Fisheries and Oceans Canada Pêches et Océans Canada

Science Sciences

Canadian Science Advisory Secretariat (CSAS)

Research Document 2013/015

Central and Arctic Region

Recovery potential modelling of Silver Chub (*Macrhybopsis storeriana*) in Ontario

Jennifer A.M. Young and Marten A. Koops

Fisheries and Oceans Canada
Great Lakes Laboratory for Fisheries and Aquatic Sciences
867 Lakeshore Rd.
Burlington ON L7R 4A6

July 2013

Canada

Foreword

This series documents the scientific basis for the evaluation of aquatic resources and ecosystems in Canada. As such, it addresses the issues of the day in the time frames required and the documents it contains are not intended as definitive statements on the subjects addressed but rather as progress reports on ongoing investigations.

Research documents are produced in the official language in which they are provided to the Secretariat.

Published by:

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

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

ISSN 1919-5044

Correct citation for this publication:

Young, J.A.M., and Koops, M.A. 2013. Recovery potential modelling of Silver Chub (*Macrhybopsis storeriana*) in Ontario. DFO Can. Sci. Advis. Sec. Res. Doc. 2013/015. v + 22 p.

TABLE OF CONTENTS

ABSTRACT

The Committee on the Status of Endangered Wildlife in Canada (COSEWIC) has assessed the Great Lakes - Upper St. Lawrence population of Silver Chub (*Macrhybopsis storeriana*) as *Endangered*, due to a substantial decline in abundance (COSEWIC 2012). Here we present population modelling to assess population sensitivity, and determine population-based recovery targets and allowable harm in support of a recovery potential assessment (RPA) for Silver Chub. Our analyses demonstrated that the dynamics of a growing Silver Chub population would be very sensitive to perturbations that affect fecundity, or the survival of young-of-the-year. A stable or declining population, however, will be more sensitive to changes in adult survival. Based on an objective of demographic sustainability (i.e., a self-sustaining population over the long term), and a 15% probability of catastrophic decline per generation, we propose a population abundance recovery targets of ~444,000 adult Silver Chub (ages 1+). This abundance requires, at minimum, 84 km^2 of suitable habitat. The current abundance of Silver Chub in this DU (Western Basin of Lake Erie only) is estimated at approximately 660,000 adults, but has been as low as 251,000 within the last five years (Ohio Division of Wildlife 2013; OMNR 2013). The potential habitat (surface area) in the Western Basin is estimated to be in excess of 3000 km^2. If the Silver Chub population is stable, the risk of extirpation from Ontario for a population of 251,000 (the lowest measured abundance) is 1% within the next 100 years. Since 2000, however, Silver Chub has been declining, on average, at a rate of 20% annually. At this rate, Silver Chub would become extirpated from Ontario within 36-95 years. The rate of decline has decreased since 2000, and the Silver Chub population may be stabilizing. If so, some harm may be allowed. Transient harm should not exceed a 15% reduction in adult abundance, or a 23% reduction in young-of-the-year (YOY) abundance, or an 8% reduction in total abundance within a 7 year period (approximately three generations).

Modélisation du potentiel de rétablissement du méné à grandes écailles (*Macrohybopsis storeriana*) en Ontario

RÉSUMÉ

Le Comité sur la situation des espèces en péril au Canada (COSEPAC) a attribué à la population de méné à grandes écailles (*Macrhybopsis storeriana*) des Grands Lacs et du haut Saint-Laurent le statut d'espèce *en voie de disparition*, en raison d'un déclin important de son abondance (COSEPAC 2012). Nous présentons ici une modélisation de la population pour évaluer sa sensibilité et déterminer des cibles de rétablissement en fonction de la population ainsi que les dommages admissibles en appui à une évaluation du potentiel de rétablissement du méné à grandes écailles. Nos analyses ont montré que la dynamique d'une population croissante de méné à grandes écailles serait très sensible aux perturbations affectant la fécondité et la survie des jeunes de l'année. Une population stable ou en déclin est en revanche plus sensible aux modifications de la survie des poissons adultes. En nous basant sur un objectif de durabilité démographique (c.-à-d. une population autonome à long terme) et une probabilité de 15 % de déclin catastrophique par génération, nous proposons des cibles de rétablissement de l'abondance d'environ 444 000 ménés à grandes écailles adultes (âgés d'un an ou plus). Cette abondance nécessite au moins 84 km^2 d'habitat propice. L'abondance actuelle du méné à grandes écailles dans cette unité désignable (UD) (bassin ouest du lac Érié seulement) est estimée à environ 660 000 adultes, mais elle a chuté à 251 000 au cours des cinq dernières années (Ohio Division of Wildlife 2013; OMNR 2013). Selon les estimations, l'habitat potentiel (superficie) dans le bassin ouest mesure plus de 3 000 km^2. Si la population de méné à grandes écailles est stable, le risque de disparition en Ontario d'une population de 251 000 individus (abondance mesurée la plus faible) est de 1 % dans les 100 prochaines années. Cependant, depuis 2000, le méné à grandes écailles décline en moyenne à un taux de 20 % par an. À ce taux, le méné à grandes écailles disparaîtrait de l'Ontario dans les 36 à 95 ans qui viennent. Le taux de déclin a diminué depuis 2000 et la population de méné à grandes écailles peut être en train de se stabiliser. Si c'est le cas, certains dommages pourraient être autorisés. Les dommages temporaires ne doivent pas excéder une diminution de 15 % de l'abondance des adultes, ou une diminution de 23 % de l'abondance des jeunes de l'année, ou une diminution de 8 % de l'abondance totale sur une période de 7 ans (soit trois générations environ).

INTRODUCTION

In Canada Silver Chub (*Macrhybopsis storeriana*) can be found in rivers and lakes in the Saskatchewan-Nelson watershed (Saskatchewan – Nelson River populations) and in Lake Erie (Great Lakes – Upper St. Lawrence populations). The Great Lakes – Upper St. Lawrence populations were designated as *Endangered* by the Committee on the Status of Endangered Wildlife in Canada (COSEWIC 2012) due to a substantial decline in abundance over the last 10 years. 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 from Canada, Fisheries and Oceans Canada (DFO) 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. Here, we contribute to components two and three by identifying population sensitivity, and quantifying recovery targets, required habitat, and allowable harm, with associated uncertainty, for the Great Lakes – Upper St. Lawrence populations of Silver Chub. 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 extirpation, time to extirpation, and to estimate the minimum viable population (MVP) and the minimum area for population viability (MAPV; i.e., the amount of suitable habitat required to support the MVP); and (iv) projection matrices were used to quantify the effects of allowable harm on the population growth rate.

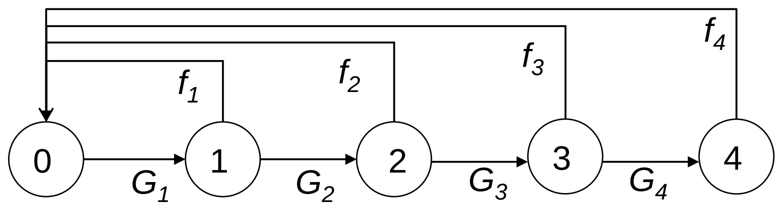
SOURCES

Growth patterns and annual mortality of Silver Chub in Canada were determined using aged samples collected in Lake Erie from 1952-1954 (Kinney 1954) and also in 2000 (N. Mandrak, unpubl. data). Fecundity-at-size was estimated based on Kinney (1954). Population trajectory was estimated using Interagency trawling index data collected from 1988 to 2012 (Ohio Division of Wildlife 2013; OMNR 2013). All analyses and simulations were conducted using the statistical program R (R Development Core Team 2012).

