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Recovery Potential Modelling of Warmouth (*Lepomis gulosus*) in Canada

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Foreword

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

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ABSTRACT

The Committee on the Status of Endangered Wildlife in Canada (COSEWIC) has assessed the Warmouth (*Lepomis gulosus*) as Endangered in Canada. Here a population model is presented to assess stage-specific harm, inform population-based recovery targets, and quantify required habitat in support of a recovery potential assessment (RPA). Data were lacking for Canadian populations of Warmouth with model parameters taken from American populations. As well, simulations accounted for uncertainty in the extent of intra-annual correlation among vital rates through inclusions of three levels of parameter correlation (independent, medium correlation, and strong correlation) which strongly influenced model outputs. Warmouth populations were sensitive to perturbations to the adult stage (and age-1+). Harm affecting this portion of the life cycle should be minimized to avoid jeopardising survival and recovery of Canadian populations. Results of population viability analysis were highly dependent on the extent of intra-annual correlation among stochastic variables included in analysis. To achieve demographic sustainability (i.e., a self-sustaining population over the long term) population sizes ranging from 6,302 (using an independent correlation structure) to 383,291 (using a strong correlation structure) were required. Populations of these sizes required 41 to 2,477 ha of Warmouth exclusive habitat (assuming shared young-of-the year and age-1+ habitat). Values estimated with use of an independent correlation structure are consistent with the approaches implemented in previous RPA analysis.

INTRODUCTION

Warmouth (*Lepomis gulosus*) has been designated as Endangered by the Committee on the Status of Endangered Wildlife in Canada (COSEWIC 2015). 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, b) 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 - that are further broken down into 22 elements. This report contributes to components two and three and elements 3, 12, 13, 14, 15, 19, 20, 21, and 22 by assessing stage-specific harm, informing recovery targets and quantifying required habitat with associated uncertainty for Canadian populations of Warmouth. This work is based on a demographic approach developed by Vélez-Espino and Koops (2009, 2012) and Vélez-Espino et al. (2010) which determines a population-based recovery target based on long-term population projections.

METHODS

This analysis consisted of four parts:

- (i) information on vital rates was compiled to build projection matrices incorporating variability within stochastic simulations.

With these projection matrices:

- (ii) stochastic sensitivities of the population growth rate to changes in each vital rate were determined and used to estimate total allowable chronic harm following Vélez-Espino and Koops (2009);
- (iii) simulation analysis was used to estimate the impact of transient harm (a one-time removal of fish of various life stages) on population growth; and,
- (iv) population viability analysis was conducted 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).

SOURCES

Few studies have been conducted on Warmouth in Canada. No data exist relating to the life history characteristics of Canadian populations of Warmouth. As a result, the population model was parameterised using data from studies of American populations of Warmouth from the primary literature. All analyses and simulations were conducted using the statistical program R 3.3.2 (R Core Team 2016).

THE MODEL

Warmouth life cycle was modelled using a birth-pulse, post-breeding, age-structured matrix model with annual projection intervals (Caswell 2001). Matrix population models use estimates of vital rates (growth, survival, and fecundity) to project age- or stage-specific population sizes. The dominant eigenvalue of the matrix represents the population growth rate (λ) and indicates the long term status of the population based on current conditions (Caswell 2001). A $\lambda > 1$ indicates that the population is growing exponentially, a $\lambda = 1$ indicates a population that is stable, and a $\lambda < 1$ indicates a population that is declining towards 0. The dominant right

eigenvector of the matrix represents the stable-stage or age structure of the population and indicates the proportional distribution of individuals among stages/ages. This can be used to estimate the number of individuals in all other stages/ages if one is known.

The matrix structure is defined by Warmouth longevity (t_{max}) and age-at-maturity (t_{mat}). Within the model Warmouth is assumed to live to a maximum age of 8 years and reach maturity at age-2 (COSEWIC 2015). The life cycle of Warmouth is represented in Figure 1.

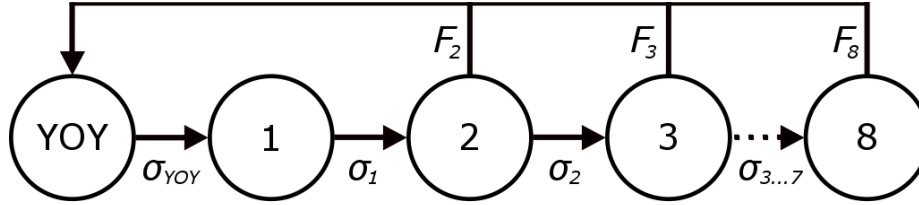


Figure 1. Generalized life cycle used to model the population dynamics of Warmouth. F_t represents age-specific annual fertility and σ_t represents the age-specific annual survival.

Elements within the age-structured matrix include age-specific annual survival (σ_t) and fertility rate (F_t). Fertility coefficients (F_t) represent the contribution from an adult in age class t to the next census of age-0 individuals. Multiple variables are incorporated into estimates of annual age-specific fertility rate. Fertility is dependent on mean age-specific fecundity (f_t) or the mean number of eggs produced per spawning season per female in age class t . It also accounts for the proportion of the population that are female (ϕ) and the proportion of the population that are mature at age- t (P_t). As well, fertility includes spawning periodicity (T) or the number of years between spawning events (1 year for Warmouth). Finally, because the model uses a post-breeding matrix structure, the survival coefficient is included to account for mortality occurring before the next spawning event. Fertility is calculated as:

$$F_t = \frac{\phi P_t f_t \sigma_t}{T}. \quad (1)$$

The age-structured projection matrix (\mathbf{B}) has nine columns representing young-of-the-year (YOY) through age-8 Warmouth:

$$\mathbf{B} = \begin{bmatrix} 0 & F_2 & F_3 & \cdots & F_8 & 0 \\ \sigma_0 & 0 & 0 & \cdots & 0 & 0 \\ 0 & \sigma_1 & 0 & \cdots & 0 & 0 \\ 0 & 0 & \sigma_2 & \cdots & 0 & 0 \\ \vdots & \vdots & \vdots & \ddots & \vdots & \vdots \\ 0 & 0 & 0 & \cdots & \sigma_7 & 0 \end{bmatrix}. \quad (2)$$

Due to the post-breeding matrix structure the population census occurs directly after reproduction has occurred. This results in individuals growing and maturing over the course of the year and spawning immediately prior to the next census. To account for this, the fertility coefficients for age- $t+1$ are incorporated into column t of the projection matrix (i.e., fertility of age-2 fish is represented in the age-1 column of the matrix). As well, the matrix structure includes a column of 0s to represent age-8 fish. This allows for age-8 fish to exist but not survive to the next census (or spawn as age-9 fish).

Parameter Estimates

All model parameters are outlined in Table 1.

Table 1. Values, symbols, descriptions, and sources for all parameters used to model Warmouth populations.

