \\ 0 & \sigma_2 & 0 & 0 & .... & 0 & 0 \\ 0 & 0 & \sigma_3 & 0 & .... & 0 & 0 \\ 0 & 0 & 0 & \sigma_4 & .... & 0 & 0 \\ .... & .... & .... & .... & .... & .... & .... \\ 0 & 0 & 0 & 0 & 0 & \sigma_{10} & P_{10+} \end{pmatrix}$$

c)

$$M_{SL} = \begin{pmatrix} 0.92 & 153 & 153 & 0 \\ 0.00075 & 0 & 0 & 0 \\ 0 & 0.12 & 0 & 0 \\ 0 & 0 & 0.12 & 0 \end{pmatrix}$$

$$M_{LL} = \begin{pmatrix} 0 & 0 & 180 & 531 & 727 & 940 & 1164 & 1396 & 1629 & 1861 & 930 \\ 0.002 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0.46 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0.51 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0.55 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0.58 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0.60 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0.62 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0.63 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0.65 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0.66 & 0.33 \end{pmatrix}$$

Figure 1. Generalized life cycle (a), corresponding the age-structured projection matrix (b), and mean values of matrix elements (c) used to model the population dynamics of Silver Shiner. Life cycle and matrices are shown for both long-lived (LL) and short-lived (SL) scenarios, and represent populations at equilibrium. F_i represents annual effective fecundities, σ_i the survival probabilities from age j-1 to age j, and P_j, the probability of remaining in stage j. Note that fecundity is positive for the age 0 class (SL) and for the age 2 class (LL) since some individuals recorded as immature in census t will mature upon their next birthday (if they survive) and produce offspring that will be counted at census t+1 (Caswell 2001).

Fecundity coefficients (F_j) represent the contribution of an adult in age class j to the next census of age-0 individuals. Since a post-breeding model is assumed, the coefficient F_j includes the annual survival probability of adults from age j-1 to age j (σ_j), as well as the age-specific annual number of female offspring for an individual on their j^{th} birthday (f_j) such that

(2) $$F_j = \sigma_j f_j \quad ,$$

where f_j is the product of the average fertility (total annual egg count) for a female of age j (n_j), the proportion of females in the population (φ, assumed to be 50% for Silver Shiner), the proportion of fish that reproduce at age j (ρ_j), and the inverse of the average spawning periodicity (T, assumed to be 1):

(3) $$f_j = \eta_j \varphi \rho_j \frac{1}{\mathrm{T}} \quad .$$

Parameter Estimates

Estimates of survival and fertility (Table 1, Table 2) were based on length measurements of Silver Shiner sampled from Ontario in 2011 (Figure 2; DFO, unpubl. data). Two subsets of individuals were aged by independent interpreters. Both interpreters were provided with specimens of various lengths captured using the same protocol during the same sampling periods. Both interpreters utilized the right or left lapillus otolith to interpret age. Age analysis results varied greatly between interpreters with one interpreter determining maximum age (T_{max}) to be 3, and the other determining maximum age to be greater than 10 years (Figure 3). This difference in life history had a large effect on population dynamics. We therefore present model results for both scenarios, henceforth referred to as the short-lived model (T_{max} = 3) and the long-lived model (T_{max} > 10).

Growth patterns for both models were established by fitting a von Bertalanffy growth curve by the method of non-linear least squares to the appropriate subset of individuals (Figure 3). The growth curve relates size and age using the formula: $L_t = L_\infty (1 - e^{-k(t-t_0)})$, where L_t is size at time t, t_0 is the hypothetical age at which the fish would have had length 0, L_∞ is the asymptotic size, and k is a growth parameter. Since fish were collected throughout the summer, the age interpretations were adjusted based on sampling date to simulate a single sample. A spawn date of May 23, 2011 was estimated based on an analysis of mean daily water temperature at Springbank Dam in the Thames River (Upper Thames River Conservation Authority, Unpubl. data), and an estimated spawning temperature of 18-23ºC (Baldwin 1983).

Short-lived Model

The short-lived model represents 4 age classes (ages 0-3, Figure 1), and is based on aging analysis of a subset of 50 individuals. The set included 30 specimens from Sixteen Mile Creek, 12 from Bronte Creek, and 8 from the Thames River. Because the sample size of young-of-the-year (YOY) aged by this interpreter was small (n=4), YOY caught by Baldwin (1983) were included in the fit of the von Bertalanffy growth curve. In addition, the curve was forced to pass through an approximated hatch size of 6mm, (size of 2 day-old Emerald Shiner; Schapp 1989). This allowed a more meaningful representation of first year growth (Table 1, Figure 3). Size-at-age predicted by this curve (Table 2) was used for all subsequent short-lived model calculations.

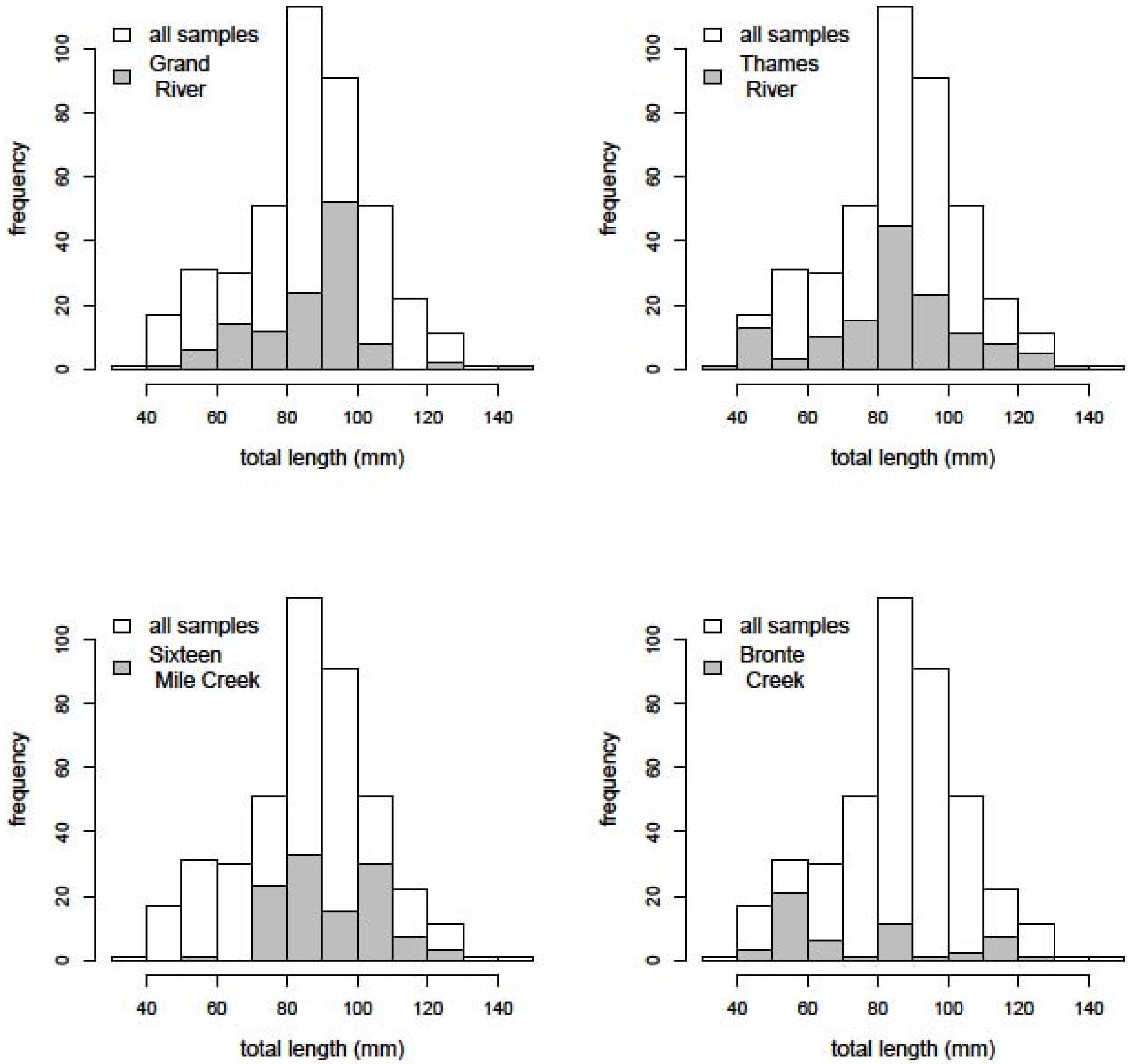


Figure 2. Length frequency (total length) of Silver Shiner collected from four Canadian populations between May 31 and July 13, 2011.

All fish not included in the short-lived aging data set were assigned ages based on an age-length key with 5 mm bins, using the R package "FSA" (Ogle 2012). Ages were assigned randomly with probabilities based on the proportion of aged fish of each age within the appropriate length category. Adult mortality was determined using weighted catch curve analysis on the resulting age frequency (Hilborn and Walters 1992, Maceina and Bettoli 1998). Because ages were assigned randomly, the age distribution differed slightly with each trial. We therefore repeated this process 1000 times to accumulate a distribution of adult mortality from which a mean and standard deviation were determined.

Table 2. Mean and standard deviation or range (in brackets) of age-specific vital rates for two Silver Shiner model scenarios assuming a lifespan of either 3 years (short) or >10 years (long): Total length (mm), survival of a growing population, survival of a population at equilibrium, and annual fertility.