THE MODEL

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

a)



b)

$$M = \begin{pmatrix} F_1 & F_2 & F_3 & F_4 & 0 \\ \sigma_1 & 0 & 0 & 0 & 0 \\ 0 & \sigma_2 & 0 & 0 & 0 \\ 0 & 0 & \sigma_3 & 0 & 0 \\ 0 & 0 & 0 & \sigma_4 & 0 \end{pmatrix}$$

c)

$$M = \begin{pmatrix} 0.2 & 853.7 & 2149.1 & 3327.0 & 0 \\ 0.0003 & 0 & 0 & 0 & 0 \\ 0 & 0.38 & 0 & 0 & 0 \\ 0 & 0 & 0.47 & 0 & 0 \\ 0 & 0 & 0 & 0.51 & 0 \end{pmatrix}$$

Figure 1. Generalized life cycle (a), corresponding age-structured projection matrix (b), and mean values of matrix elements for a stable population (c) used to model the population dynamics of Silver Chub. F_i represents annual effective fecundities, and σ_i the survival probabilities from age j-1 to age j. Note that fecundity is positive for the age-0 class since 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).

Elements of the age-structured matrix include the fecundity coefficient of age class j (F_j), and the age-specific annual probability of surviving from age j-1 to age j (σ_j).

Fecundity coefficients (F_j) represent the contribution of an adult in age class j to the next census of age-0 individuals. Since a post-breeding model is assumed, the coefficient F_j includes the annual survival probability of adults from age j-1 to age j (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

$$F_j = \sigma_j f_j \quad , \tag{1}$$

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 Chub), the proportion of fish that reproduce at age j (ρ_j; assumed to be 1 for Silver Chub), and the inverse of the average spawning periodicity (T):

$$f_j = \eta_j \varphi \rho_j \frac{1}{\mathrm{T}} \quad . \tag{2}$$

Parameter Estimates

All model parameters are defined in Table 1 and Table 2.

Population Trajectory

Population trajectory of Silver Chub was estimated based on a time series of annual trawling data from the Western Basin of Lake Erie between 1988 and 2012 (Ohio Division of Wildlife 2013; OMNR 2013) (Figure 2). These data consisted of total abundance estimates for the Western Basin, with abundance extrapolated from the geometric mean Silver Chub per hectare. 95% confidence bounds were estimated by fitting quasi Poisson models to fish per hectare data each year. There were two large booms in Silver Chub abundance, followed by large crashes. We estimated the population growth rate (λ) by fitting a line through the logged abundances from the first year after the most recent large crash (2000) to 2012, where the slope of this line is the instantaneous growth rate (*r*). The annual population growth rate is $\lambda = e^{r}$, giving an average population growth rate of λ=0.8 (95% confidence interval: 0.72 – 0.90), or 20% annual decline. The rate of decline has slowed since 2000; if only the last 6 years are included, the Silver Chub population in Lake Erie would be considered stable, with slight growth (λ=1.04; 95% confidence interval: 0.69 – 1.55) (Figure 2). It should be noted that the latter trajectory estimate is quite uncertain due to large variation in abundance over the last 6 years, and suggests a recent trajectory anywhere from 31% annual decline to 55% annual growth). In addition, variation around the catch per hectare estimates is also large, and confidence intervals around annual population estimates often varied by orders of magnitude.

Individual Growth and Mortality

Silver Chub were assumed to mature at age 1 and live to a maximum age of 4 (COSEWIC 2012). Estimates of growth and survival were based on collections of Silver Chub sampled from Lake Erie in the 1950s and in 2000. Kinney (1954) sampled, measured, and aged 1,720 Silver Chub each month between 1952 and 1954, and reported the mean length for each age class in each month. Ages reported in Kinney (1954) were adjusted for sampling month and lengths were converted from standard length (SL) to total length (TL) using the relationship reported by Kinney (1954). Silver Chub were sampled from Lake Erie in 2000, and were also aged (n=110). Growth of Silver Chub appears not to have changed since Kinney's sampling. Data from both sources were therefore pooled to determine growth patterns for Silver Chub.

The growth pattern was determined by fitting a von Bertalanffy growth curve to the length-at-age data by the method of non-linear least squares (Baty and Delignette-Muller 2009) (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 total length (TL) 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.

Table 1. Values, symbols, descriptions, and sources for all parameters used to model Silver Chub.

Vital Rate	Description	Symbol	Estimate	Source / Reference
Growth	Asymptotic size	L_∞	219.4 (211–231)	von Bertalanffy growth model fitted to Canadian data
	Growth coefficient	k	0.596 (0.499–0.689)	
	Age at 0 mm	t_0	-0.12 (-0.26-0.02)	
Mortality	Instantaneous mortality at stage *j*	M_j	Mean adult: 0.88 (+/-0.05)	(Froese and Pauly 2012)
	Mean annual environmental temperature	C	10.8ºC	(Kinney 1954)
	Instantaneous mortality at unit size	m_0	128.4 (+/- 7.2)	Equation (2)
Mean annual survival	Young-of-the-year (YOY)	σ_1	0.00018 – 0.00189	Equation (3), Table 2, Kinney (1954), Mandrak unpubl. data
	Adult	σ_2, σ_3	0.38 – 0.51	
Fecundity	Fertility (egg count per year)	η_j	1083 – 12923	(Kinney 1954)
	Proportion female	φ	0.5	Assumed
	Proportion reproductive at age *j*	ρ_j	$\rho_{1,2,3} = 1$	Assumed
	Spawning periodicity	T	1	Assumed
	Annual female offspring of age *j*	f_j	541 – 6462	Equation (2)
Matrix	Effective fecundity (average female offspring for class *j*)	F_j	0.1 – 3327	Equation (1), (Caswell 2001)
	Maximum age	T_{max}	4	(COSEWIC 2012)
	Age at maturity	T_{mat}	1	(COSEWIC 2012)
Analysis	Annual population growth rate	λ	0.8	(Caswell 2001; Ohio Division of Wildlife 2013; OMNR 2013)
	Generic vital rate (survival, maturity, fertility)	v		(Caswell 2001; Morris and Doak 2002)
	Elasticity (proportional sensitivity of rate *v*	ε_v		Equation (4), (Caswell 2001)
	Allowable chronic harm	H_c		Equation (5)
	Allowable transient harm	H_t		

Table 2. Age specific life history values (length, fertility at age j, survival from age j-1 to age j) used in the population model for Silver Chub. Standard deviation (fertility and survival) or 95% bootstrapped confidence (growth) are in brackets.

Age		1	2	3	4
Growth (TL mm)		106.6 (102.7 – 110.1)	157.2 (154.3 – 160.0)	185.1 (183.0 – 187.1)	200.6 (197.1 – 203.8)
Fertility (*η*)		1,083 (84.5)	4,491 (211.0)	9,062 (338.5)	12,923 (719.0)
Survival (*σ*)	growing	0.00189 (0.25)	0.38 (0.018)	0.47 (0.018)	0.52 (0.020)
	stable	0.000335 (0.25)	0.38 (0.018)	0.47 (0.018)	0.52 (0.020)
	declining	0.000185 (0.25)	0.38 (0.018)	0.47 (0.018)	0.52 (0.020)

Mean adult mortality (*M*) was estimated from the von Bertalanffy parameters and mean annual temperature in ºC (*C*) using the following equation from the Life History Tool in Fishbase (Froese and Pauly 2012) (an update of the Pauly (1980) equation):

(1) $$\log_{10} M = -0.65 - 0.287 \cdot \log_{10} L_\infty + 0.604 \cdot \log_{10} k + 0.513 \cdot \log_{10} C \quad .$$

Mean annual temperature was approximated from Figure 13 in Kinney (1954), using image software (Tummers 2006), to be 10.8 ºC.