	Symbol	Description (units)	Value	Source
Age	t_{max}	Longevity (y)	8	COSEWIC (2016)
	t_{mat}	Age-at-maturity (y)	2	COSEWIC (2016)
	ζ	Generation time (y)	4.5	Estimated
Growth	L_{∞}	Asymptotic length (mm)	275.37	Fitted/Carlander (1977)
	K	Growth coefficient (y^{-1})	0.228	Fitted/Carlander (1977)
	t_0	Age at 0 mm	-0.042	Fitted/Carlander (1977)
	sd_L	log standard deviation of growth	0.1	Fitted/Carlander (1977)
Fecundity	α_F	Fecundity allometric intercept	2.1×10^{-5}	Panek and Cofield (1978)
	β_F	Fecundity allometric exponent	3.89	Panek and Cofield (1978)
	sd_F	log standard deviation of fecundity	0.05	Panek and Cofield (1978)
	φ	Proportion female	0.5	COSEWIC (2015)
	T	Spawning periodicity (y)	1	COSEWIC (2015)
	$P_{0,1}$	Proportion reproductive at age-0 to age-1	0	COSEWIC (2015)
	P_2	Proportion reproductive at age-2	0.5	COSEWIC (2015)
$P_{1,\dots,4}$	Proportion reproductive at age-1 to age-4	1	COSEWIC (2015)	
Weight	α_w	Length-weight allometric intercept	9.1×10^{-6}	Fitted
	β_w	Length-weight allometric exponent	3.17	Fitted
Mortality	$m_{0,\lambda min}$	Mortality at 1 unit of length with $\lambda = 0.82$	129.27	Fitted
	$m_{0,\lambda equil}$	Mortality at 1 unit of length with $\lambda = 1$	124.36	Fitted
	$m_{0,\lambda mean}$	Mortality at 1 unit of length with $\lambda = 1.14$	116.71	Fitted
	$m_{0,\lambda max}$	Mortality at 1 unit of length with $\lambda = 1.67$	98.16	Fitted
	$CV_{M, YOY}$	Coefficient of variation of mortality for YOY	0.1	Fitted
	$CV_{M, 1+}$	Coefficient of variation of mortality for age-1+	0.2	Mertz and Myers (1995)

Growth

Back calculated length-at-age data were available from various locations in the United States (Carlander 1977). The data were fitted with a von Bertalanffy growth curve (Figure 2):

$$L_t = L_{\infty}(1 - e^{-K(t-t_0)}), \quad (3)$$

Where L_t is total length (TL) in mm at age t , t_0 is the hypothetical age at which the fish would have had a length of 0, L_{∞} is the asymptotic size, and K is a growth parameter. To properly represent early life growth the relationship was forced through length-at-hatch, L_0 , at age-0. Length-at-hatch for Warmouth ranges from 2.3–2.9 mm (Warren 2009); the median, 2.6 mm, was used as the value for L_0 . The data were compiled from multiple back calculated length-at-age data sets from various location with uneven sample sizes. To account for inherent biases in the data set the growth model was fit as a generalized non-linear model to incorporate weighting to reflect the uneven sample sizes and an AR1 correlation structure to account for the lack of independence among back calculated length within a location. Inclusion of an AR1 correlation structure provided a superior fit to assuming independence among observations ($\Delta AIC = 345$).

This resulted in an L_{∞} value of 275.4, a K value of 0.228 and a t_0 value of -0.042 (Table 1). Maximum recorded length of Warmouth is 310 mm (Holm et al. 2009).

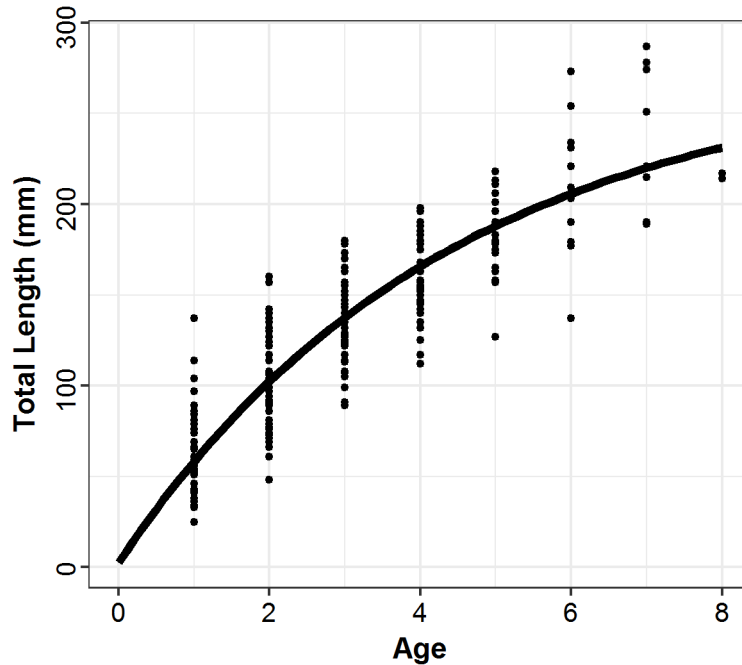


Figure 2. Length-at-age data for Warmouth. The black line represents the best fit of the von Bertalanffy growth curve forced through size-at-hatch. $L_t = 275.3(1 - e^{-0.227(t+0.042)})$.

Various length-weight relationships were available for Warmouth populations throughout the United States (Carlander 1977, Hill and Cichra 2005). The available relationships were compiled into a single model by fitting the predicted values giving the relationship:

$$W = 9.06 \times 10^{-6} L^{3.17}, \quad (4)$$

Where W is body weight in grams and L is total length in mm.

Reproduction

No information on Warmouth reproduction is available for Canadian populations; however, data are available for American populations. Warmouth may spawn several times over the spawning season between May and early July (COSEWIC 2015). Warmouth reproduction was simplified through the use of a birth-pulse matrix model which assumes a single annual reproductive event. This simplification is valid if YOY Warmouth experience equal growth and mortality regardless of spawning time; however, this has not been validated.

First spawning occurs at age-2 once a length > 89 mm is reached (Larimore 1957). It is unknown what proportion of individuals become mature at age-2; P_t is assumed to be 0 at ages 0 and 1, 0.5 at age-2 and 1 at ages > 2 (Table 1). The sex ratio was assumed to be 1:1 sex ratio with ϕ set to 0.5.

Warmouth fecundity is size-dependent (Larimore 1957). Panek and Cofield (1978) measured the egg count in a South Carolina population with individuals ranging in size from 96 to 220 mm (Figure 3). A relationship between total length, mm, and fecundity was best fit as a power curve:

$$f = 2.10 \times 10^{-5} L^{3.89}. \quad (5)$$

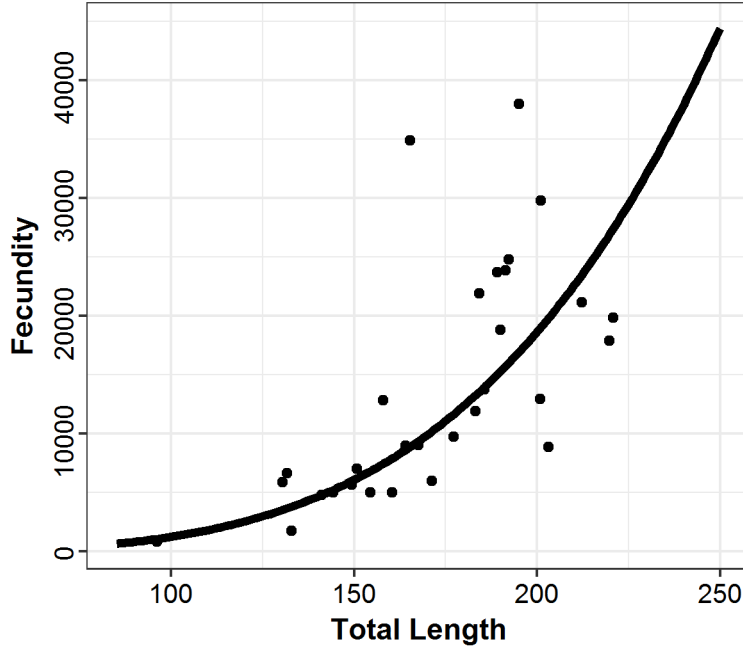


Figure 3. Fecundity data from a South Carolina population for Warmouth from Panek and Cofield (1978). The black line represents the best fit relationship: $f = 2.10 \times 10^{-5} L^{3.89}$.