	Demographic Trait / Model Scenario							
	Total length (TL)		Survival (σ_j)		Equilibrium survival		Fertility (η)	
Age	short	long	short	long	short	long	short	long
0	6.0	44.3 (41.7-46.2)	NA	NA	NA	NA	0	0
1	86.8 (86.5-87.0)	54.8 (53.1-56.1)	0.0096 (0.003)	0.31 (.037)	0.00075 (0.0002)	0.00187 (0.0002)	2452 (97)	0
2	88.7 (88.4-89.0)	64.3 (63.0-65.2)	0.25 (0.02)	0.457 (0.045)	0.117 (0.010)	0.457 (0.045)	2626 (110)	0
3	88.8 (88.5-89.0)	72.9 (71.7-73.6)	0.25 (0.02)	0.507 (0.043)	0.117 (0.010)	0.507 (0.043)	2630 (111)	1421 (65)
4	NA	80.7 (79.4-81.3)	NA	0.545 (0.041)	NA	0.545 (0.041)	NA	1950 (89)
5	NA	87.6 (86.4-88.2)	NA	0.575 (0.040)	NA	0.575 (0.040)	NA	2527 (128)
6	NA	93.9 (92.8-94.5)	NA	0.599 (0.038)	NA	0.599 (0.038)	NA	3138 (173)
7	NA	99.6 (98.3-100.3)	NA	0.618 (0.037)	NA	0.618 (0.037)	NA	3767 (229)
8	NA	104.7 (103.2-105.7)	NA	0.634 (0.036)	NA	0.634 (0.036)	NA	4403 (229)
9	NA	109.3 (107.3-110.8)	NA	0.647 (0.035)	NA	0.647 (0.035)	NA	5036 (386)
10+	NA	113.4 (110.9-115.5)	NA	0.658 (0.034)	NA	0.658 (0.034)	NA	5656 (481)

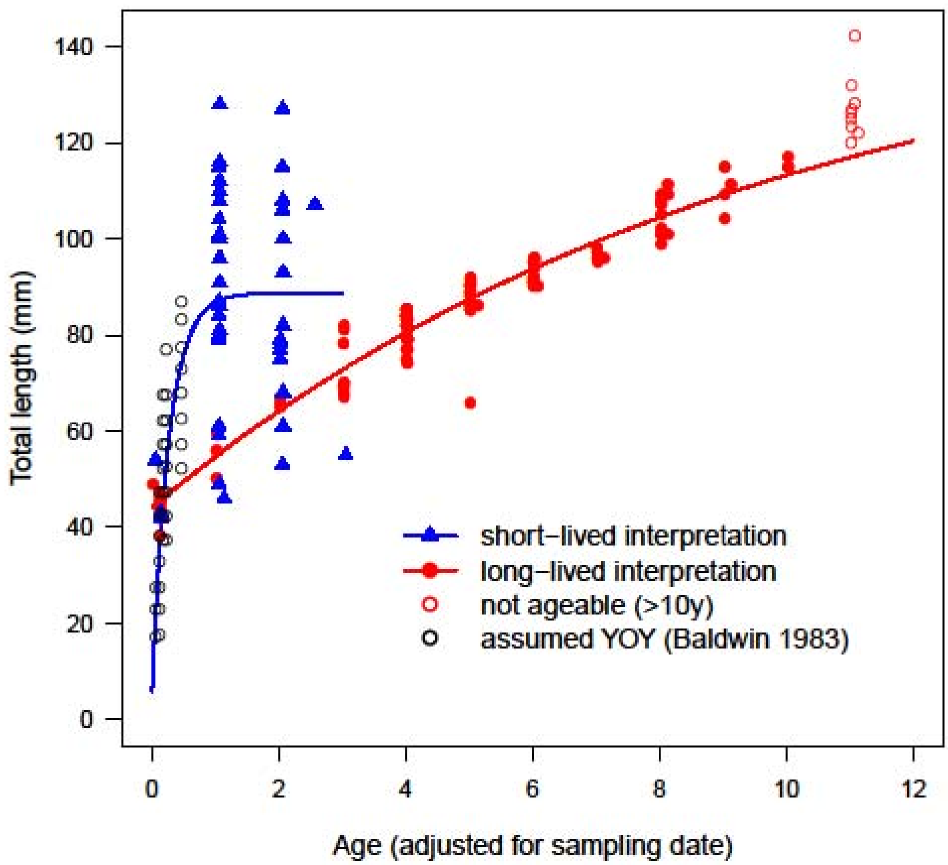


Figure 3. Comparison of size-at-age of Silver Shiner from Ontario sampling in 2011 as interpreted by two independent consultants. Young of the year from previous Ontario sampling are included (Baldwin 1983). Fitted von Bertalanffy growth curves for both interpretations overlaid.

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

$$M_t = \frac{m_0}{L_t^c}, \qquad (4)$$

where M_t and L_t are the instantaneous mortality and mean length at time *t*, m_0 is the mortality at unit size (i.e., at $L_t = 1$), and *c* is an exponent describing the relationship between length and mortality. Lorenzen (2000) concluded that an exponent of 1 best represented the overall relationship across species. However, given the rapid first year growth of Silver Shiner apparent in the short-lived interpretation, this exponent resulted in an obvious overestimation of first year survival. We therefore chose the lower 95% confidence limit of *c* (1.66) found by Lorenzen (2000) to acquire a more reasonable rate. The parameter m_0 was estimated by substituting mean adult size and mortality into equation (4). Substituting von Bertalanffy growth for L_t in equation (4), YOY mortality was calculated by integrating equation (7) and evaluating from 0 to 1.

Variation in size at age was determined by fitting a separate von Bertalanffy curve to each of the 1000 trial age assignments (Table 2). 95% bootstrap confidence intervals of mean size-at-age were used as boundaries when estimating fertility-at-size. Fertility-at-size was determined by extrapolating the following length-weight and fertility-at-weight relationships for the closely related Emerald Shiner, pictured in Schapp (1989), and extracted using image software (Tummers 2006):

(5) $$\log_{10} W = 3.114 \log_{10} TL$$

(6) $$\eta = 539.5W - 11$$

Here, *W* is weight in grams, and *TL* is total length in mm. Uncertainty in fertility incorporated both uncertainty in size-at-age (using confidence intervals from the fitted von Bertalanffy curves), and uncertainty in fertility-at-size (using confidence intervals from the linear fertility regression). The combined uncertainty bounds were assumed to contain all possible fertility values within 4 standard deviations of the mean (i.e., variance was calculated assuming that the range of uncertainty was a 95% confidence interval).

Silver Shiner are reported to mature at age 1 or 2 (Baldwin 1983, McKee and Parker 1982). McKee and Parker (1982) reported that most individuals >60 mm standard length (~75 mm TL; conversion estimated from measurements reported by Baldwin 1983) were mature. In our sample, 88% of age 1 individuals met this requirement, and were considered mature for this model (i.e., $\rho_1 = 0.88$), as well as all age 2+ individuals. Generation time was calculated from the age-specific survival and fecundity estimates as per Caswell (2001), and yielded a generation time of 1.3 years for Silver Shiner in the short-lived model.

Long-lived Model

The long-lived model was based on all fish sampled from the Thames River in 2011. Nine out of 128 individuals included in the long-lived aging data set were determined to be older than 10 years, but could not be aged accurately beyond this point. We therefore set the maximum age for the long-lived model to be 11 years and assessed the sensitivity of this assumption. The 11th age class includes all individuals 10 years or older. It is therefore possible for individuals to remain in this class for more than one year (see Figure 1, Equation (1)).

Mean size-at-age was determined by fitting a von Bertalanffy curve to the 128 aged individuals (Figure 3; Table 1; Table 2). Data from Baldwin (1983) were not included in this fit because Baldwin assumed a short lifespan. Nor was the curve forced to pass through the same size at hatch as the short-lived model (6 mm), because doing so resulted in a poor fit to the aged data. The predicted hatch size is therefore an overestimate. The lengths-at-age predicted by this curve were used for all subsequent calculations. Uncertainty in mean size-at-age was incorporated by calculating bootstrapped confidence intervals on the fitted growth curve (Baty and Delignette-Muller 2009).

Fertility-at-age was determined by substituting the long-lived size-at-age into the same fertility-at-size equations as the short-lived model (Equations (5) and (6)). Uncertainty in fertility was determined in the same manner as for the short-lived model.

Size-dependent mortality was estimated (Table 2) by combining the size-dependent mortality model (Equation (4)) with a catch curve analysis of the age-frequency data from the long-lived interpreter (Hilborn and Walters 1992). Ages were adjusted based on sampling date as in the short-lived model. Again substituting the von Bertalanffy growth equation for L_t, and using a mortality coefficient of c = 1, we can integrate equation (4) and estimate survival from age j to age j+1 as follows:

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

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 (8). m_0 can thus be described by the slope of the catch curve regression (β), scaled by the von Bertalanffy parameters (Equation (9)).

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

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

Survival from stage j to stage j+1 was calculated using Equation (7). 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 (7) to estimate the variance of the transformed parameter. Survival and fertility 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 fertility estimates as per Caswell (2001), and yielded a generation time of 5.4 years.

Age at maturity for the long-lived model was based on the assumed size at maturity of 75 mm TL (McKee and Parker 1982). All individuals assessed as age 4 by the long-lived interpreter were >75 mm, as were 3 out of 9 age 3 individuals. Size at age 3 was predicted by the growth curve to be 73 mm. We therefore assume that all age 4 individuals are mature (ρ_{4+} = 1), and approximately half of age 3 individuals (ρ_3 = 0.5, with a range of 0.33 – 1).