Age-dependent survival was estimated from mean adult mortality by combining a size-dependent mortality model (Lorenzen 2000) with the estimated growth parameters. Mortality was assumed to decline proportionally with increases in size (Lorenzen 2000) such that

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

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

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

The parameter m_0 was estimated from equation (2) using the geometric mean size of adults between ages 1 and 4 and the mean instantaneous mortality (equation (1)). YOY survival was estimated in three ways: i) by assuming a stable population growth rate (λ=1) and solving for first year survival, ii) by assuming the population growth rate equals the maximum rate of growth at low densities for a fish of this size, based on the allometric relationship for freshwater fishes between production per unit biomass and adult weight (λ=2.2) (Randall and Minns 2000), and iii) by assuming the average rate of decline since 2000 (λ=0.8). Variation in the fitted growth curve parameters was estimated using bootstrap resampling and translated into variance in length-at-age and annual survival-at-length.

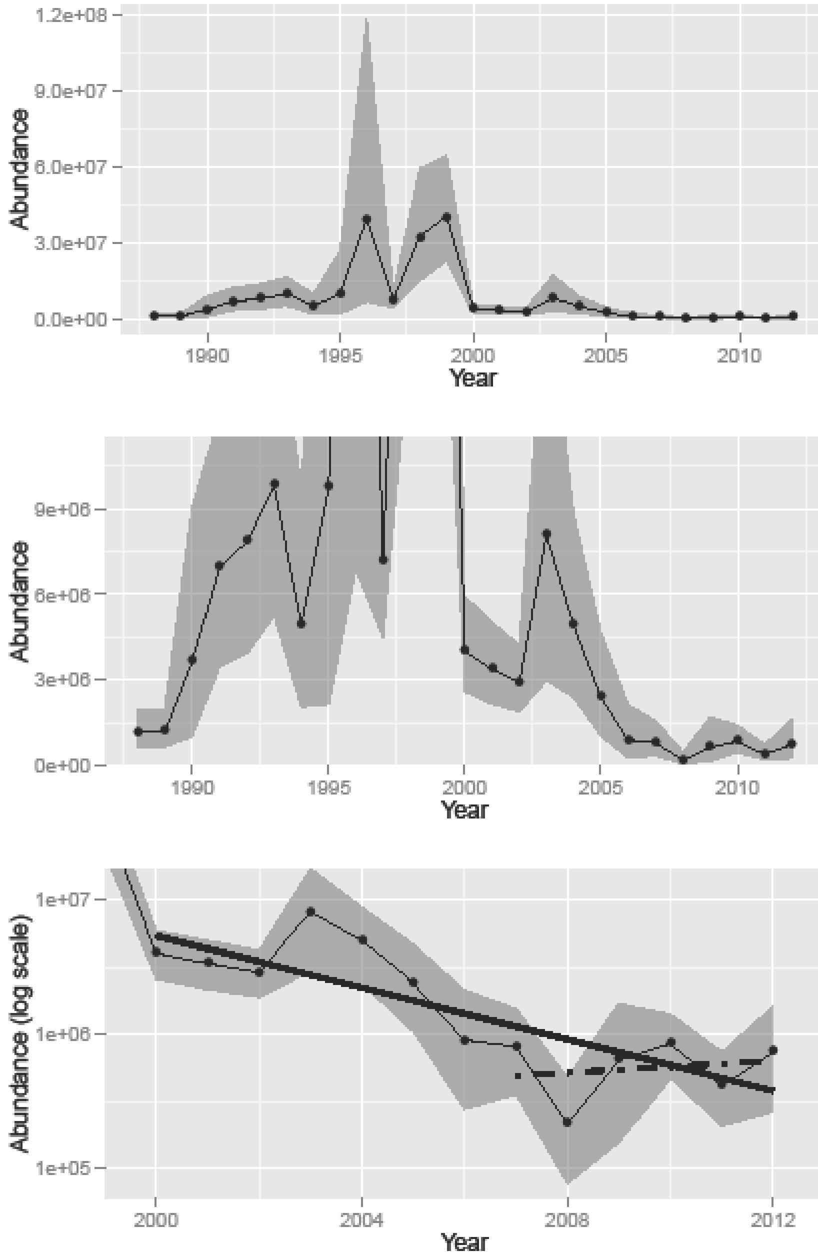


Figure 2. (top) Abundance of Silver Chub in the Western basin of Lake Erie from 1988 – 2012. (middle) Abundance with high range (boom years) excluded. (bottom) Logged abundance from 2000 – 2012 with lines of best fit from 2000 – 2012 (solid) and from 2007 – 2012 (dashed) showing trends of long-term decline and more recent slight growth, respectively. Abundances based on geometric mean fish per hectare and 95% quasi Poisson confidence intervals (shaded).

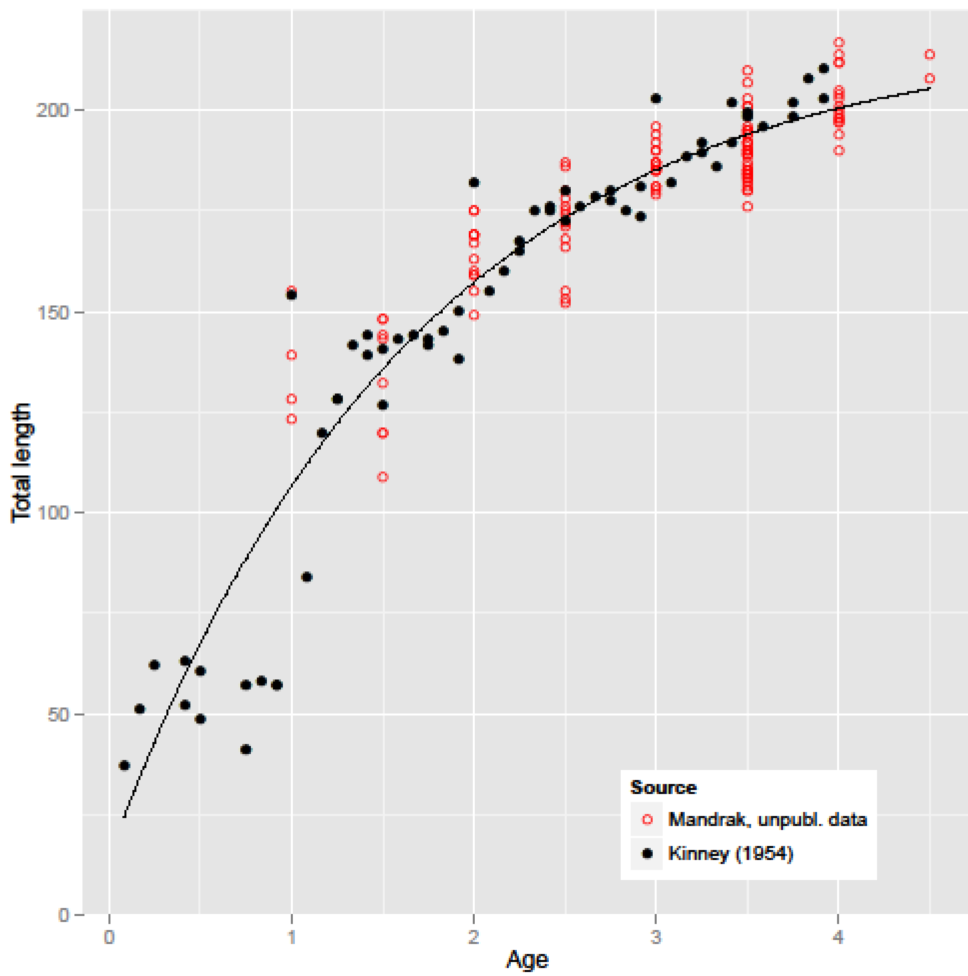


Figure 3. Size at age of Canadian Silver Chub with fitted von Bertalanffy growth curve; actual observations (2000) and mean monthly size (1952-1953). Ages from Kinney (1954) have been adjusted for sampling month.

Fecundity

Age-specific fecundity was based on relationships reported by Kinney (1954) between total length, standard length, body weight, ovary weight, and fecundity. Variance in length-at-age was combined with variance in ovary weight by body weight to provide boundaries for fecundity-at-age. These boundaries were assumed to contain four standard deviations of the mean fecundity-at-age. Generation time was calculated from the age-specific survival and fecundity estimates as per Caswell (2001), and equaled 2.5 years.