Mortality

Mortality rate for Warmouth is unknown. Warmouth was assumed to follow a size-dependent mortality schedule and mortality rates that resulted in particular population growth rates were solved for through an optimization procedure. Size-dependent mortality assumes that instantaneous mortality decreases linearly with body size (Lorenzen 2000), such that:

$$M_t = m_0 L_t^{-1}, \quad (6)$$

where m_0 is the mortality at a single unit of length. If L_t is described by the von Bertalanffy growth curve (Equation 7), survival from age t to $t+1$ can be calculated by combining Equations 3 and 6 and integrating (van der Lee and Koops 2016) resulting in:

$$\sigma_t = \left[\frac{L_t e^{-K}}{L_{t+1}} \right]^{m_0 / K L_\infty}. \quad (7)$$

The value of m_0 (Table 1) that resulted in particular average (mean of $\log(\lambda)$ or geometric mean) population growth rates (minimum, equilibrium, mean, and maximum) was solved for. These λ values are not meant to represent exact realized population growth rates but potential trends of a declining (minimum), stable (equilibrium), moderately growing (mean), and rapidly growing (maximum) population.

Minimum population growth rate represents the smallest average population growth rate possible over the long term and was defined based on the COSEWIC definition of an endangered species. COSEWIC Criterion A defines an endangered species as one where there is indication of a 70% decline in population size over the previous 10 years or 3 generations, whichever is longer. Generation time (ζ) for Warmouth was estimated from the projection matrix to be 4.55 years. From this, minimum population growth rate was estimated as: $\lambda_{min} = 0.3^{1/\zeta^3}$ resulting in a λ_{min} of 0.92. Based on the best available information and expert opinion it is thought that Canadian Warmouth populations have remained relatively stable (Burrige et al.

2020). Therefore it is not necessarily expected that Canadian population of Warmouth are experiencing minimum rates of population growth as long term averages.

An equilibrium population growth rate indicates a stable population over the long term with a geometric mean λ value of 1.

Maximum population growth rate was estimated from an allometric relationship (Randall and Minns 2000):

$$\lambda_{max} = e^{2.64W^{-0.35}}, \quad (8)$$

where W represents average adult weight, giving a λ_{max} value of 1.67. A long term average population growth at λ_{max} would likely only be possible at lower population densities when a surplus in resources is available.

Mean population growth rate is meant to represent a reasonable level of long term growth of a recovering population. Mean population growth rate was estimated through balancing conservative and optimistic estimates of λ by taking the geometric mean of minimum, equilibrium, and maximum λ (Vélez-Espino and Koops 2007). This resulted in a population growth rate of 1.15. Other average λ_{mean} values are possible and likely to occur; however, elasticity values will be similar in magnitude.

STOCHASTICITY

Random, inter-annual variability was incorporated into simulations to account for the environmental stochasticity experienced by populations of Warmouth. Variability was incorporated into age-specific growth (length), fecundity and annual age-specific mortality (Figure 4). Additionally, various levels intra-annual correlation among variables were incorporated to represent the impacts of 'bad' or 'good' years acting on the population as a whole.

Length

Stochastic growth was simulated by applying variability to the inter-annual length increment, L_i , between simulation years. Mean L_i was calculated by subtracting L_{t-1} from L_t based on the von Bertalanffy growth curve (Equation 3). Age-specific growth increments were varied using a log-normal distribution with a mean of $\ln(L_i)$ and a standard deviation of 0.1. The random L_i value was then added to the L_{t-1} from the previous iteration to give the current L_t , with age-specific length probabilities (Figure 4, left panel). Initial L_t values were based on the mean von Bertalanffy growth curve.

Fecundity

Stochastic fecundity was incorporated by varying the intercept parameter of the fecundity relationship (α_F , Equation 5). This allows age-specific fecundity to vary identically intra-annually and assumes the impact of 'good' or 'bad' is the same across age classes. The parameter α_F was varied using a log-normal distribution with a mean value of $\ln(2.01 \times 10^{-5})$ and a log standard deviation of 0.05. Additionally, as fecundity is length dependent age-specific fecundity values, f_t , were affected by stochastic length-at-age values giving the age-specific probability distributions (Figure 4, middle panel).

Mortality

Age-specific instantaneous mortality was varied following a stretched-beta distribution (a beta distribution rescaled to extend outside of the 0 to 1 range; Morris and Doak 2002). Use of a

stretched-beta distribution allows the parameter to vary with the appropriate distributional shape while truncating the distribution so that the simulation is not affected by extreme values of the tails of a typically distribution (e.g., normal) while maintaining the appropriate mean and standard deviation (Morris and Doak 2002). The inter-annual variability in mortality for Warmouth was unknown. Bradford (1992) found that across species and life-stages the variance in mortality increases as a function of M ($sd(M) = 0.39M^{1.12}$). Mertz and Meyers (1995) concluded that this variance estimate was likely inflated due to error from field estimates of M and proposed that the inter-annual variability in M could be represented by a constant coefficient of variation (CV) of 0.2. The stochastic distribution of M was based on a normal distribution with means converted from Equation 7 and a CV of 0.2 for age classes 1+. A CV of 0.2 applied to YOY mortality resulted in a very broad distribution and often unreasonably low or high λ values. As a result, a CV value of 0.1 was used to represent the stochasticity of YOY mortality which allows for a more reasonable distribution of λ values (van der Lee et al. 2020). The normal distribution for each age-specific mortality value was converted to a stretched-beta distribution with unique ranges and distribution parameters (Figure 4, right panel). Although the mean mortality schedule was length dependent the stochastic mortality values were not affected by stochastic length-at-age. This was done to maintain a constant mean mortality schedule across years and replicates with random variability around the mean trend rather than allowing the mortality schedule itself to vary inter-annually.