POPULATION SENSITIVITY

While the growth curves for both the short- and long- lived model fit the aged samples well, both final models resulted in what are almost certainly overestimates of first year survival. Thus, population growth rates are likely unreasonably high as well (see Discussion for possible reasons for this overestimate). Because estimates of allowable harm are based on the estimated population growth rate, we did not assess allowable harm here, but instead focused on quantifying sensitivity of the model to perturbations, and identifying those parts of the life cycle that are most sensitive to change.

We are interested in the sensitivity of the estimated annual population growth rate (λ) to perturbations in vital rate v. Annual population growth rate can be estimated as the largest eigenvalue of the projection matrix (Caswell 2001). Model sensitivity is quantified by elasticities, which 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:

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

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 (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; Table 2); (ii) calculate λ for each matrix; (iii) calculate the ε_v of σ_j and f_j for each matrix; and (iv) estimate mean stochastic elasticities and their parametric, bootstrapped 95% confidence intervals. To test the robustness of sensitivities to the status of growth or decline, we also repeated the elasticity estimation for a hypothetical population at equilibrium.

RECOVERY TARGETS

We used demographic sustainability as a criterion to set recovery targets for Silver Shiner. Demographic sustainability is related to the concept of a minimum viable population (MVP; Shaffer 1981), and was defined as the minimum adult population size that results in a desired probability of persistence over 100 years (approximately 77 or 18 generations for the short- or long-lived model, respectively).

Both short- and long-lived models predict that the population of Silver Shiner is growing. Since population growth is not sustainable over time, we simulated the probability of persistence of a stable population over the long term. To achieve stability in the model, vital rates were reduced to achieve a geometric mean growth rate (in stochastic simulations) of $\lambda=1$. For the long-lived model, the most uncertain survival estimate (YOY) was reduced. Adult survival was more uncertain for the short-lived model because there were fewer ages on which to perform catch-curve analysis. Therefore, we reduced m_0 (therefore reducing all survival estimates) to achieve equilibrium for the short-lived model.

We estimated recovery targets as follows. (i) 50 000 projection matrices were generated by randomly drawing vital rates based on the means, variances, and distributions as in the population sensitivity analysis, and based on a geometric mean 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 (P_k) of 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. Adults refer to mature individuals: ages 1+ in the case of the short-lived model, and ages 3+ for the long-lived model.

MINIMUM AREA FOR POPULATION VIABILITY

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

$$(11) \qquad MAPV_j = MVP_j \cdot API_j.$$

MVP_j is the minimum number of individuals per age-class required to achieve the desired probability of persistence over 100 years, as estimated for the recovery target. Individuals were distributed among age classes according to the stable age distribution, which is represented by the dominant right eigenvector (w) of the mean projection matrix based on the growth rate $\lambda = 1$ ($\mathbf{M}\, w = \lambda \cdot w$) (De Kroon *et al*. 1986). API_j is the area required per individual in class j. API was estimated using an allometry for river environments from Randall *et al*. (1995). This allometry approximates API_j for freshwater fishes based on the mean total length (TL) in mm of class j:

$$(12) \qquad API = e^{-13.28} \cdot TL^{2.904}$$

Total lengths from Table 2 were used to calculate API_j (see Table 4). MAPVs for each age class were estimated from equations (11) and (12), and the MAPV for the entire population was estimated by summing across all stages.

MAPV for both short- and long-lived models was compared with the area available for the four Canadian populations. In addition, the estimated current population abundances and associated extinction risks were compared with the extinction risks of a population at habitat saturation, where saturation abundance was based on API and extinction risk was based on the results of simulations.

POPULATION ABUNDANCE

Current population abundance was estimated based on the densities of fish captured in 2011 within each of the four populations. A total of 54 sampling locations were sampled during the 2011 survey. A minimum of three sampling sites (each representing a riffle, run and pool) were sampled at each sampling location. At locations in larger rivers (Grand and Thames), additional sampling sites (two) were sampled when habitat complexity allowed for additional sampling. Each sampling site was sampled using a 3-pass repeated seining technique. Each sampling site measured 100m^2. Sampling locations were chosen randomly within the current or suspected range of Silver Shiner**.** Depletion analysis was attempted for the 64 of 270 sites where Silver Shiner were caught. For 26 of these sites, either depletion was not observed, or the confidence interval around initial population size included zero. In addition, the populations were not closed prior to sampling. We therefore did not use depletion methods to estimate density. Instead, all hauls within a given location were totaled, and averaged over the 300 (or 500) m^2 to provide a rough density at each site.

Mean densities for each waterbody were extrapolated over the total area of the waterbody. An approximate area for each waterbody was determined based on an average stream width for the waterbody, as measured at each sample location, times the length of the known range within that waterbody (J. Barnucz, Pers. Comm.). In addition to this known habitat (KH) a suspected habitat (SH) was determined by extending the estimated length to unsampled but likely habitat (J. Barnucz, Pers. Comm). The Grand and Thames River populations consisted of smaller segments: the Grand River, the Nith River, and Conestogo River (Grand River population); and the Main Thames, the Middle Thames, the North Thames, the South Thames, and Medway Creek (Thames River population). Mean densities were considered separately for each segment of habitat and their abundances totaled. 95% quasi-Poisson confidence intervals for mean abundance were determined for each habitat segment. A Quasi-Poisson model was used because the means and variances of counts were not equal.

DENSITY DEPENDENCE

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) reduces survival by the proportion h_j, which is a function of the ratio between available (A_j) and required (r_j) habitat. Specifically, σ_j is multiplied by

$$h_j = \frac{d^3}{d^3 + 0.25} \qquad (13)$$

where, $d = A_j / r_j$.

In the simulations, habitat required was calculated at each time step as the sum of the number of individuals in each stage (N_j) times API_j. For each available habitat size, projection matrices were randomly generated as for the recovery targets. We then used 3000 realizations of population size over 100 years, averaged over five runs, to estimate the mean population trajectory (with confidence bounds) over time, as well as the expected extinction risk.

POPULATION PROJECTIONS

Projections of the growing Silver Shiner population were performed to assess the effects of harm to vital rates on population growth. These projections were simulated in a similar manner to the recovery targets. Projection matrices were drawn to determine status quo dynamics (i.e., in the absence of harm or recovery). We then used 3,000 realizations of population size over

100 years to generate a median abundance, averaged over 5 runs. The effects of harm on vital rates to recovery was explored by decreasing the vital rate by an increment before randomly generating projection matrices. All projections assumed density dependence based on available habitat was in effect. The statistical program R was used for all simulations and statistical analysis (R Development Core Team 2012).

RESULTS

SHORT-LIVED MODEL

The geometric mean population growth rate (from stochastic simulations) was estimated at λ = 11.3, with a 95% bootstrap confidence interval of (6.7 - 19.2). If, however, Silver Shiner do not spawn until age 2, the population growth rate is reduced to λ = 1.9 (1.4 – 2.5).

Population Sensitivity

Population growth of a short-lived Silver Shiner is extremely sensitive to perturbations of YOY survival, the fecundity of first time spawners, and the proportion of individuals that spawn at age 1 (Figure 4, Table 3). Changes in any of these rates affect the growth rate at nearly the same magnitude. On the other hand, the population is virtually insensitive to changes in survival or fertility of age 2 or 3 individuals; all of these rates could be set to 0 with very little effect on population growth. The sensitivity of the short-lived model does not differ significantly based on population status (growth or equilibrium; Figure 4). Elasticities are not very sensitive to stochasticity (error bars in Figure 4b).

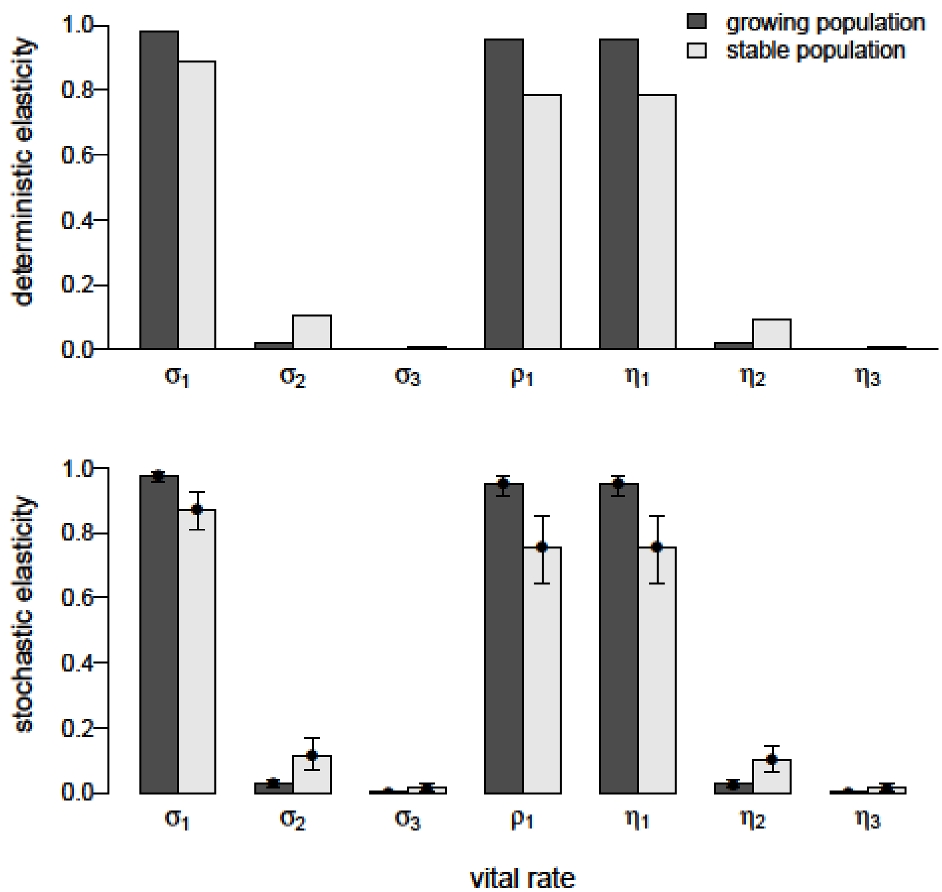


Figure 4. Results of the deterministic (panel 1) and stochastic (panel 2) perturbation analysis showing elasticities (ε_v) of vital rates for the short-lived model: annual survival probability of age j-1 to age j (σ_i), fertility (η_j), and the proportion of reproductive age 1 individuals (ρ_1). Stochastic results include associated bootstrapped 95% confidence interval. Exact values listed in Table 3.