POPULATION SENSITIVITY

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:

$$\varepsilon_v = \frac{v}{\lambda} \sum_{i,j} \frac{\partial \lambda}{\partial a_{ij}} \frac{\partial a_{ij}}{\partial v}, \tag{4}$$

where, 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 to (i) generate 5,000 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. The elasticity estimation was repeated for both growing and stable populations.

ALLOWABLE HARM

Allowable harm is defined as harm to the population that will not jeopardize population recovery or survival. Chronic harm refers to a negative alteration to a vital rate (survival, fecundity, etc.) that reduces the annual population growth rate permanently or over the long term. Transient harm refers to a one-time removal of individuals such that survival (and therefore population growth rate) is only affected in the year of the removal.

Estimates of allowable chronic harm are based on the population growth rate. We estimate allowable chronic harm assuming the estimated mean growth rate over the last 6 years (λ=1.04), and a minimum acceptable population growth rate of stability (λ=1). Maximum allowable chronic harm (H_c) was estimated analytically as:

$$\mathrm{H} = \left(\frac{1}{\varepsilon_v}\right)\left(\frac{1-\lambda}{\lambda}\right) \tag{5}$$

where ε_v is the elasticity of vital rate v, and λ is population growth rate in the absence of additional harm.

We modelled the effects of transient harm as follows: (i) annual projection matrices were generated for a given timeframe by randomly drawing vital rates based on the means, variances, and distributions as in the sensitivity analysis; (ii) survival of either juveniles, adults, or both was reduced for one of the random matrices, simulating a one-time removal of individuals; (iii) the mean population growth rates before and after removal were compared over the timeframe considered; (iv) this simulation was repeated 5,000 times to create a distribution of changes in population growth rate as a result of removal; (v) several rates of removal (number of individuals as a proportion of total abundance) were considered.

We defined allowable transient harm as a one-time removal of individuals, within a time-frame of 10 years or three generations (whichever is shorter), that does not reduce the average population growth rate over that time-frame more than a pre-determined amount. The population growth rate was considered to be “reduced” when the lower confidence bound of the distribution of differences in growth rate pre- and post-removal exceeded the designated amount.

RECOVERY TARGETS

Abundance

We used demographic sustainability as a criterion to set recovery targets for Silver Chub. Demographic sustainability is related to the concept of a MVP (Shaffer 1981), and was defined as the minimum adult population size that results in a desired probability of persistence over 100 years (40 generations for Silver Chub).

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, YOY survival was reduced to achieve a geometric mean growth rate (in stochastic simulations) of λ=1.

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 λ=1; (ii) projection matrices were drawn at random from these to generate 5,000 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, 0.01, 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 (age 1+) individuals.

Risk at Current Abundance

Projections were repeated assuming the average rate of decline since 2000 (λ=0.8). We used 3,000 realizations of population size over 250 years to generate a median (and 95% bootstrapped confidence) time to extirpation and results were averaged over 5 runs. This process was repeated for various population abundances.

Habitat: Minimum Area for Population Viability

Following Vélez-Espino et al. (2010), we estimate the 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:

$$MAPV_j = MVP_j \cdot API_j. \tag{6}$$

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 λ = 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 lake environments from Randall et al. (1995). This allometry approximates API_j for freshwater fishes based on the mean TL in mm of class j:

$$API = e^{-13.28} \cdot TL^{2.904} \tag{7}$$

Mean TL at each age was used to calculate API_j). MAPVs for each age class were estimated from equations (6) and (7), and the MAPV for the entire population was estimated by summing across all stages. MAPV was compared to the total area available for the Canadian population.

RESULTS

POPULATION SENSITIVITY

Silver Chub population growth is most sensitive to changes in survival in the first year (Figure 4). This is especially true if the population is growing. Stable or declining populations are more sensitive to changes in cumulative adult survival than YOY survival (Table 3). Fecundity has less influence on population growth rate of declining or stable populations than of growing populations. Uncertainty in population sensitivity (error bars in Figure 4) is driven by uncertainty in YOY survival.

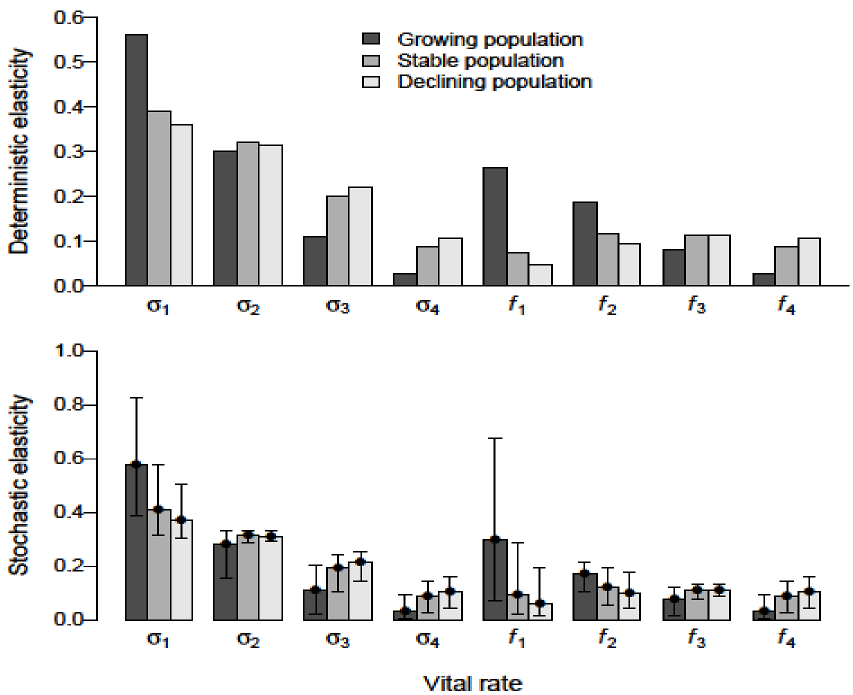


Figure 4. Results of the deterministic (upper panel) and stochastic (lower panel) perturbation analysis showing elasticities (ε_v) of vital rates for Silver Chub: annual survival probability from age j-1 to age j (σ_j) and fecundity at age j (f_j). Results for a growing, stable, or declining population are compared. Stochastic results include associated bootstrapped 95% confidence interval. Exact values listed in Table 3.

Table 3. Summary of elasticities of Silver Chub vital rates (ε_v), and allowable chronic harm (as a proportion of the vital rate, H_c) for a population at maximum growth (λ=2.2), a population at mean growth rate since 2007 (λ=1.04), a stable population (λ=1) and a declining population (λ=0.8). Shown are elasticities for: annual survival of YOY (σ_1), cumulative adult survival (σ_a), fecundity of first time spawners (f_1) and cumulative fecundity of all ages (f_n). Recommended values for allowable chronic harm (based on the precautionary principle) are highlighted.