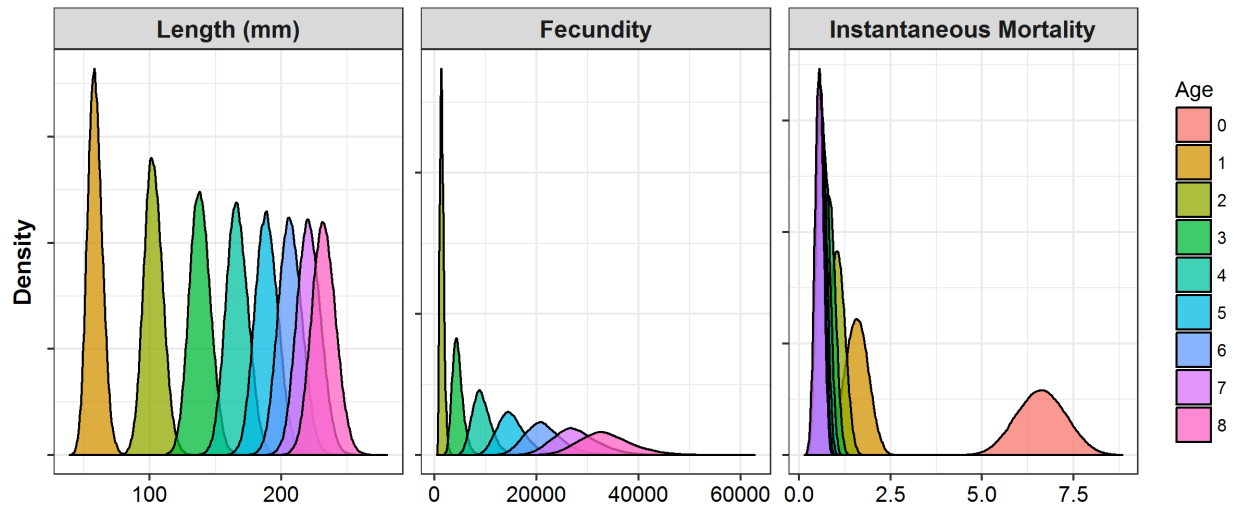


Figure 4. Density graph representing the realized probability distributions for age-specific stochastic parameters (length, fecundity, and instantaneous mortality) incorporated into model simulations. Length and fecundity values are based on log-normal distributions and mortality was based on stretch-beta distribution. NOTE: age increases along the x-axis from left to right for length and fecundity but decreased from left to right for instantaneous mortality.

Correlation

Individual intra-annual correlation structures were applied to growth and mortality such that age-specific variables were related to each other depending on the magnitude of the correlation parameter, ρ . For each, an AR1 correlation structure was used such that age-classes that are closer together were more correlated than age classes further apart (i.e., ρ between ages 1 and 2 was equal to ρ^1 while ρ between ages 1 and 8 was equal to ρ^7):

$$cor_{ij} = \rho^{|j-i|}, \quad (9)$$

where i is the row number and j is the column number of the entry in the correlation matrix (cor).

Three levels of correlations were used: independent (no correlation, $\rho = 0$); medium ($\rho = 0.25$ for growth and $\rho = 0.5$ for mortality); and strong ($\rho = 0.5$ for growth and $\rho = 0.9$ for mortality). Actual values of intra-annual correlations among variables were unknown. The values chosen are meant as representations of possible correlations to demonstrate the effects on model outputs.

This incorporation of stochasticity and correlation structures into model simulations resulted in unique distributions of population growth rate (Figure 5). As population growth is a multiplicative process the distribution of annual population growth rates is log-normally distributed. The long-term average population growth rate (geometric mean over 100 years) has an approximately normal distribution. The impact of stronger intra-annual correlations among parameters was broader distributions with the standard deviations increasing with the strength of the correlation structure included. The $\log_e(sd)$ of the annual population growth rate distributions were 0.17, 0.22, and 0.29 for independent, medium, and strong correlation structures respectively. The standard deviations of long term population growth rate distributions were 0.016, 0.022, and 0.030.

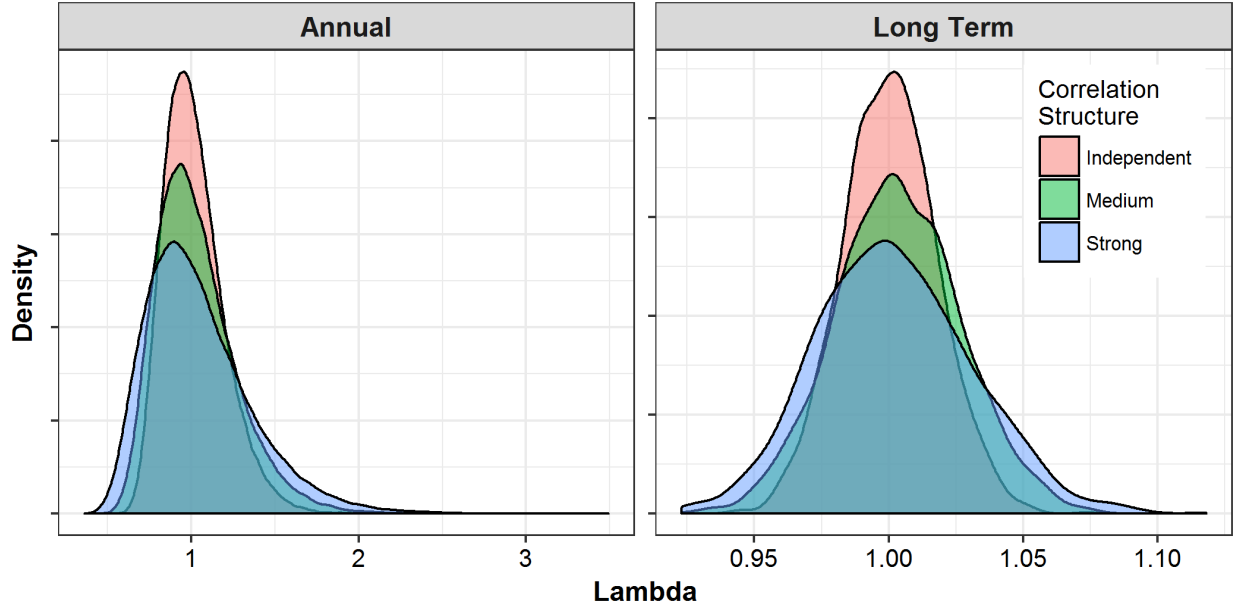


Figure 5. Density graph of the annual and long term average values of population growth rate (λ) that result from stochastic variation in parameter values with differing levels of intra-annual correlation. The annual values represent the distribution of lambda values for any given year. The long term average values represent the distribution of the geometric mean of λ values over 100 years. The distributions were based on a matrix with an average λ of 1.

SENSITIVITY ANALYSIS

Sensitivity analysis of matrix population models determines the impact of changes to vital rates and lower level parameters on annual population growth rate (λ). Sensitivities were quantified through estimation of elasticity values which describe the proportional change in λ following a proportional perturbation in a vital rate (v). Elasticities (ϵ_v) are calculated by taking the scaled partial derivatives of λ with respect to the vital rate:

$$\epsilon_v = \frac{v}{\lambda} \sum_{i,j} \frac{\partial \lambda}{\partial a_{i,j}} \frac{\partial a_{i,j}}{\partial v} \quad (10)$$

where a_{ij} is the projection matrix element in row i and column j .

Variation in model parameters was incorporated to determine effects on population responses from demographic perturbations (see Vélez-Espino and Koops 2007). Computer simulations were used to:

- (i) generate 50,000 matrices with stochastic parameters (L_t , f_t , and σ_t) drawn from distributions described above using a strong correlation structure;
- (ii) calculate the ε_v of λ with respect to σ_t and f_t for each matrix;
- (iii) estimate mean stochastic elasticities and their 95% confidence intervals; and
- (iv) repeat steps i to iii for matrices with λ of 0.92, 1, 1.15, and 1.67.

RECOVERY EFFORT AND ALLOWABLE HARM

Allowable harm and minimum required recovery effort were assessed within a demographic framework following Vélez-Espino and Koops (2009). Recovery effort is defined as the minimum improvement in vital rate(s) that will allow a population to begin recovery. Allowable harm is defined as the maximum harm to a population (decline in vital rate(s)) that will not prevent population recovery. Recovery effort applies when a population has an initial $\lambda < 1$ and allowable harm applies when a population has an initial $\lambda > 1$. Estimates of allowable chronic harm and transient harm are provided. Chronic harm refers to a permanent negative alteration to vital rate(s) while transient harm refers to a one time (temporary) mortality event impacting one or more life stages.