Table 3. Summary of elasticities of Silver Shiner vital rates (ε_v) for a growing population and a population at equilibrium. Shown are annual survival probability (σ_j), annual fertility (η_j) and percent reproductive at age 1(ρ_1).

	σ_1	σ_2	σ_3	ρ_1	η_1	η_2	η_3
Growing Population							
Deterministic mean	0.978	0.022	0.000	0.956	0.956	0.021	0.000
Lower 95% confidence	0.986	0.043	0.002	0.973	0.973	0.042	0.002
Upper 95% confidence	0.956	0.014	0.000	0.912	0.912	0.013	0.000
Stochastic mean	0.974	0.025	0.001	0.949	0.949	0.025	0.001
Equilibrium Population							
Deterministic mean	0.886	0.104	0.010	0.782	0.782	0.094	0.010
Lower 95% confidence	0.924	0.164	0.026	0.853	0.853	0.140	0.026
Upper 95% confidence	0.811	0.071	0.005	0.648	0.648	0.066	0.005
Stochastic mean	0.872	0.115	0.013	0.757	0.757	0.102	0.013

Recovery Targets

Probability of extinction decreases as a power function of population size (Figure 5). 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 26,000 adults (ages 1-3) per population when the probability of catastrophic decline (50%) was assumed to be 5% per generation (3.9% annually). If catastrophes occurred at 10% per generation (7.8% annually), MVP was 780,000 adults. In both scenarios, the cumulative probability of extinction for the respective MVPs was approximately 0.01 over 100 years (Figure 5). The extinction risk, P(ext.), for the 5% (Equation (14)) or 10% (Equation (15)) per generation catastrophe scenario can be defined as a function of initial adult population, N, as:

(14) $$P(ext.) = 542 \cdot N^{-1.07}$$

(15) $$P(ext.) = 3310 \cdot N^{-0.94}.$$

MVP simulations assumed an extinction threshold of 1 adult female (or 2 adults). We observed that assuming a higher, quasi-extinction threshold (i.e., if the population is considered effectively extinct before it declines to 1 female) results in a roughly linear increase in MVP. For example, if the quasi-extinction threshold is defined as 50 adults, and the chance of catastrophe is 5% per generation, mean MVP increases from ~26,000 to ~624,000 (see Table 5 for examples of using these equations to calculate MVP for a different extinction risk). Thus, if the true extinction threshold is greater than 1 adult female, larger recovery targets should be considered. Equations describing extinction risk at a threshold of 50 adults, and a probability of catastrophe of 5 and 10%, respectively, are as follows:

(16) $$P(ext.) = 1783 \cdot N^{-1.01}$$

(17) $$P(ext.) = 6138 \cdot N^{-1.01}$$

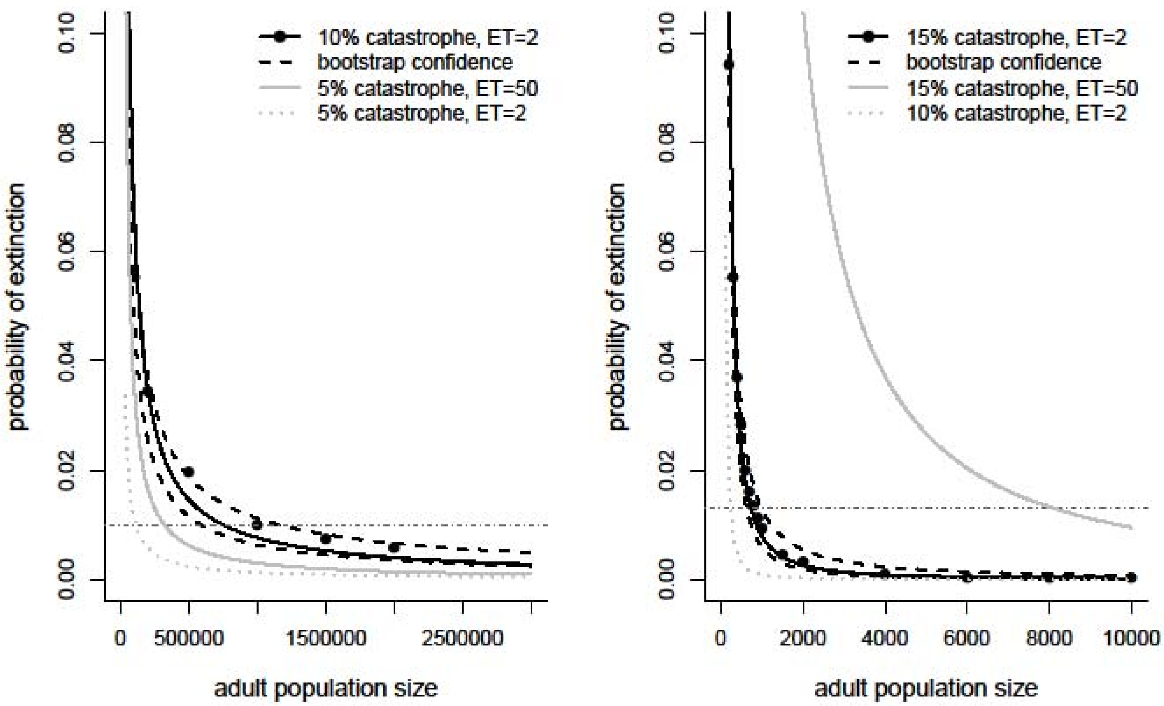


Figure 5. Probability of extinction within 100 years of 10 simulated Silver Shiner populations, at equilibrium, as a function of adult population size. Curves represent different combinations of probability of catastrophe per generation (%), and quasi-extinction thresholds (ET). Dashed horizontal reference line is at 0.01 (left) and 0.014 (right) and intersects curves at the associated MVPs (Table 5). Left panel: short-lived model (adults include ages 1-3); right panel: long-lived model (adults include ages 3-10+).

Minimum Area for Population Viability

The stable stage distribution of Silver Shiner is predominantly YOY (Table 4). MAPV ranged from 0.029 km^2 for an MVP of ~26,000 adults to 3.040 km^2 for a target of 2.7 million adults (Table 5). We recommend the MAPV that corresponds with a probability of catastrophe of 10%, an extinction threshold of 2 adults, and an extinction risk of ~0.01, which equals 0.87 km^2 for ~780,000 adults. These areas assume that each individual requires the areas (API) listed in Table 4, and does not account for any overlapping of individual habitats (sharing) that may occur. It also assumes that habitat is of suitable quality, and should be increased if the quality of habitat is low in some, or all, of the considered habitat.

The smallest of the habitat requirements listed in Table 5 are exceeded by both Thames River and Grand River known available habitats. However, the suspected habitats of Bronte Creek and Sixteen Mile Creek are only 30% and 65% of the recommended habitat target, respectively (Table 6). Habitat requirements for less conservative risk scenarios are met by both Bronte Creek and Sixteen Mile Creek habitats (see Table 5 for examples).

Table 4. Stable stage distribution (SSD; percentage of the population in each stage), and area per individual (API) for the short- and long-lived models.

Age	SSD (%)		API (m^2)	
	short	long	short	long
0	99.919	99.622	0.0003	0.10
1	0.072	0.188	0.73	0.19
2	0.008	0.086	0.78	0.30
3	0.001	0.044	0.78	0.44
4	NA	0.024	NA	0.58
5	NA	0.014	NA	0.74
6	NA	0.008	NA	0.91
7	NA	0.005	NA	1.08
8	NA	0.003	NA	1.25
9	NA	0.002	NA	1.41
10+	NA	0.002	NA	1.57

Table 5. Number of individuals of each stage required to support a minimum viable population (MVP), under the short-lived model, and the resulting estimate of required habitat for each stage and for the entire population, based on estimated Area per Individual (Table 4). Results for three different extinction thresholds, two probabilities of catastrophe, and two levels of extinction risk are shown.