Vital rate	**σ_1**		**σ_a**		**f_1**		**f_n**	
Measurement	**ε**	**H**	**ε**	**H**	**ε**	**H**	**ε**	**H**
Maximum growth								
Deterministic mean	0.56	-0.96	0.44	-2.06	0.26	-1.24	0.56	-0.97
Stochastic mean	0.57	-0.99	0.43	-1.94	0.29	-1.32	0.57	-0.99
Lower confidence	0.82	-0.68	0.63	-0.83	0.67	-0.90	1.1	-0.51
Upper confidence	0.39	-1.46	0.17	-8.26	0.07	-3.38	0.19	2.96
Possible current growth								
Deterministic mean	0.40	-0.03	0.60	-0.02	0.08	-0.13	0.40	-0.03
Stochastic mean	0.41	-0.09	0.59	-0.06	0.10	-0.38	0.41	-0.09
Lower confidence	0.58	-0.06	0.72	-0.05	0.30	-0.13	0.76	-0.05
Upper confidence	0.32	-0.12	0.41	-0.09	0.02	-1.20	0.17	-0.21
Stable								
Deterministic mean	0.39	0	0.61	0	0.07	0	0.39	0
Stochastic mean	0.41	0	0.59	0	0.09	0	0.41	0
Lower confidence	0.58	0	0.72	0	0.29	0	0.75	0
Upper confidence	0.32	0	0.42	0	0.02	0	0.17	0
Declining								
Deterministic mean	0.36	0	0.64	0	0.05	0	0.36	0
Stochastic mean	0.37	0	0.63	0	0.06	0	0.37	0
Lower confidence	0.5	0	0.74	0	0.19	0	0.65	0
Upper confidence	0.3	0	0.48	0	0.01	0	0.18	0

ALLOWABLE HARM

Allowable Chronic Harm

Estimates of the maximum allowable harm to vital rates depended on the population growth rate and the stochastic element (e.g., mean or upper or lower 95% confidence level). From a precautionary perspective (i.e., assuming a lower 95% confidence level), and assuming the mean population growth rate from 2007-2012 (λ=1.04), our results suggest a maximum allowable reduction of 3% to juvenile survival, 2% to survival of adults (ages 1+) *or* 3% to fecundity of all ages (Table 3). Allowable chronic harm is larger if the population is growing at a faster rate, and is 0 if it is not growing. If human activities are such that harm exceeds just one of these thresholds, the future persistence of populations is likely to be compromised. In addition simulations suggest that recovery time can be severely delayed by any levels of harm within the maximum allowable harm suggested in Table 3 (Young and Koops 2011).

Allowable Transient Harm

The generation time for Silver Chub was estimated to be 2.5 years. Therefore, a time-frame of 7 years (~ 3 generations) was considered for transient harm. The decline in average growth rate increased exponentially with larger removal rates of individuals. The change in growth rate was similar when either YOY *or* adults were removed, and larger if both YOY and adults were removed (). The change in growth rate was similar for initial growth rates of λ=1 and λ=1.04 (Figure 6). Allowable transient harm (allowable one time removal, performed no more frequently than every 7 years) can be extracted from Figure 6 by determining the percent removal that is associated with an acceptable reduction in the population growth rate over that time period (following the curve for the life stage being removed). We suggest that the lower confidence bounds be used, as they represent a true change in the population growth rate beyond that which might result simply from environmental stochasticity (Figure 6). Allowable transient harm may also differ depending on the population growth rate; a growing population may be able to sustain a larger removal, without going into decline, than a stable population. For example, if an acceptable change in the population growth rate is 0.01 for a stable population, the allowable one-time removal every 7 years is 23.5% of YOY or 15% of adults or 8.5% of all individuals (Figure 6 left, Table 4). An acceptable change in population growth rate for a population growing at a rate of λ=1.04 may be 0.04. This would yield an allowable removal of 66.5% of YOY or 54% of adults or 33.5% of all individuals every 7 years (Figure 6 right, Table 4).

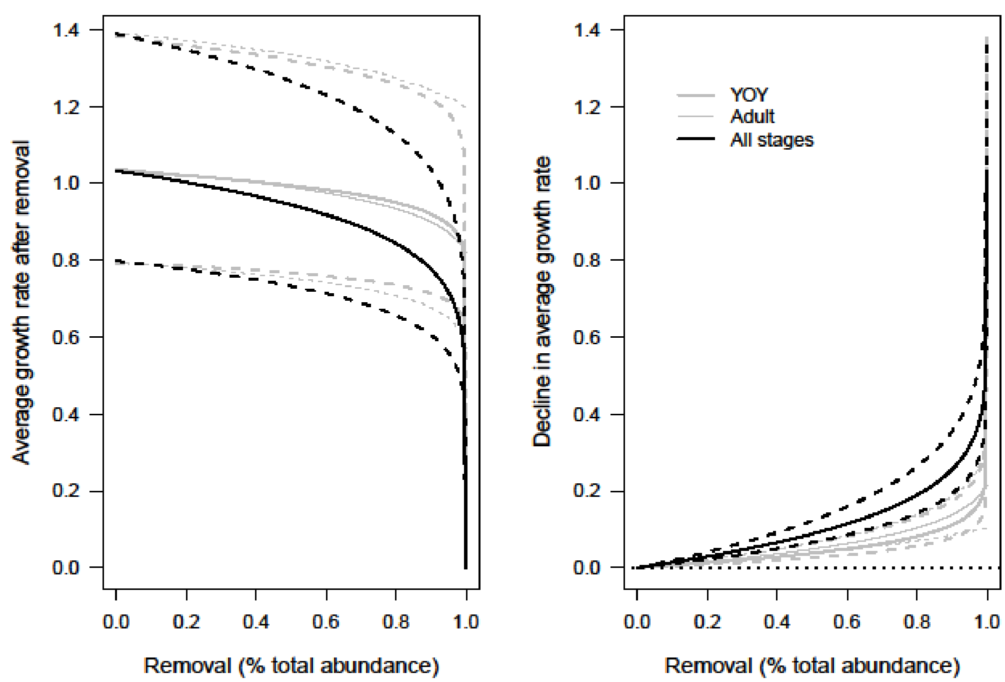


Figure 5. Average growth rate (left) and decline in average growth rate (right) for a population growing at a rate of λ=1.04 over 7 years, as a function of the percent of individuals removed from the population in one of 7 years. Means (solid lines), bootstrap 95% confidence intervals (dashed lines) and a reference line at 0 change (dotted line) are shown. Results for removal of YOY only, adults only, or all stages are compared.