Recovery effort (ψ_v) and allowable chronic harm (τ_v) were estimated analytically as:

$$\psi_v \text{ or } \tau_v = \left(\frac{1}{\varepsilon_v} \right) \left(\frac{1-\lambda}{\lambda} \right) \quad (11)$$

where ε_v is the elasticity of vital rate v and λ is the initial population growth rate. If the recovery effort or harm affect more than one vital rate they are calculated by summing the elasticity values (ε_v) of each vital rate before inclusion in Equation 11.

The effects of transient harm were modelled as follows:

- (i) annual projection matrices were generated for 10 years by randomly generating parameter values as in the sensitivity analysis;
- (ii) survival of one or all stages was reduced in the first random matrix, simulating a one-time removal of individuals;
- (iii) the average population growth rate with and without removal were compared over the timeframe considered;
- (iv) this simulation was repeated 1,000 times to create a distribution of changes in population growth rate resulting from removal; and
- (v) rates of removal (number of individuals as a proportion of total abundance) from 0.01 to 0.99 (all individuals) with increments of 0.01 were considered.

Allowable transient harm was defined as a one-time removal of individuals, within a time-frame of 10 years that does not reduce the average population growth rate over that time-frame more than a pre-determined amount (see Results). 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: Minimum Viable Population (MVP)

The concept of demographic sustainability was used to identify potential recovery targets for Warmouth. 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 (~ 22 generations for Warmouth). Since population growth is not sustainable over time, the probability of persistence was simulated for a stable population over the long-term, λ_1 .

Important elements incorporated in population viability analysis include: the choice of time frame over which persistence is determined, the severity and probability of a catastrophic event, and the quasi-extinction threshold below which a population is deemed unviable. The choice of time frame is arbitrary and without biological rationale; however, 100 years is likely reasonable for making management decisions. The rate and severity of catastrophic events occurring within Warmouth populations is not known. Reed et al. (2003), through a meta-analysis, determined that among vertebrate populations catastrophic die-offs that result in a 1 year decrease in population size of 50% or greater occurred at a rate of 14%/generation on average. This result was used as a basis within the MVP simulations. Quasi-extinction results from the compounding effects of Allee effects, demographic stochasticity and inbreeding depression (Lande 1988, Morris and Doak 2002) leading a population to extinction once the threshold is crossed. Use of a quasi-extinction threshold is a simplifying assumption that allows for the inclusion of these effects without including them explicitly in the simulation model, which would require a number of unverifiable assumptions and increased computation time (Morris and Doak 2002). The value on the quasi-extinction threshold cannot be empirically measured; therefore, 50 adults were used as a reasonable approximation (Morris and Doak 2002).

Recovery targets were estimated as follows:

- (i) 100,000 projection matrices were generated by randomly drawing vital rates as in the population sensitivity analysis, based on a geometric mean growth rate of $\lambda = 1$;
- (ii) Individual simulations were conducted by randomly drawing projection matrices and projecting the population with various initial adult densities over 100 years with impacts from random catastrophes;
- (iii) Catastrophes were simulated based on a pre-defined probability of occurrence and resulted in a 50% decline to total population abundance;
- (iv) Simulations were repeated 1,000 times and the number of extinctions (when the adult population dropped below the quasi-extinction threshold) were counted;
- (v) This process was repeated 10 independent times and these realizations were used to generate a cumulative distribution function of extinction probability;
- (vi) Simulations were replicated using a probability of catastrophe of 0.10 or 0.15/generation

From these simulations, the minimum number of adults necessary for the desired probability of persistence (see Results) over 100 years (MVP) was calculated. MVP analysis was repeated using each level of stochastic parameter correlation.

Habitat: Minimum Area for Population Viability (MAPV)

Following Velez-Espino et al. (2010) and Young and Koops (2014), the minimum area for population viability (MAPV) was estimated as a first order quantification of the amount of habitat required to support a viable population, and is calculated as:

$$MAPV = \sum_{t=0}^{t_{max}} MVP_t \cdot API_t, \quad (12)$$

where MVP_t is the age-specific minimum number of individuals required to achieve the desired probability of persistence over 100 years, as estimated for the recovery target; and API_t is the area required per individual of age t (Minns 2003). Individuals were distributed among stage classes according to the stable-stage distribution, which is represented by the dominant right eigenvector (w) of the mean projection matrix based on the $\lambda = 1$ ($Aw = \lambda w$) (de Kroon et al. 1986, Table 2). API_t was estimated by taking the inverse of density ($API_t = 1/D_t$). Fish community density ($\text{no} \cdot \text{ha}^{-1}$) has been found to relate to the mean weight, W (g), of the fish in the community (Randall et al. 1995) following:

$$D = a_D W^{b_D}, \quad (13)$$

with $a_D = 30200$ and $b_D = -1.01$ in lentic environments. Although this allometry was initially estimated based on community estimates of density and weight, it was applied here to make age-specific estimates of Warmouth density. As a result, MAPV values using these parameters provide estimates of Warmouth exclusive habitat requirements. In natural environments, interactions with other species will result in increased spatial requirements per individual Warmouth. In addition, density relationships were created from Warmouth specific density data. Mean and error estimates of Warmouth population density and biomass were available from data from 60 Florida Lakes (Willis et al. 2009). Warmouth density was assumed to follow the same slope as the Randall et al. (1995) relationship and new intercept values were estimated to represent maximum and mean density relationships which were used to provide additional estimates of MAPV. Maximum density was estimated from the upper 90th percentile of the density data (assuming a normal distribution) and mean density was estimated from the mean. MAPV estimates from maximum Warmouth density represent the potential minimum space requirements of a Warmouth population. MAPV estimates from mean Warmouth density represent the average space requirement of a typical Warmouth population. As the density data available from Warmouth were from Florida lakes and populations in more southerly latitudes are expected to be more productive than those in the Great Lakes (Schlesinger and Regier 1982), the resultant MAPV values are likely to represent underestimates for Great Lake populations.

Table 2. Stable-stage distribution of the age-structured matrix models for Warmouth.

Age	Proportion of Population
0	0.9964
1	0.0084
2	0.00051
3	0.00015
4	0.00005
5	0.00002
6	0.000007
7	0.000003
8	0.000001

Space requirements of cohort will change over time depending on the growth function and mortality schedule experienced (Young and Koops 2014). As well, the population level spatial requirements will depend on the species-specific habitat requirements and how individual cohorts interact (i.e., which age-classes share habitat). The temporal variation in population level space requirements was incorporated into estimates of MAPV through calculation of the daily space requirements of a cohort, summing the daily values to the stage level and taking the maximum annual values to represent MAPV.

The daily space requirement of a cohort was estimated by first calculating the daily length-at-age (Equation 3). This was converted to weight-at-age (Equation 4) and used to estimate the daily area-per-individual (API_d) based on the inverse of density (Equation 13). Daily population abundance (MVP_d) was estimated from age-specific MVP estimates and the mortality schedule (Equation 7). Daily space requirement ($MAPV_d$) of an individual cohort was then the product of API_d and MVP_d .