Extinction Threshold	Generational Catastrophe	Extinction Risk	Reference Equation	Life Stage	MVP	MAPV (km^2)
2 adults	5%	0.01	(13)	YOY	32,106,808	0.010
				1+	25,984	0.019
				Total		0.029
2 adults	10%	0.05	(14)	YOY	166,110,240	0.051
				1+	134,433	0.099
				Total		0.150
50 adults	5%	0.01	(15)	YOY	770,600,463	0.238
				1+	623,646	0.457
				Total		0.696
2 adults	10%	0.01	(14)	YOY	963,493,382	0.298
				1+	**779,754**	0.572
				Total		0.870
50 adults	10%	0.05	(16)	YOY	3,367,610,481	1.042
				1+	2,725,403	1.998
				Total		3.040

Population Abundance

Available habitat for the four populations was estimated as, approximately (Table 6): 0.3 km^2 (Bronte Creek), 0.2 km^2 (Sixteen Mile Creek), 3.9 km^2 (Thames River), and 8.0 km^2 (Grand River). Including suspected habitat extends the total estimates of Bronte Creek (0.35 km^2), Sixteen Mile Creek (0.6 km^2) and the Grand River (8.4 km^2; see Table 6 for areas broken into sub-habitats).

Abundances of the four Silver Shiner populations in known habitat were estimated to be approximately (Table 7ii): 5,700 (2,100 - 15,300) in Bronte Creek; 31,600 (18,300 - 54,500) in Sixteen Mile Creek; 53,800 (31,000 - 188,300) in the Thames River population, and 135,100 (51,700 - 355,600) in the Grand River. These estimates were based on sampling densities of 0.0190, 0.1775, 0.0139 and 0.0169 respectively (Table 6). If densities were extended to include suspected habitat, approximate abundance estimates were, respectively: 6,600 (2,500 - 17,700); 101,100 (58,700 - 174,300); 53,700 (31,000 - 188,300); and 140,500 (53,900 - 368,500). For the purpose of comparison with MVP, all sampled individuals were considered to be adults in the short-lived model, since there was little distinction between ages in the short-lived aged sample. None of these abundances meet the recommended MVP target of 780,000. If, however, Silver Shiner populations reach saturation of known plus suspected available habitat, the MVP target will be exceeded by both Grand and Thames River populations (Table 7iii).

Table 6. Area of known (KH) and known plus suspected (SH) available habitat for four Silver Shiner populations. Areas are the product of the occupied river reach and the mean river width at sampling locations. Grand and Thames river habitats are further broken down into their composite waterbodies. Estimated densities (in fish per m^2) for each waterbody are also shown with confidence intervals (quasi-Poisson) in brackets.

Watershed (sample size)	Occupied River Reach (km)		Mean River Width (m)	Total Area (km^2)		Estimated Density (fish/m^2)
	KH	KH + SH		KH	KH + SH	
Bronte Creek (10)	16	18.5	18.75	**0.300**	**0.347**	0.0190 (0.0071 - 0.0511)
Sixteen Mile Creek (8)	10	32	17.80	**0.178**	**0.570**	0.1775 (0.1030 - 0.3060)
Thames River				**3.875**	**3.875**	0.0139 (0.0080 - 0.0486)
main branch (11)	28	28	44.25	1.239	1.239	0.0136
Middle Thames (3)	10	10	26.50	0.265	0.265	0.12
North Thames (1)	14	14	53.00	0.742	0.742	0.0300
South Thames (1)	39	39	40.00	1.560	1.560	0.0100
Medway Creek (1)	6	6	11.50	0.069	0.069	0.0433
Grand River				**8.002**	**8.376**	0.0169 (0.1165 - 0.0444)
Grand River (8)	93	93	63.75	5.929	5.929	0.0304
Nith River (5)	75	92	22.00	1.650	2.024	0.0196
Conestogo River (3)	11	11	38.50	0.424	0.424	0.0122

Table 7.(i) Recommended MVP for comparison with (ii) Estimated adult abundance for four Silver Shiner populations, based on densities and available habitat estimated from 2011 Ontario sampling (see Table 6) and (iii) Possible abundance assuming saturation of available habitat and required area per individual (see Table 4). Abundance estimates are shown for known available habitat (KH) and known plus suspected (SH) available habitat. Confidence intervals (quasi-Poisson) are in brackets. Abundance of 1+ adults and of 3+ adults are shown separately for comparison with MVP values for the short- and long-lived models respectively.

Available Habitat (Model Scenario)	Population			
	Bronte Creek	**Sixteen Mile Creek**	**Thames River**	**Grand River**
(i) Recommended MVP				
short-lived: 779,754 age 1+				
long-lived: 728 age 3+; 2,646 age 1+				
(ii) Estimated Adult Abundance				
KH (Adult=1+)	5,700 (2,120 - 15,320)	31,595 (18,328 - 54,462)	53,727 (31,015 - 188,331)	135,066 (51,680 - 355,637)
KH + SH (Adult=1+)	6,591 (2,451 - 17,714)	101,104 (58,650 - 174,279)	53,727 (31,015 - 188,331)	140,451 (53,931 - 368,503)
KH + SH (Adult=3+)	2,926 (1,088 - 7,865)	100,194 (58,122 - 172,710)	42,606 (24,595 - 149,347)	114,749 (44,062 - 301,067)
Estimated Density	0.0190 (0.0071 - 0.0511)	0.1775 (0.1030 - 0.3060)	0.0139 (0.0080 - 0.0486)	0.0169 (0.1165 - 0.0444)
(iii) Adult Abundance at Saturation (Allometry)				
KH + SH (Adult=1+)	311,022	510,726	3,474,479	7,510,703
KH + SH (Adult=3+)	3,509	5,762	39,201	84,741

The risk of extinction for the four populations (Figure 6) differs dramatically based on the assumed risk scenario (probability of catastrophe and quasi-extinction threshold; Table 8 ii and iii). In some cases, risk at current densities could be greatly reduced by saturating the available habitat (Table 8). The Bronte Creek population is at greatest risk under any scenario. Assuming a risk scenario of 10% per generation probability of catastrophe and an extinction threshold of 2 adults, the risk of extinction at current abundance, over the next 100 years, is 97.6% (range 38.5-100%) based on current density. This risk is high because Bronte Creek is both the smallest habitat, and one of the least dense populations. Increasing the density of Bronte Creek to saturation can reduce this risk to as little as 2.3%. Sixteen Mile Creek and Thames River populations are at some risk of extinction over the next 100 years (3.6-32.5%). The Sixteen Mile Creek population has the highest density of the four, but the smallest known habitat. Its risk of extinction falls in the lower end of this range if suspected habitat is indeed suitable (3.9-10.9%), and a saturation density can further reduce risk to 1.4%. Risk to the Thames River population can be reduced to 0.2% by saturating the suspected habitat. The Grand River population is currently at lowest risk of extinction over the next 100 years (1.9-12.3%), and can also reduce risk to 0.1% through increased density. The overall probability of persistence of all four populations is low due to the risk to Bronte Creek (~12%, range 0-60%). However, if catastrophes happen at a rate of 5% probability per generation (with an extinction threshold of 2 adults), persistence is much more likely (82-98%). In addition, if saturation is achieved in all four populations, probability of persistence is large (92%) even under the more conservative risk scenario (10% catastrophe and extinction threshold of 50).

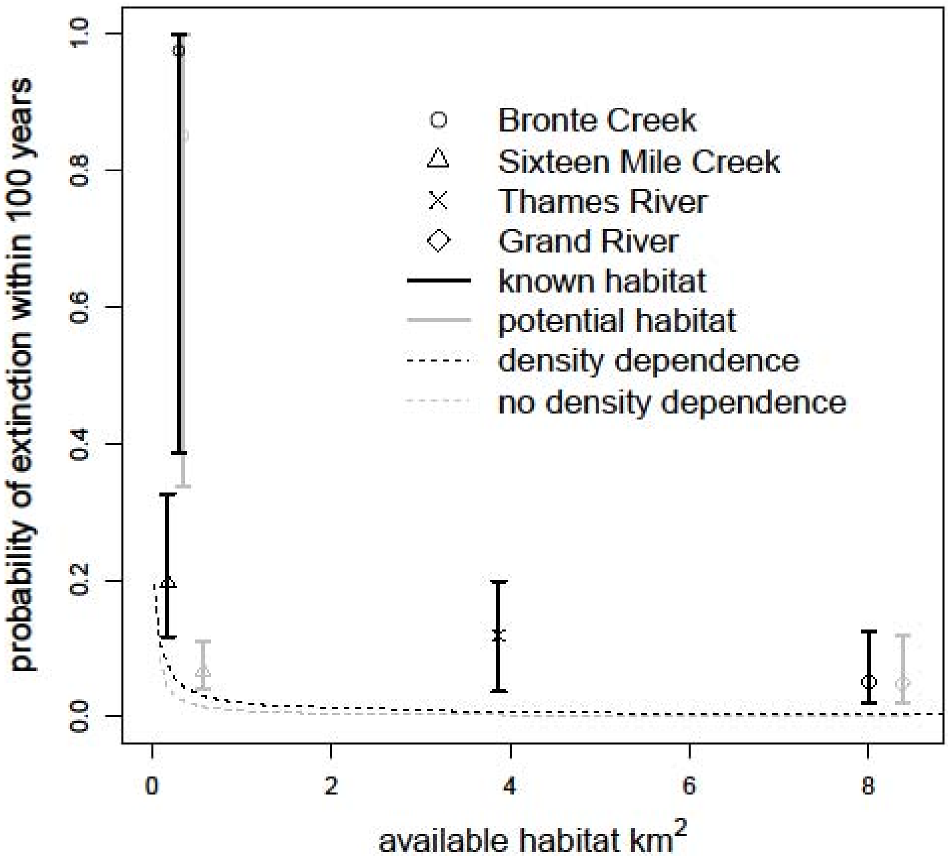


Figure 6. Probability of extinction within 100 years of 10 simulated Silver Shiner populations as a function of available habitat. Simulations assume no population growth or decline, on average, and a short lifespan. Dashed curves assume saturation of the available habitat and either density dependence (black) or no density dependence (grey). Error bars show ranges of extinction risk for each of four Silver Shiner populations given current estimates of density and either known (black) or suspected plus known available habitat (grey).