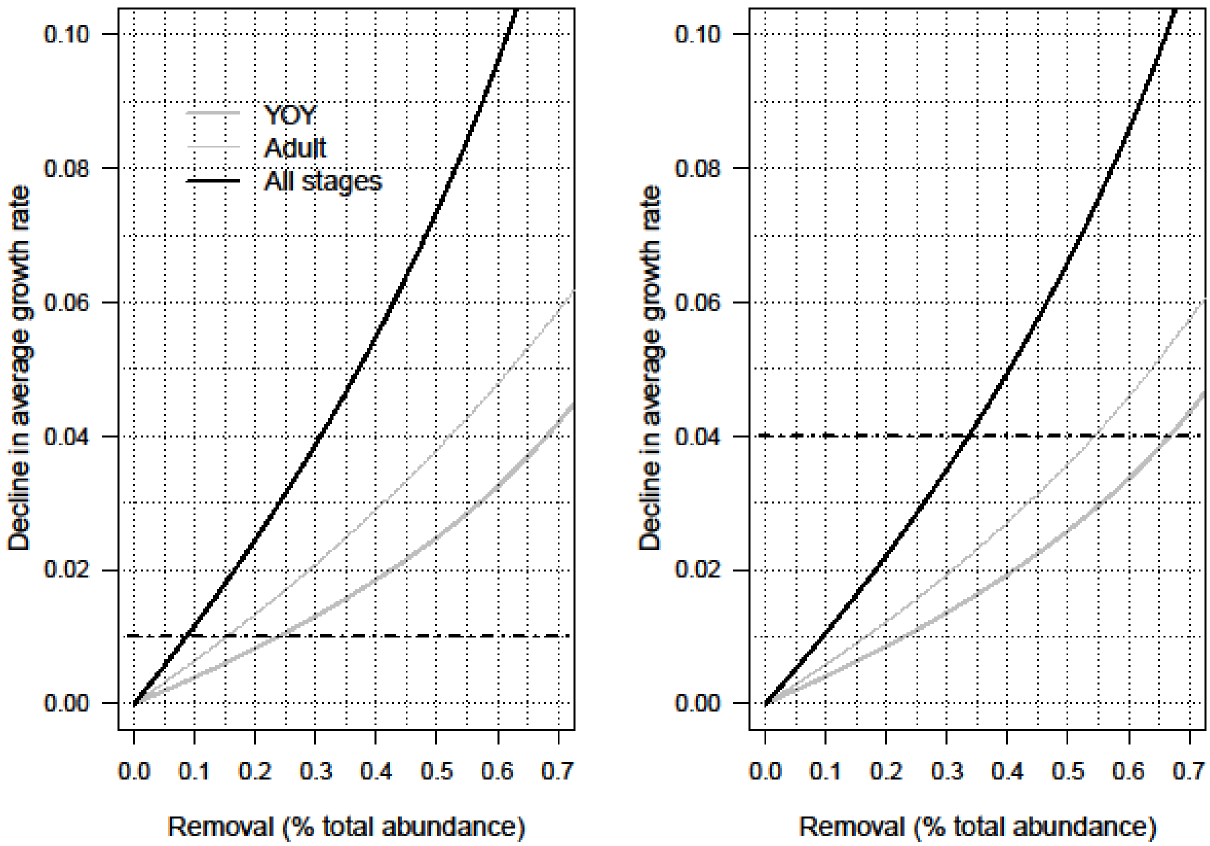


Figure 6. Decline in average population growth rate of a stable population (left) or a population growing at a rate of λ=1.04 (right) over 7 years, as a function of the percent of individuals removed from the population in one of 7 years. Results for removal of YOY only, adults only, or all stages are compared. Values shown are the lower confidence bounds from.

The figures here represent removal rates (i.e., a percent of the total population). Absolute numbers can be determined from the removal rates by multiplying by the total population abundance for the appropriate life stage. For example, the current population is estimated at ~662,000 (95% confidence: 266,000 – 1,619,700) (Ohio Division of Wildlife 2013; OMNR 2013). Assuming a stable population and an acceptable reduction in growth rate of 1%, using the mean estimate of population abundance implies an allowable transient harm of 99,300 adults (harm to adults only) *or* 2.65×10^8 fry (harm to YOY only) *or* 56,300 adults and 9.6×10^7 YOY (harm to all life stages) over 7 years (see Table 4 for allowable transient harms based on the abundance confidence interval, and for examples of transient harms to growing populations resulting in 1, 2 and 4% changes in growth rate). Absolute numbers of individuals can also be calculated deterministically (i.e., ignoring environmental variation) given the population abundance (N_0), acceptable change in mean population growth rate (Δλ), and the survival rate of stage class j (σ_j):

(8) $h_j = \Delta\lambda \cdot N_0 \cdot \sigma_j$.

Table 4. Transient allowable harm: Removal rates per 7 years that result in a 1, 2 or 4% change in mean population growth rate over 7 years, where a change in growth rate is considered to have occurred when the lower confidence bound (Figure 6) of simulated changes in growth rate () reaches the threshold change. Absolute numbers correspond to the estimated population abundance of 662,000, (95% confidence: 266,000 – 1,619,700). Two population growth rates are compared: stability (λ=1) and slight growth (λ=1.04).

Model	**Removal**	**YOY only**	**Adult only**	**YOY and adult (total)**	**Change in growth rate**
Stable	Rate	0.235	0.15	0.085	-0.01
	Number	2.65 E8 (1.06 E8 – 6.48 E8)	99,300 (39,900 – 243,000)	56,270 adults (22,600 – 137,700)	
Growing	Rate	0.225	0.165	0.09	-0.01
	Number	1.4 E8 (1.02 E8 – 6.21 E8)	109,200 (43,900 – 267,300)	56,600 adults (23,900 – 145,800)	
Growing	Rate	0.41	0.305	0.18	-0.02
	Number	2.6 E8 (1.86 E8 – 1.13 E9)	201,900 (81,100 – 494.000)	119,200 adults (47,900 – 291,500)	
Growing	Rate	0.665	0.54	0.335	-0.04
	Number	4.2 E8 (3.01 E8 – 1.84 E9)	357,500 (143,600 – 874,600)	221,800 adults (89,100 – 542,600)	

RECOVERY TARGETS

Abundance Targets (MVP)

Probability of extinction decreases as a power function of population size (Figure 7). 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 recovery effort, longer time to recovery, 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 approximately 6,800 adults (ages 1+) (range 3,400 – 10,600) when the probability of catastrophic decline (50% decline) was assumed to be 10% per generation (4.1% annually). If catastrophes occurred at 15% per generation (6.3% annually), MVP was approximately 30,400 adults (range 20,400 – 52,800). In both scenarios, the cumulative probability of extinction for the respective MVPs was approximately 0.01 over 100 years (Figure 7). The extinction risk, P(ext.), for the 10% (Equation (9)) or 15% (Equation (10))

per generation catastrophe scenario can be defined as a function of initial adult population, N, as:

(9) $P(ext.) = 7 \cdot N^{-0.770}$

(10) $P(ext.) = 24 \cdot N^{-0.771}$.

If catastrophes occur at 15% per generation and the recovery target is set based on an assumption that catastrophes occur at 10% per generation, the risk of extinction will be 3 times greater than expected.

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 10% per generation, mean MVP increases from ~6,800 to ~101,100 (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 10 and 15%, respectively, are as follows:

(1) $P(ext.) = 27 \cdot N^{-0.709}$

(2) $P(ext.) = 46 \cdot N^{-0.671}$

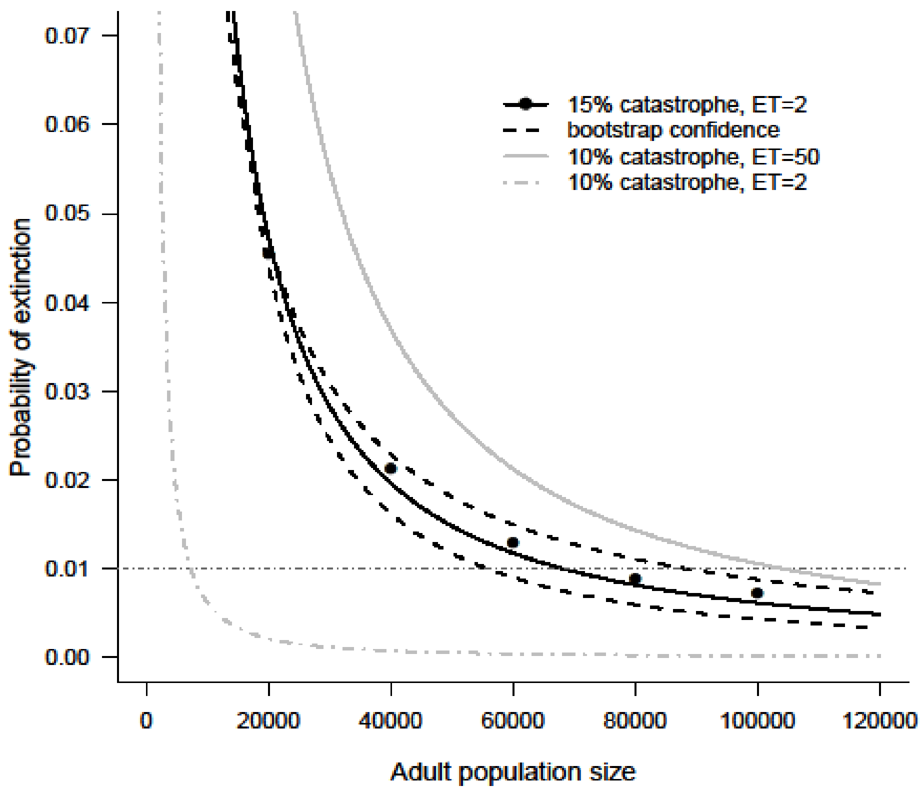


Figure 7. Probability of extinction within 100 years of 10 simulated Silver Chub populations, at equilibrium, as a function of adult population size. Curves represent different combinations of the probability of catastrophe per generation (%), and quasi-extinction thresholds (ET). Dashed horizontal reference line is at 0.01 and intersects curves at the associated MVPs (Table 5).