$MAPV_d$ was then summed to the stage level ($MAPV_s$) by summing age-specific $MAPV_{d,t}$, each day (day 1 to 365 where day 1 is the recurring 'birthday' of the fish) and the stage-specific MAPV value reported in the maximum value that occurs over the course of the year. Values are reported for each life stage (YOY, juvenile, and adult) which represent stage-exclusive habitat. As there is not necessarily a difference between juvenile and adult habitat for Warmouth (Burrige et al. 2020), estimates of age-1+ habitat are provided assuming shared habitat between juvenile and adult. Finally, an estimate of MAPV is provided assuming all age-classes' share habitat. Due to the age-specific growth and mortality curves the stage-specific values will not necessarily sum (i.e., $MAPV_j + MAPV_A \neq MAPV_{1+}$). Population level habitat requirements are estimated as the summation of the stage-specific habitat requirements are thought to be independent.

RESULTS

SENSITIVITY ANALYSIS

Use of different correlation structures in stochastic sensitivity estimates resulted in similar elasticity values; for simplicity only values estimated using a strong correlation structure are presented as they provide the most conservative estimates of allowable harm. Warmouth population growth rate was most sensitive to pre-adult (YOY and age-1) survival rate with elasticity decreasing with age (Figure 6). Greater average λ values resulted in larger elasticities at younger ages and lower values at older ages. When summed to the stage level, population growth rate was primarily sensitive to adult survival due to the length of the adult stage (Table 3), except at λ_{max} when the population was more sensitive to juvenile survival.

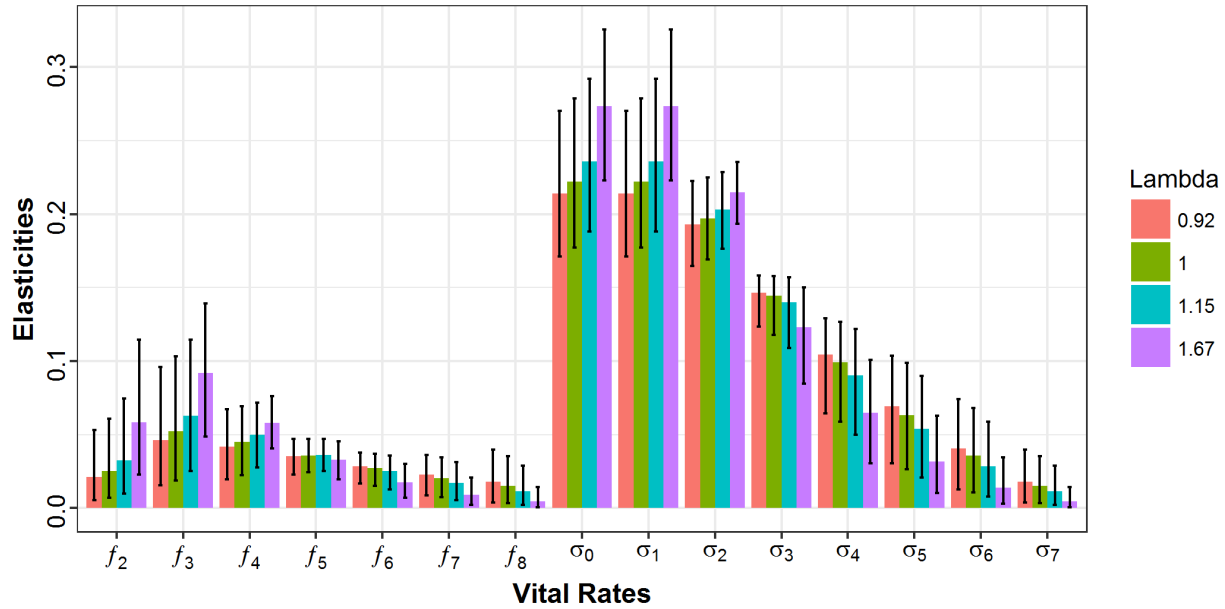


Figure 6. Results of the stochastic sensitivity analysis of Warmouth population growth rate (λ) to perturbation of age-specific vital rates (survival (σ) and fecundity (f)). The results are reported as elasticity (ϵv) values (mean, upper and lower confidence intervals) and were estimated for various values of λ , representing minimum, equilibrium, mean, and maximum λ respectively.

RECOVERY EFFORT AND ALLOWABLE HARM

Recovery effort and allowable chronic harm

Estimates of recovery effort and allowable harm are provided for a variety of population growth rates to provide a range of potential consequences of anthropogenic impacts on Warmouth populations. Realised population growth rates of natural populations will likely differ from these estimates; however, the estimates may guide management on the impacts of harm (or recovery effort) on populations with growth rates within the range of those evaluated. Recovery effort estimates are provided for a population that is in decline at a rate of 70% over three generations ($\lambda = 0.92$) which represents an expected minimum long term average decline for an Endangered population. As well, estimates are provided for a population growing at a 'mean' rate ($\lambda = 1.15$); this represents a recovering population growing at a reasonable rate. Finally, estimates are provided for a population growing at a maximum rate ($\lambda = 1.67$). This rate represents a low density population with surplus resources and is unlikely to be maintained by a population in a natural environment over a long term.

Recovery effort and allowable chronic harm estimates (Table 4) were based on the lower and upper confidence intervals of stage-specific elasticity values from stochastic sensitivity analysis respectively, following a precautionary approach. Values represent the proportional change to vital rates that would result in $\lambda = 1$. Values below -1 indicate a lack of significant impacts of harm to that vital rate if all others are held constant for a given level of population growth.

Table 3. Summary of the stochastic sensitivity analysis of Warmouth population growth rate (λ) to perturbation of stage-specific (YOY (y), juvenile (j) and adult (a)) vital rates (survival (σ) and fecundity (f)). The results are reported as elasticity (ε_v) values (mean, lower and upper confidence intervals) and were estimated for various values of λ .

Population Growth Rate (λ)		Estimate	Elasticity			
			σ_y	σ_j	σ_a	f
Minimum	0.916	Mean	0.214	0.310	0.476	0.214
		LCI	0.177	0.262	0.332	0.177
		UCI	0.270	0.380	0.575	0.270
Equilibrium	1	Mean	0.222	0.320	0.458	0.222
		LCI	0.177	0.262	0.332	0.177
		UCI	0.279	0.389	0.561	0.279
Mean	1.152	Mean	0.235	0.337	0.428	0.235
		LCI	0.188	0.276	0.305	0.188
		UCI	0.292	0.403	0.535	0.292
Maximum	1.671	Mean	0.273	0.380	0.347	0.273
		LCI	0.223	0.322	0.241	0.223
		UCI	0.326	0.434	0.456	0.326

Table 4. Summary of recovery effort and allowable chronic harm estimates of individual vital rates for Warmouth. Recovery effort applies to populations with population growth rates < 1 and allowable harm applies to populations with population growth rates > 1 . Recovery effort values represent the minimum proportional increase in individual vital rates required to stop population decline. Allowable chronic harm values represent the maximum proportional decrease in individual vital rates that would not jeopardize population recovery. Values were estimated using the lower (recovery effort) or upper (allowable chronic harm) confidence intervals of vital rate elasticities (Table 3).

Population Growth Rate (λ)	Vital Rate					
	σ_y	σ_j	σ_a	σ_{1+}	σ	f
Recovery Effort						
0.916	0.538	0.363	0.264	0.126	0.092	0.538
Allowable harm						
1.152	-0.452	-0.328	-0.247	-0.163	-0.132	-0.452
1.671	-1.233	-0.925	-0.881	-0.517	-0.401	-1.233

Recovery effort and allowable harm estimates are provided for stage-specific vital rates (YOY, juvenile, and adult survival and fecundity), changes to survival of all age-classes (σ), as well as age-classes 1 and older (σ_{1+}) as individual life stages (especially juvenile and adult) may not be impacted independently.