Density Dependence

When populations experienced reduced survival at high densities as a result of density dependence, the risk to extinction increased 30-173% (Figure 6). The additional risk is insignificant if available habitat greatly exceeds MAPV, but should be considered for populations where available habitat is close to or smaller than MAPV. Density dependence causes the population to oscillate around saturation abundance (Figure 7).

Table 8. Extinction risk (probabilities) over 100 years for four populations of Silver Shiner, based on extinction probability curves: (i) Equations (14), (ii) Equation (15), and (iii) Equation (18). Model simulations assumed a 5, 10, or 15% per generation probability of catastrophe, an extinction threshold of 2 adults, and either short- (i, ii) or long-lived (iii) life history. Risk for three different population abundance values are compared: Current population estimates extrapolated over known available habitat (Estimated KH), current population estimates applied to known plus suspected available habitat (Estimated KH + SH), and abundance at saturation of known plus suspected available habitat assuming the allometry based required area per individual (Table 4). Probability of persistence of all four populations as well as the risk of total extirpation from Canada are also shown.

Abundance Assumptions	Bronte Creek	Sixteen Mile Creek	Thames River	Grand River	Persistence (all)	Extinction (all)
(i) Short-lived (5% catastrophe, ET=2)						
Estimated (KH)	0.053 (0.018 - 0.152)	0.008 (0.005 - 0.015)	0.005 (0.001 - 0.009)	0.002 (0.001 - 0.005)	0.933 (0.824 - 0.975)	3.9E-9
Estimated (KH + SH)	0.045 (0.016 - 0.130)	0.002 (0.001 - 0.004)	0.005 (0.001 - 0.009)	0.002 (0.001 - 0.005)	0.946 (0.855 - 0.981)	9.2E-10
Saturation (KH + SH)	0.0007	0.0004	0.0001	0.0000	0.9987	4.4E-16
(ii) Extinction Risk: Short-Lived (10% catastrophe, ET 2)						
Estimated (KH)	0.976 (0.385 - 1.0)	0.195 (0.117 - 0.325)	0.118 (0.036 - 0.198)	0.050 (0.020 - 0.123)	0.016 (0 - 0.513)	0.001
Estimated (KH + SH)	0.851 (0.336 - 1.0)	0.065 (0.039 - 0.109)	0.118 (0.036 - 0.198)	0.048 (0.019 - 0.118)	0.117 (0 - 0.603)	3.2E-4
Saturation (KH + SH)	0.0227	0.0143	0.0024	0.0011	0.9600	8.7E-10
(iii) Extinction Risk: Long-Lived (15% catastrophe, ET 2)						
Estimated (KH)	0.002 (0 - 0.009)	0.000	0.000	0.000	0.998 (0.991 - 1)	4.0E-18
Estimated (KH + SH)	0.001 (0 - 0.007)	0.000	0.000	0.000	0.999 (0.993 - 1)	4.5E-19
Saturation (KH + SH)	0.001	0.000	0.000	0.000	0.999	6.3E-17

Recovery Projections

Given the likely overestimation of population growth rate, we do not present projected times to recovery as they likely underestimate the true times. We instead note some potentially relevant effects of harm (reduction of vital rates) on population dynamics.

If populations of Silver Shiner reach saturation of available habitat, in the long term we would expect the population abundance to exceed MVP anywhere from 42% (Bronte Creek; Figure 7) to 67% of the time (Grand River) as the populations oscillate around the saturation abundance.

Given current estimates of fertility and YOY survival, a Silver Shiner population could continue to grow even if adult survival is 0 (i.e., fish spawn on their first birthday and die). However, this life-history was more sensitive to environmental and density-based fluctuations and occasionally went extinct (1/3 simulations).

A reduction in YOY survival delayed time to recovery significantly (75% reduction resulted in a 4x delay) and reduced the expectation of abundance exceeding MVP (from 41% to 25% of the time). Reducing fertility of first year spawners more than 75% caused the population abundance to oscillate in a predictable way under density dependence (i.e., the same pattern of oscillation was seen in nearly all trials, despite stochasticity (Figure 7).

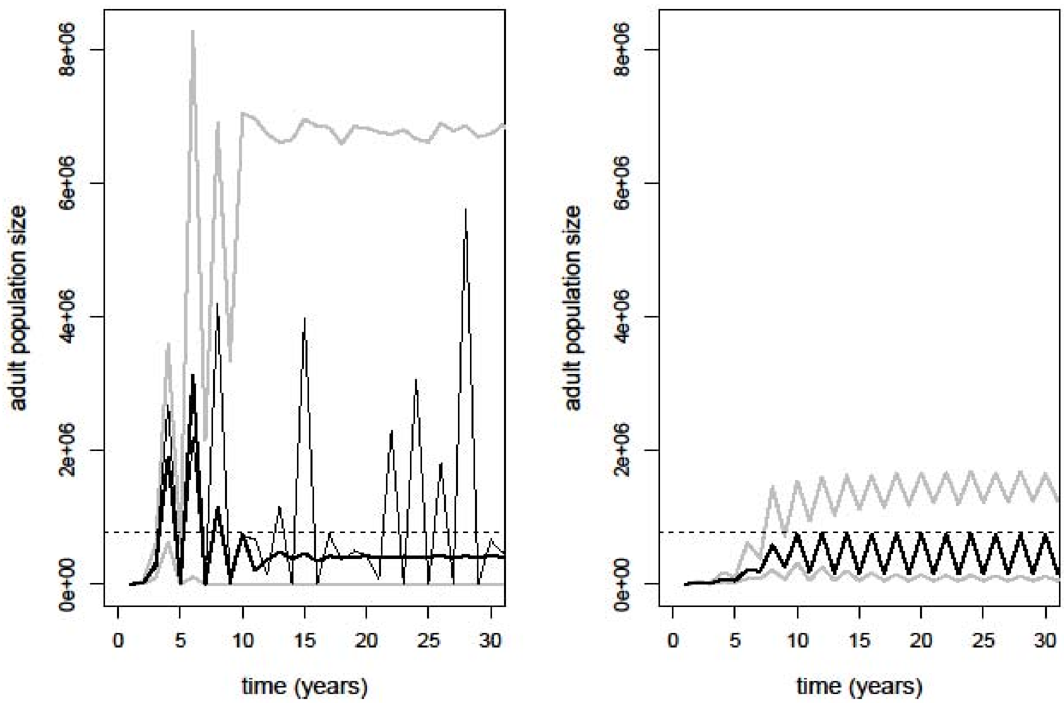


Figure 7. Population size over time of the Bronte Creek Silver Shiner population, experiencing density dependence, and 10% per generation catastrophic decline. An example population (narrow solid line), and mean (thick black lines) and 95% confidence interval (grey lines) of 15,000 simulated populations are shown. Horizontal reference line is at the minimum viable population size (MVP ~780,000 adults). Simulation assumed that habitat area was at Minimum Area for Population Viability (MAPV = 0.87 km^2). Left panel: status quo vital rates as in Table 2; right panel: age 1 do not spawn (ρ_1=0).

LONG LIVED MODEL

The geometric mean population growth rate (from stochastic simulations) was estimated at λ = 3.57, with a bootstrap 95% confidence interval of λ = 3.03 to 4.18.

Population Sensitivity

If a long lifespan is assumed, the population growth of Silver Shiner is most sensitive to changes in the survival of immature individuals, and is sensitive to changes in proportion of individuals who spawn for the first time at age 3 (ρ_3), as well as the fertility of those who do so. It is likely impossible to isolate harm or recovery to individual age classes, but the additive nature of elasticities allows us to consider the collective effects of perturbations on different life stages. When rates affecting juvenile or adult life stages were considered cumulatively, population growth rate of a growing population was found to be very sensitive to cumulative changes to juvenile survival, somewhat sensitive to cumulative changes to fertility, and not very sensitive to cumulative changes to adult survival (Figure 8, Table 9)