Risk at Current Abundance

Based on the current population estimate of 662,000 (266,000 – 1,619,700), if the Silver Chub population is at least stable (and not in decline) the current risk of extirpation is 0.57% (0.31 - 1.05%) over the next 100 years (assuming 15% per generation catastrophes and an extinction threshold of 50 adults; Equation (2)).

Since 2000, the average growth rate for Silver Chub has been 20% annual decline (λ=0.8). If this trend continues, and assuming a current abundance of 662,000 adults, the time to extirpation is expected to be 73 years (95% bootstrap confidence: 40 – 120 years) if no catastrophic events occur. If there is a 15% probability of catastrophe per generation, the time to extirpation is expected to decrease to 58 years (95% bootstrap confidence: 36 – 95 years). This time could decrease dramatically if the true abundance is lower (Figure 8).

Table 5. 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 6). Results for two different extinction thresholds, four probabilities of catastrophe, and two levels of extinction risk are shown.

Extinction Threshold	Generational Catastrophe	Extinction Risk	Equation	Age Class	MVP	MAPV
				YOY	5,016,959	0.5
2 adults	15%	0.05	(10)	1+	2,945	0.0
				Total		0.6
				YOY	8,221,841	0.8
50 adults	0%	0.01		1+	4,826	0.1
				Total		0.9
				YOY	11,475,823	1.2
2 adults	10%	0.01	(9)	1+	6,736	0.1
				Total		1.3
				YOY	32,372,861	3.3
50 adults	5%	0.01		1+	19,002	0.3
				Total		3.6
				YOY	44,067,714	4.5
50 adults	15%	0.05	(2)	1+	25,867	0.4
				Total		4.9
				YOY	51,729,795	5.3
2 adults	15%	0.01	(10)	1+	30,364	0.4
				Total		5.8
				YOY	172,181,645	17.8
50 adults	10%	0.01	(1)	1+	101,066	1.4
				Total		19.1
				YOY	755,595,058	77.9
50 adults	15%	0.01	(2)	1+	443,514	6.1
				Total		84.0

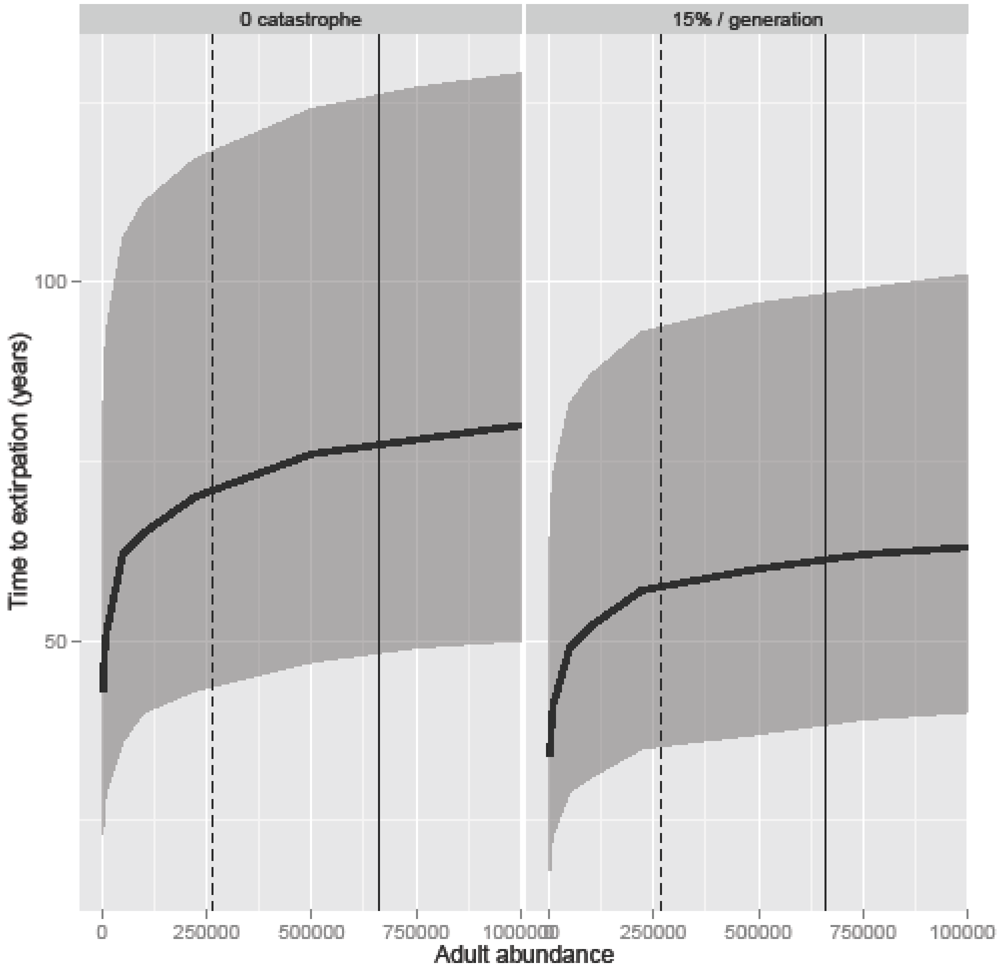


Figure 8. Median time to extirpation of simulated Silver Chub populations in decline (λ = 0.8), as a function of adult population size, with 95% bootstrapped confidence interval (shaded). Two catastrophe scenarios are shown: no catastrophes (left), and 15% probability per generation (right). Vertical reference lines represent the current estimated population abundance (662,000, solid) and lower confidence bound (266,000, dashed).

Table 6. Stable stage distribution (SSD; percentage of the population in each stage, assuming a post-breeding census. i.e., the YOY class is newly hatched, age 1 have just had their first birthday, etc.) and required area per individual (API) for each age class.

Age class	**SSD (%)**	**API (m^2)**
YOY	99.942	0.1
1	0.034	8.8
2	0.013	18.0
3	0.006	24.6
4	0.003	28.8

Habitat Targets (MAPV)

The stable stage distribution of Silver Chub is 99.942% YOY, and 0.058% adults (Table 6). Note that this distribution assumes a post-breeding census such that the YOY class consists of individuals that are newly hatched, the age-1 class have just had their first birthday, etc. MAPV ranged from 0.6 km^2 for an MVP of ~3,000 adults to 84 km^2 for a target of 444,000 adults (Table 5). We recommend the MAPV that corresponds to a probability of catastrophe of 15%, an extinction threshold of 50 adults, and an extinction risk of ~0.01 (the most conservative scenario). These areas assume that each individual requires the areas (API) listed in Table 5, and does not account for any overlapping of individual habitats (sharing) that may occur. It is important to note that this area is based on an allometry of fish density per fish size and does not include any additional space requirements for the completion of life stages.

The estimated available habitat (i.e., total lake surface area) for Silver Chub in the West Basin of Lake Erie is over 3000 km^2, which greatly exceeds the required area. This estimate assumes, however, that the entire basin is suitable Silver Chub habitat. If certain areas of the current available habitat are deemed partially unsuitable, the total minimum required area should be increased.

DISCUSSION

Our results show that to avoid jeopardizing the survival and future recovery of Silver Chub, human-induced harm to the annual survival of juveniles should be minimal. For a population in decline, harm to the survival of adults should be minimized also.

If the Silver Chub population is growing, chronic harm may be allowed but should not exceed 3% reduction of juvenile survival, 2% of adult survival (ages 1+) *or* 3% of fecundity of all ages. Transient harm may be allowed if the population is not in decline. Removal of 23.5% of YOY or 15% of adults or 8.5% of all individuals will result in a 1% decline in population growth rate for a stable population. Removal of 66.5% of YOY or 54% of adults or 33.5% of all individuals every 7 years will reduce the growth rate by 0.04 if the population is growing at λ=1.04 (i.e., this removal will result in a stable population). Absolute numbers for removal should be chosen based on the population abundance (see Table 4 for absolute numbers given estimates of current population abundance). Allowable transient harm may be greater if population abundance is determined to be higher than the current estimate, or if the population is growing at a faster rate. We caution that any removal affects population growth rate and will delay recovery, and that current population abundance estimates are very uncertain.