Warmouth were most affected by harm or recovery efforts to survival rate when all life stages were affected simultaneously; closely followed by age-1+. The effects of harm to YOY survival were less than that of other life stages when harm is applied at the stage level. This is due to the relative length of the life stage (1 year) as Warmouth population growth was most sensitive to YOY survival (Figure 5) when affected by age-specific perturbations.

To further examine the effects of harm on Warmouth populations, simulations of Warmouth populations under varying levels of harm were conducted. Simulations began with a Warmouth population with a λ value of 1.15 and harm applied (deaths per 100 individuals per year) to

various life stages (YOY, age-1+, and all age-class) and the probability of population decline ($\lambda < 1$) estimated on an annual and long term basis. The harm applied ranged from 1 to 95 deaths per 100 individuals. The harm implemented in simulations was in addition to the mean natural mortality rates of an unharmed population and did not take into account density-dependence. Therefore estimates likely represent 'worst case' scenarios in the absence of compensatory density-dependence. This may be of particular importance in relation to harm to YOY aged fish.

Projection matrices were generated for 1,000 replicates of 100 years in the same manner as sensitivity analysis using a strong correlation structure. The λ value of each projection matrix and the geometric means of the lambda values for each 100 year replicate were calculated. The proportion of all λ values < 1 provides an estimate of the annual probability of decline under different levels of harm and the proportion of average λ values < 1 provides an estimate of the long term (100 year) probability of population decline for the given amount of variability incorporated in the simulation at the initial λ value.

The annual and long term λ probability distributions are compared (Figure 7) for an unharmed population ($\lambda = 1.15$) and a population at maximum allowable harm (14 deaths per 100 individuals). The annual λ distributions are broad, extending from approximately < 0.5 to > 2.5 with the values for the harmed population shifted left. On a long term basis the distributions are much narrower. The unharmed population with an average $\lambda = 1.15$ experienced growth rate values ranging from 1.04 to 1.22 while the harmed population with an average $\lambda \approx 1$ ranged from 0.91 to 1.12 with 423 average lambda estimated > 1 . Therefore despite having an expected mean population growth rate of approximately 1 there was a 42% chance that the population will experience decline.

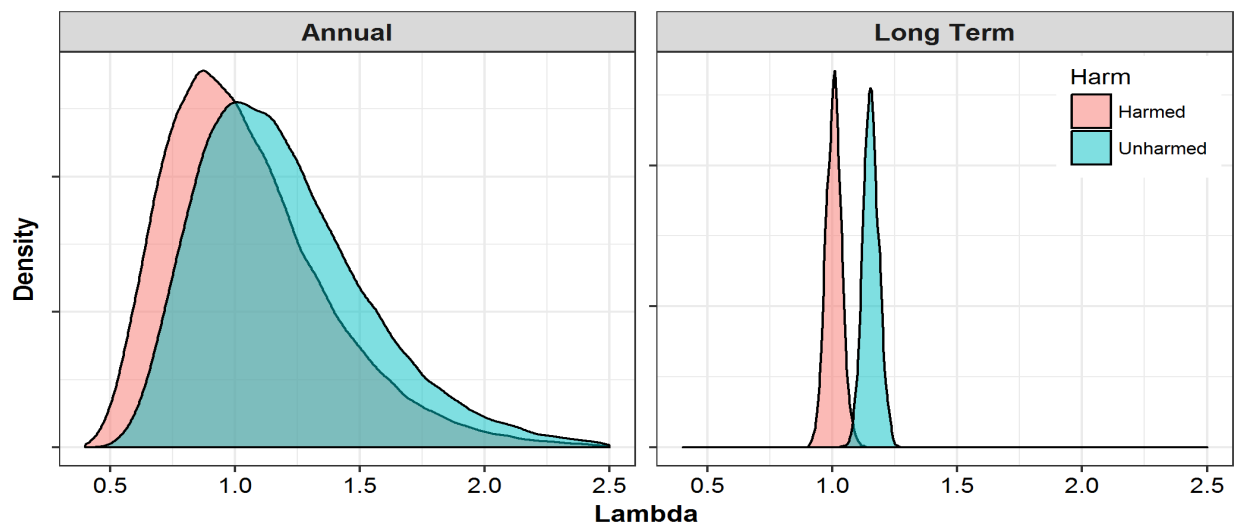


Figure 7. Annual and long term (100 year geometric mean) λ distributions for an unharmed (average $\lambda = 1.15$) and harmed (maximum allowable harm; average $\lambda \approx 1$) Warmouth population.

Extending this to other levels of harm to various life stages (YOY, age-1+, and all age-class) reveals the probability of population decline (Figure 8). From Figure 8 the risk (in the form of probability of decline) associated with rates of fish death can be determined on an annual and long term (100 year) basis. The probability of observing an annual population decline of an unharmed population ($\lambda = 1.15$) was 33%; however there was a 0% probability of observing a decline over 100 years. As the level of harm increases the risk of population decline increases. On a long term basis the probability of population decline exceeds 50% following 13 deaths per

100 individuals per year of all age-classes, 17 deaths per 100 individuals of age classes 1+, and 47 deaths per 100 individuals of YOY Warmouth. These values reach 100% following the deaths of 23, 28 and 66 Warmouth per 100 individuals respectively.

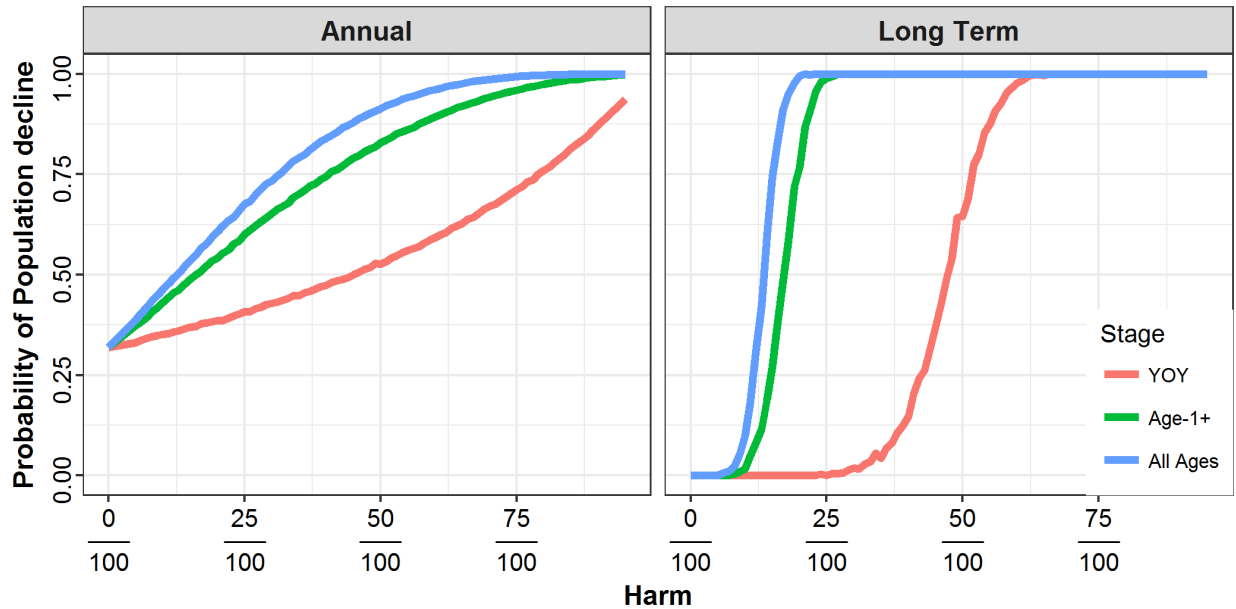


Figure 8. The probability of Warmouth population decline ($\lambda < 1$) on an annual and long term (100 year geometric mean) basis after experiencing increasing levels of harm to YOY, age-1+ and all age-class survival rate.