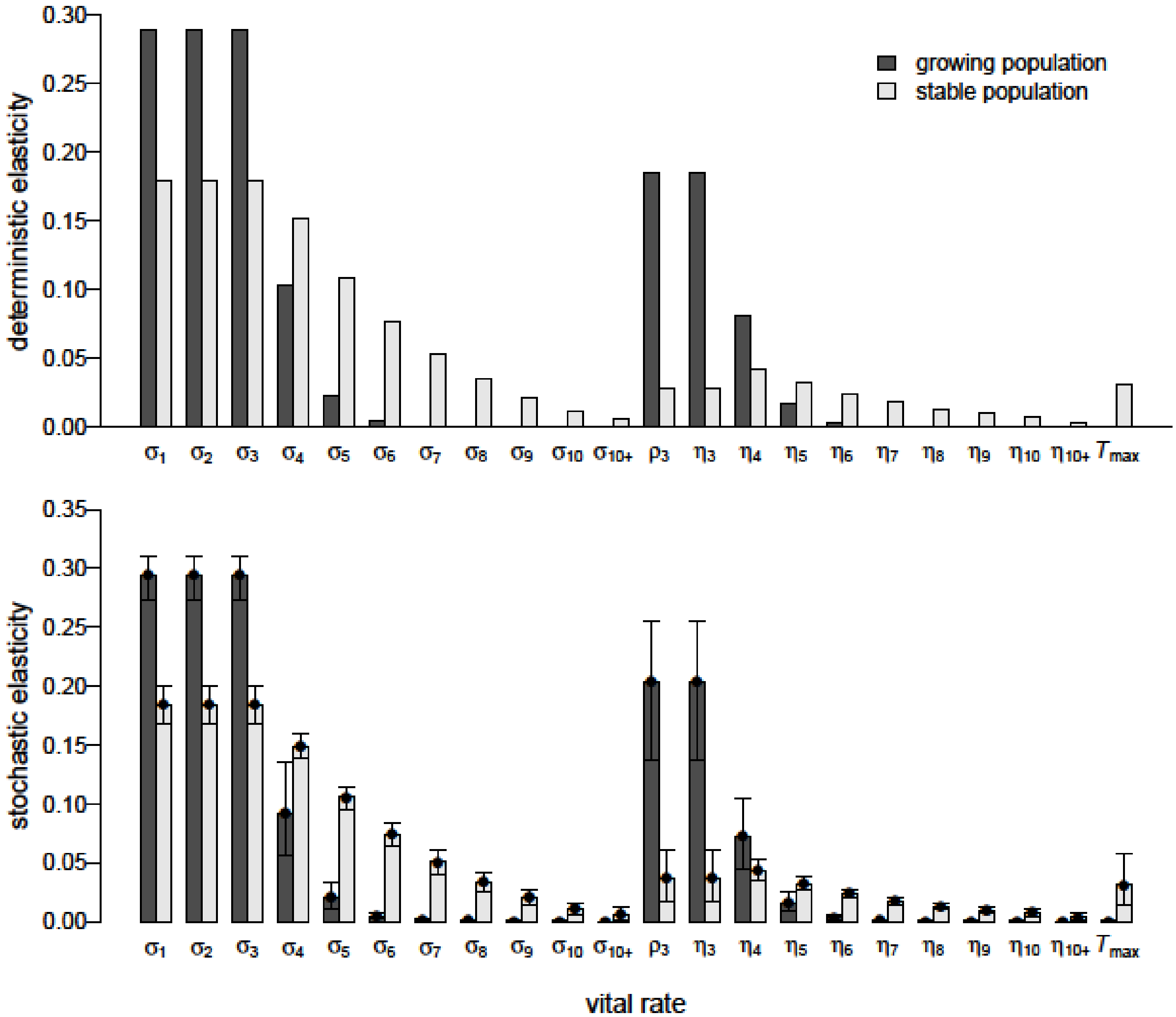


Figure 8. Results of the deterministic (panel 1) and stochastic (panel 2) perturbation analysis showing elasticities (ε_v) of the vital rates for the long-lived model: annual survival probability of age j-1 to age j (σ_i), fecundity (f_j), and the proportion of reproductive age 3 individuals (ρ_3). Stochastic results include associated bootstrapped 95% confidence interval.

Elasticities for the long-lived model were very sensitive to the value estimated for proportion of reproductive age-3 individuals (error bars in Figure 8). This parameter was highly correlated with the elasticities for all parameters (R^2=0.36-0.90). The correlation was positive for the survival of immature individuals and the fertility of age-3 spawners, and negative for the remaining parameters (i.e., if fewer individuals spawn at age 3, then early survival and fertility becomes less important, and the survival and fertility of older adults become more important). This trend is mirrored by changes in sensitivity between a growing population and one at equilibrium (Figure 8). Growing populations are more sensitive to changes in early survival and fertility, but as the population growth rate is decreased, the sensitivity shifts towards older adults, and lifespan (T_{max}) becomes relevant. At equilibrium, the population sensitivity to cumulative changes in juvenile survival was roughly equivalent to that of cumulative changes to adult survival.

Table 9. Summary of elasticities for vital rates of Silver Shiner for a long-lived growing population and a population at equilibrium. Shown are age specific annual survival probabilities (σ_j), fertilities (η_j), percent reproductive at age 3 (ρ_3), maximum age (T_{max}), stage specific survival (σ_{juv}, σ_{adult}) and overall fertility (f_n)

	$\sigma_1, \sigma_2, \sigma_3$	$\sigma_4 - \sigma_{10+}$	ρ_3, η_3	$\eta_4 - \eta_{10+}$	T_{max}	σ_{juv}	σ_{adult}	η_n
Growing Population								
Deterministic mean	0.29	0-0.1	0.19	0-0.19	0.00	0.87	0.13	0.29
Lower 95% confidence	0.29	0-0.09	0.20	0-0.2	0.00	0.88	0.12	0.29
Upper 95% confidence	0.31	0-0.14	0.25	0-0.25	0.00	0.93	0.18	0.39
Stochastic mean	0.27	0-0.06	0.14	0-0.14	0.00	0.82	0.07	0.19
Equlibrium Population								
Deterministic mean	0.18	0.01-0.15	0.03	0-0.03	0.03	0.54	0.46	0.18
Lower 95% confidence	0.18	0.01-0.15	0.04	0-0.04	0.03	0.55	0.45	0.18
Upper 95% confidence	0.20	0.01-0.16	0.06	0.01-0.06	0.06	0.60	0.51	0.24
Stochastic mean	0.17	0-0.14	0.02	0-0.02	0.01	0.50	0.38	0.13

Recovery Targets

Recovery targets were chosen in the same manner as for the short-lived model. MVP was 220 (range 180 – 290) adults (ages 3-10+) per population when the probability of catastrophic decline (50%) was assumed to be 10% per generation (1.9% annually). If catastrophes occurred at 15% per generation (3% annually), MVP was 728 (range 612 – 1,094) adults. In both scenarios, the probability of extinction for the respective MVPs was approximately 0.013 over 100 years (Figure 5). The extinction risk can be calculated as a function of initial adult population size N as follows for the 10% (Equation (18)) or 15% (Equation (19)) per generation catastrophe scenario:

(18) $$P(ext.) = 354 \cdot N^{-1.88}$$

(19) $$P(ext.) = 549 \cdot N^{-1.61}.$$

MVP simulations assumed an extinction threshold of 1 adult female (or 2 adults). As with the short-lived model, if the quasi-extinction threshold is defined as 50 adults, and the chance of catastrophe is 15% per generation, mean MVP increases from ~700 to 8,200 adults aged 3-10+ (see Table 10 for examples of using these equations to calculate MVP for a different extinction risk). Thus, if the true extinction threshold is greater than 1 adult female, larger recovery targets should be considered. Equations describing extinction risk at a threshold of 50 adults, and a probability of catastrophe of 10 and 15%, respectively, are as follows:

(20) $$P(ext.) = 8489 \cdot N^{-1.71}$$

(21) $$P(ext.) = 8637 \cdot N^{-1.49}$$

Minimum Area for Population Viability

The stable stage distribution of Silver Shiner is predominantly YOY (Table 4). MAPV ranged from 0.02 km^2 for an MVP of ~200 adults to 0.81 km^2 for a target of ~8,200 adults (Table 10). We recommend an MAPV of at least 0.07 km^2 for ~700 adults, which corresponds with a probability of catastrophe of 15%, an extinction threshold of 2 adults, and an extinction risk of ~0.013. These areas assume that each individual requires the areas listed in Table 4, and does not account for any overlapping of individual habitats (sharing) that may occur. It also assumes that habitat is of suitable quality throughout, and should be increased if the quality of habitat is low in some or all of the considered habitat.

Each of the four available habitats exceeds this recommended minimum MAPV. Both the Grand and Thames River habitats exceed the most conservative suggested MAPV, however Bronte and Sixteen Mile Creek habitats do not (Table 10, Table 6).

Population Abundance

The estimated abundance for the four Silver Shiner populations is not dependent on the growth model. However, because the definition of adult differs for the two models, we also provide population estimates of age 3+ individuals for the purpose of comparison with the recovery targets, which account only for adults as defined in the long-lived model. Estimates of 3+ individuals are based on the proportion in each population of individuals that were larger than 72mm (the mean size of age 3 individuals as predicted by the long-lived von Bertalanffy growth curve). These proportions were: 43.4% (Bronte Creek), 99.1% (Sixteen Mile Creek), 79.3% (Thames River), and 80.7% (Grand River), which were multiplied by the total abundance estimates Table 7 ii. Resulting approximate adult abundance estimates, extrapolating to known plus suspected available habitat were, approximately: 2,900 (1,100 – 7,900) for Bronte Creek; 100,200 (58,100 – 172,700) for 16 Mile Creek; 42,600 (24,600 – 149,300) for Thames River and 114,700 (44,100 – 301,100) for the Grand River. All of these abundances exceed the recommended minimum MVP target of ~700 adults. All but the Bronte Creek population exceed the more conservative target of ~8,200 (Table 10).

The risk of extinction is very low (< 0.2%) for each of the populations at their estimated abundance, assuming a risk scenario of 15% per generation catastrophe and an extinction threshold of 2 (Table 8iii). The overall probability of persistence for all four populations under this scenario is 99.9%. Under a more conservative scenario (extinction threshold of 50 adults), the extinction risk of all but Bronte Creek remain very low (< 0.3%; not shown in table). The risk to Bronte Creek is 5.9% (range 1.4-25.8%), giving an overall persistence probability of 93.9% (73.9-98.6).