Recovery targets, based on the concept of MVP, were presented for a variety of risk scenarios. Recommended MVP targets for Silver Chub were 444,000 adults (ages 1+), assuming the probability of a catastrophic (50%) decline was 0.15 per generation and an extinction threshold of 50 adults. Recommended MAPV for Silver Chub was 84 km^2 of suitable habitat. This required area is met and exceeded by the estimated available habitat in the Western Basin of Lake Erie, assuming that the entire basin is suitable habitat for Silver Chub.

We emphasize that the choice of recovery target is not limited to the recommended target, or to the scenarios presented in Table 5. Required adult population sizes can be calculated for any alternative probability of extinction using one of equations (9) to (2) depending on which risk scenario (probability of catastrophe and extinction threshold) best represents the Canadian populations of Silver Chub, and what level of risk is considered acceptable.

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. Abundance time series for Silver Chub in Lake Erie suggest that catastrophic decline is occurring at a much higher frequency; 8 out of 24 years had growth rates of λ<0.53 (i.e., at least 47% annual decline). Since the large boom and crash in 2000, 5 out of 12 years have had >47% decline in abundance. This suggests an underlying problem beyond the expected frequency of catastrophic decline. We therefore modelled recovery targets assuming a stable population with the most conservative catastrophe scenario, based on Reed et al. (2003), of 15%. Time to extirpation was modelled assuming the rate of decline of $\lambda=0.8$ and therefore incorporated the increased frequency of catastrophic decline. The underlying pattern of decline will need to be addressed to ensure the persistence of Silver Chub.

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).

UNCERTAINTIES

Some elements of the life history of Canadian Silver Chub are unknown. While individual growth of Silver Chub has been well studied and seems consistent over time, annual mortality is not known for any age class, and was estimated using an allometry based on growth patterns.

Past and current population trajectory is well established. Silver Chub in Lake Erie have experienced two large booms and subsequent crashes, followed by 12 years of 20% annual decline (on average). The rate of decline has decreased over time and the population may be stabilizing. The uncertainty around the more recent estimate of stability is very large (ranging from 31% decline to 55% growth), and continued monitoring is required to confirm the current trajectory and predict future abundances. In addition, current population abundance estimates are very uncertain (large variation in annual estimates). Incorrect assumptions regarding abundance will affect estimates of population trajectory, and may result in profound changes in allowable harm advice. Uncertainty in population abundance should be reduced.

Our estimates of required habitat (MAPV) assume that habitat is of high quality throughout the range of Silver Chub. We did not have sufficient data to either confirm, or provide an alternative to this assumption. The estimated available habitat exceeds the estimated requirement for Silver Chub. However, this could be misleading if the quality of habitat is not sufficient throughout the estimated area. Further study is needed to assess the suitability of habitat.

Finally, predictions from this model assume random mating and complete mixing of the population (i.e., all individuals interact and can reproduce with one another). This assumption should be considered when applying MVP targets, and larger total targets should be set if the assumption does not hold.

REFERENCES CITED

Baty, F., and Delignette-Muller, M.L. 2009. nlstools: Tools for nonlinear regression diagnostics. R package version 0.0-9.

Beissinger, S.R., and McCullough, D.R. 2002. Population viability analysis. University of Chicago Press, Chicago, Illinois.

Caswell, H. 2001. Matrix population models: construction, analysis, and interpretation. 2nd Ed., Sinaur Associates, Sunderland, Massachusetts.

COSEWIC. 2012. COSEWIC assessment and status report on the Silver Chub *Macrhybopsis storeriana* in Canada. Committee on the Status of Endangered Wildlife in Canada. Ottawa. xiii + 34 p.

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

DFO. 2007a. Documenting habitat use of species at risk and quantifying habitat quality. DFO Can. Sci Advis. Sec. Sci. Advis. Rep. 2007/038.

DFO. 2007b. Revised protocol for conducting recovery potential assessments. DFO Can. Sci. Advis. Sec. Sci. Advis. Rep. 2007/039.

Froese, R., and Pauly, D. 2012. FishBase. World Wide Web electronic publication version 10/2012. .

Kinney, E.C., Jr. 1954. A Life History Study of the Silver Chub, *Hybopsis storeriana* (Kirtland), in Western Lake Erie with Notes on Associated Species. Thesis (PhD). Ohio State University, Columbus, Ohio. iv + 78 p.

Lorenzen, K. 2000. Allometry of natural mortality as a basis for assessing optimal release size in fish-stocking programmes. Can. J. Fish. Aquatic Sci. 57(12): 2374-2381.

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

Ohio Division of Wildlife. 2013. Ohio's Lake Erie Fisheries 2012. Annual Status Report. Federal Aid in Fish Restoration Project F-69-P. Ohio Department of Natural Resources, Division of Wildlife, Lake Erie Fisheries Units, Fairport and Sandusky.

OMNR. 2013. 2013 Status of Major Stocks. Lake Erie Management Unit, ISSN 1718-4924 (Print), ISBN 978-1-4606-1011-4 (Print), ISSN 1925-5454 (Online), ISBN 978-1-4606-1012-1 (PDF).

Pauly, D. 1980. On the interrelationships between natural mortality, growth parameters, and mean environmental temperature in 175 fish stocks. J. Cons. int. Explor. Mer 39: 175-192.

R Development Core Team. 2012. R: A language and environment for statistical computing. Vienna, Austria: R Foundation for Statistical Computing. ISBN 3-900051-07-0. .

Randall, R.G., and Minns, C.K. 2000. Use of fish production per unit biomass ratios for measuring the productive capacity of fish habitats. Can. J. Fish. Aquat. Sci. 52(3): 631-643.

Randall, R.G., Kelso, J.R.M., and Minns, C.K. 1995. Fish production in freshwaters: are rivers more productive than lakes? Can. J. Fish. Aquat. Sci. 52(3): 631-643.

Reed, D.H., O'Grady, J.J., Ballou, J.D., and Frankham, R. 2003. The frequency and severity of catastrophic die-offs in vertebrates. Anim. Conserv. 6(2): 109-114.

Shaffer, M.L. 1981. Minimum population sizes for species conservation. BioScience 31(2): 131-134.

Tummers, B. 2006. Data Thief III.

Vélez-Espino, L.A., and Koops, M.A. 2007. Recovery potential assessment of an extirpated population: Lake Ontario Atlantic Salmon (*Salmo salar*). DFO Can. Sci. Advis. Sec. Sci. Res. Doc. 2007/083: 27 p.

Vélez-Espino, L.A., and Koops, M.A. 2009a. Quantifying allowable harm in species at risk: Application to the Laurentina Black Redhorse (*Moxostoma duquensnei*). Aquat. Conserv.: Mar. Freshwat. Ecosyst. 19: 676-688.

Vélez-Espino, L.A., and Koops, M.A. 2009b. Recovery potential assessment for Lake Sturgeon in Canadian designatable units. N. Am. J. Fish. Manag. 29: 1065-1090.

Vélez-Espino, L.A., Randall, R.G., and Koops, M.A. 2010. Quantifying habitat requirements of four freshwater species at risk in Canada: Northern Madtom, Spotted Gar, Lake Chubsucker, and Pugnose Shiner. DFO Can. Sci. Advis. Sec. Res. Doc. 2009/115. iv. + 21 p.

Young, J.A.M., and Koops, M.A. 2011. Recovery potential modelling of Lake Chubsucker (*Erimyzon sucetta*) in Canada. DFO Can. Sci. Advis. Sec. Res. Doc 2011/049. iv + 20 p.