Density Dependence

Given that MAPV requirements are met for the long-lived model, density-dependence is unlikely to increase the risk of extinction beyond an acceptable level. If, however, habitat is reduced to near or below MAPV, extinction risk will increase exponentially in a manner similar to that of the short-lived model, and crowding will further increase risk beyond that predicted by the MVP curves.

Table 10. Number of individuals of each stage required to support a minimum viable population (MVP) and the resulting estimate of required habitat for each stage and for the entire population, based on estimated Area per Individual (Table 4), and the long-lived model. Results for two different extinction thresholds, two probabilities of catastrophe, and two levels of extinction risk are shown.

Extinction Threshold	Generational Catastrophe	Extinction Risk	Reference Equation	Life Stage	MVP	MAPV (km^2)
2 adults	10%	0.01	(18)	YOY	212,449	0.0217
				Juv (1-2)	585	0.0001
				Adult (3+)	222	0.0001
				Total		0.0219
2 adults	15%	0.05	(20)	YOY	305,172	0.0311
				Juv (1-2)	840	0.0002
				Adult (3+)	319	0.0002
				Total		0.0315
2 adults	15%	0.01	(20)	YOY	696,679	0.0711
				Juv (1-2)	1,918	0.0004
				Adult (3+)	728	0.0005
				Total		0.0720
50 adults	10%	0.01	(19)	YOY	2,400,098	0.2448
				Juv (1-2)	6,607	0.0015
				Adult (3+)	2,508	0.0016
				Total		0.2479
50 adults	15%	0.05	(21)	YOY	3,132,738	0.3195
				Juv (1-2)	8,624	0.0019
				Adult (3+)	3,274	0.0021
				Total		0.3236
50 adults	15%	0.01	(21)	YOY	7,889,318	0.8046
				Juv (1-2)	21,719	0.0049
				Adult (3+)	8,244	0.0054
				Total		0.8149

Population Projections

Since the estimated populations all exceed the minimum recommended MVP target, we did not simulate recovery for the long-lived model.

DISCUSSION

This work compares population dynamics, population sensitivity, and extinction risk for two competing theories of life history for the Silver Shiner: a short-lived model (maximum of 3 years) and a long-lived model (maximum of >10 years). Our results show that to avoid jeopardizing the survival and future recovery of Silver Shiner, human-induced harm to the overall survival of juveniles, and to the fertility of first time spawners, should be minimal. This is the case whether Silver Shiner are long- or short-lived, but is especially true for the short-lived model. Current estimates suggest that Canadian populations are experiencing growth, but the uncertainties surrounding YOY survival leave the exact rate of growth unclear.

Recovery targets, based on the concept of MVP, were presented for both models assuming a variety of risk scenarios. Recommended targets for the short-lived model were estimated at ~780,000 adults (ages 1+) per population, assuming the probability of a catastrophic (50%) decline was 0.10 per generation and an extinction threshold of 2 adults. For the long-lived model, the recommended target of ~700 adults (ages 3+) per population assumes a catastrophic decline of 0.15 per generation. 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 for the long-lived model. Given the short generation time of Silver Shiner under the short-lived model, however, the annual probability generated by a 15% per generation probability may be too frequent. We therefore recommend recovery targets based on a 10% probability of catastrophe for the short-lived model, but suggest that data be collected to confirm the frequency of catastrophic events for Silver Shiner.

We emphasize that the choice of recovery target is not limited to the recommended target, or to the scenarios presented in Table 5 (short-lived) or Table 10 (long-lived). Required adult population sizes can be calculated for any alternative probability of extinction using one of equations (14) to (17) (short-lived) or (18) to (21), depending on which risk scenario (probability of catastrophe and extinction threshold) and life-history (short- or long-lived) best represents the Canadian Silver Shiner populations, and what level of risk is considered acceptable.

We also emphasize that recovery targets based on MVP can be easily misinterpreted (Beissinger and McCullough 2002) as a reference point for exploitation or allowable harm. A recovery target is neither of these things because it pertains exclusively to a minimum abundance level for which the probability of long-term persistence within a recovery framework is high. Therefore, abundance-based recovery targets are particularly applicable to populations that are below this threshold, and are useful for optimizing efforts and resources by selecting those populations that are in the greatest need of recovery. We stress that these MVP targets refer to adult numbers only. If juveniles are being included in abundance estimates, then the MVP should include these age classes as well (see Table 5 and Table 10).

Model results suggest that a recovered population of Silver Shiner requires 0.03 – 3.04 (recommended 0.87) km^2 of suitable habitat for the short-lived model, or 0.02 – 0.81 km^2 (recommended 0.07) for the long-lived model. The exact value depends on the extinction risk scenario. Isolated groups having insufficient quality or quantity of habitat may be at an exponentially increased risk of extirpation due to density dependence (Young and Koops 2011). We emphasize that these areas are based on an across species allometry and may not reflect true requirements of Silver Shiner. They also assume that only suitable habitat is counted in the total available area. If certain areas of the current estimated habitat are deemed partially or wholly unsuitable, the total minimum required area should be extended.

UNCERTAINTIES

We emphasize the need for research on Silver Shiner in Canada to determine (i) unknown or uncertain aspects of life history such as fecundity, lifespan, and survival rates during the first year and (ii) the frequency and extent of catastrophic events for these populations.

Fecundity

Both models estimated fertility based on a fertility-at-size relationship for Emerald Shiner. Since Silver Shiner grow to be larger than Emerald Shiner, we assumed both that Silver Shiner fertility follows a similar relationship, and that the relationship extrapolates to larger sizes. Fertility of Silver Shiner should be confirmed since both models suggest that growing Silver Shiner populations are sensitive to fertility, especially in the first year of spawning (Figure 4 and Figure 8).

Growth and ageing interpretations

The uncertainty which has the greatest effect on recommendations is the discrepancy between the two age interpretations (short- or long-lived).

MVP

The recommended recovery targets for the short- and the long-lived models differed by orders of magnitude. This is likely due to a combination of several factors. First, catastrophic decline occurred at a higher annual rate in the short-lived model, given its shorter generation time; if there had been no chance of catastrophic events, MVP targets for the short-lived model would be only ~800 adults. Second, the variation in population growth rate calculated in the stochastic trials is much larger for the short-lived model (standard deviation of 3.3 vs 0.3), resulting in much smaller growth rates in stochastic simulations (as well as much larger ones) than in the long-lived model. That is, uncertainty in growth rates increases extinction risk. It is therefore critical to determine the true life history of Silver Shiner for setting recovery targets for this species.

First year growth and survival

In lieu of direct estimates of survival of immature individuals our analysis assumed that a size-dependent mortality schedule was representative. Ideally, recovery modelling should be based on the life history characteristics of the populations to which they are applied. This is doubly important given the population sensitivity to first year survival.

Because estimates of survival were based on assumptions about growth, uncertainty regarding the appropriateness of the von Bertalanffy growth curve for first year growth is an additional source of uncertainty for first year survival. In the short-lived model, individuals appeared to be fully grown within the first year, resulting in a very large parameter value for k, and a consequent overestimate of first year survival. In the long-lived model, a single von Bertalanffy growth curve could not be fitted that simultaneously passed through the interpreted size at age, and through a reasonable hatch size, also causing an over-estimate of hatch size and first year survival. We conclude that there is a period of rapid growth in the first yea that differs in pattern from the growth of 1+ fish. We stress the importance of experimental estimation of first year survival or, alternatively, a direct estimate of the population growth rate.

Required Area per Individual

In the case of the long-lived model, the estimated current abundance exceeds the potential abundance at habitat saturation. There was not a similar discrepancy in the short-lived model. There are several possible explanations for this discrepancy. (i) API-size allometry is inappropriate for Silver Shiner, and they can exist at higher densities than it suggests. (ii) The allometry is appropriate, and Silver Shiner are currently over-crowded but have not yet experienced density dependent decline. (iii) Silver Shiner are more densely populated at sample sites than at locations not sampled, and we have over-estimated the abundance by extrapolating densities uniformly across the system. Saturation density suggested by the allometry for the short-lived model was 0.897 1+ individuals / m^2, while saturation density for the long-lived model was only 0.037 individuals / m^2. The difference is largely due to the much larger API calculated for YOY in the long-lived model, due to the over-estimated hatch size. A hatch size of 6 mm would have resulted in a saturation density of 0.662 1+individuals / m^2 for the long-lived model. We therefore feel that hypothesis (i) is correct; the allometry for the long-lived model has underestimated the saturation population abundance due to the large predicted size-at-hatch.

Frequency of catastrophic decline

MVP targets differed dramatically based on the assumed frequency of catastrophic decline. This was particularly relevant for the short-lived model where estimates of extinction risk for current populations ranged from 1.6% to100% depending on the generational probability of catastrophe. Further research in this area is warranted.

Quality of Habitat

Our estimates of required habitat (MAPV) assume that habitat is of high quality throughout the range of Silver Shiner. We did not have sufficient data to either confirm, or provide an alternative to this assumption. If any habitat within the known or suspected range of Silver Shiner is found to be partly or wholly unsuitable, MAPV should be adjusted accordingly.

A factor which may negatively influence habitat quality is river fragmentation. Modelling of the Grand and Thames rivers assumes that there is movement and intermingling of individuals throughout the river. If existing barriers are impediments to movement (in either direction) then this may affect the viability of the sub-populations within the river and therefore the viability of the overall populations. Future modelling could consider the meta-populations structure of the systems and the importance of barriers to viability.

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