Transient allowable harm

Allowable transient harm (allowable one time removal, performed no more frequently than once every 10 years) can be extracted from Figure 9 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). Allowable transient harm may differ depending on the population growth rate; a growing population will be able to sustain a larger removal without going into decline compared to a stable population. The figure represents removal rates (i.e., a proportion of the population). 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 ($\Delta\lambda$), and the survival rate of age class t (σ_t):

$$h_j = \Delta\lambda N_0 \sigma_t . \quad (14)$$

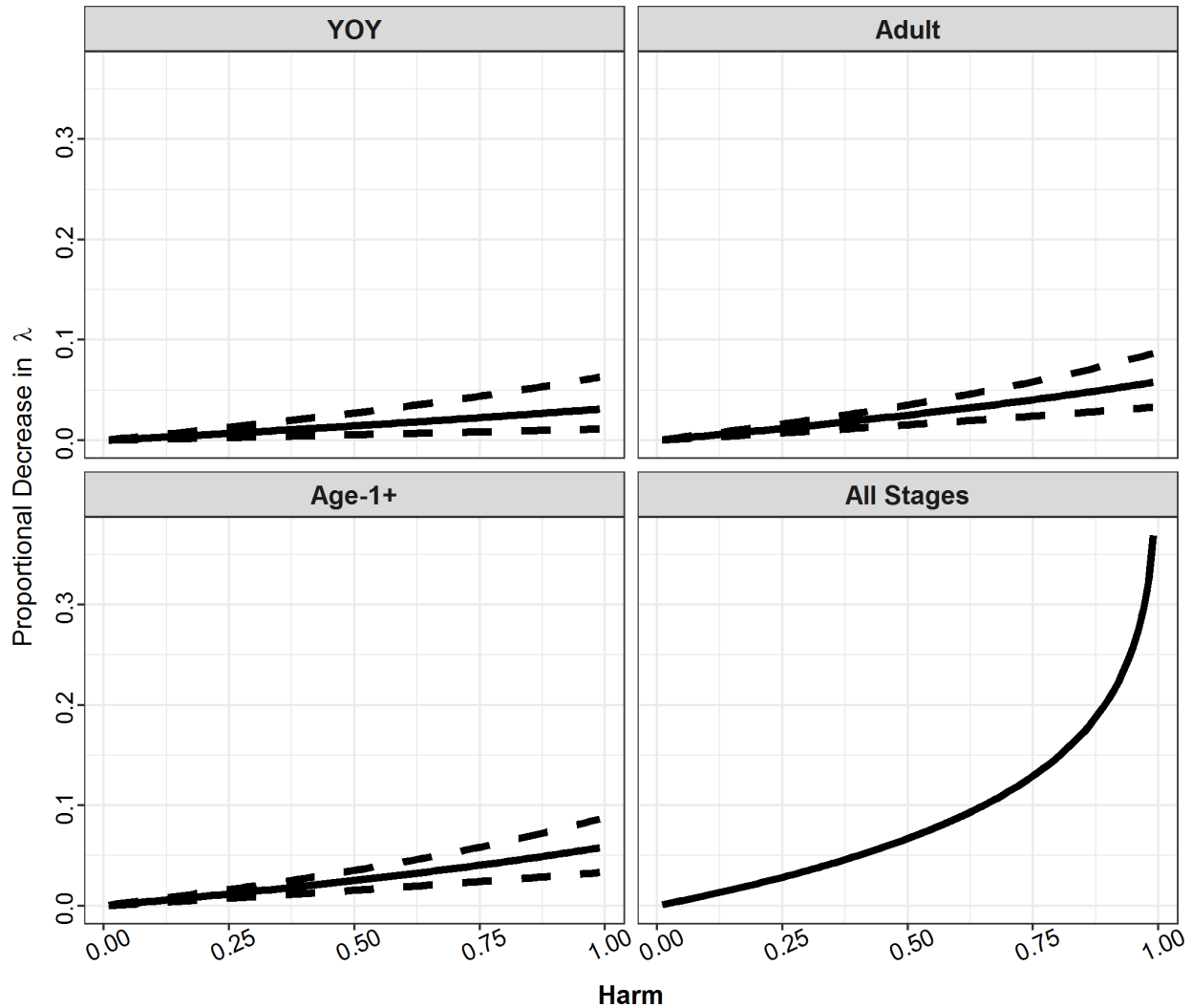


Figure 9. The average population growth rate resulting from increasing levels of transient harm (simulated as a one-time removal of individuals) impacting specified stage(s). The solid line represents mean impacts and the dashed lines represent 95% confidence intervals. Simulations were conducted with an initial λ of 1.15.

RECOVERY TARGETS

Abundance: Minimum Viable Population (MVP)

The probability of extinction ($P[ext.]$) decreases as a power function of adult population size (N_a) (Figure 10). Functions of the form: $P[ext.] = \alpha_{MVP} N_a^{\beta_{MVP}}$, were fitted using non-linear least squares to the predict extinction probabilities for each combination of quasi-extinction threshold and catastrophe rate using three levels of stochastic parameter correlation (Table 5). These equations can be rearranged and used to estimate minimum recovery target for a desired probability of persistence over 100 years given the pre-defined population, catastrophe, and quasi-extinction criteria. In choosing recovery targets, the risks associated with extinction probability must be balanced with the costs associated with an increased target (increased recovery effort, longer time to recovery, etc.). Recovery target values are presented for a 5% and 1% risk of extinction using simulation criteria of populations affected by a 0.1 and 0.15

catastrophe rate per generation with a quasi-extinction threshold of 50 adults (Table 6). Additional targets, those with different extinction risks, can be estimated with use of the functional relationships (Table 5) and stable stage distribution (Table 2).

Table 5. Parameter values for the extinction probability relationships ($P[ext.] = \alpha_{MVP} N_a^{\beta_{MVP}}$) used to estimate minimum viable population (MVP, Table 6). Relationships were fit for simulations with an quasi-extinction threshold 50 adults and probabilities of catastrophe of 0.10 and 0.15/generation using three levels of intra-annual correlation among stochastic parameters.

Catastrophe Rate	Correlation Structure	α_{MVP}	β_{MVP}
0.10	Independent	238.388	-1.307
	Medium	82.473	-0.961
	Strong	64.121	-0.729
0.15	Independent	128.697	-1.082
	Medium	74.382	-0.854
	Strong	131.090	-0.737

MVP estimates were sensitive to the choice of extinction risk, catastrophe probability and correlation structure with MVP values for adults ranging from 651 to 383,291 dependent on the risk and simulation criteria chosen (Table 6). The more precautionary estimates of MVP utilize a catastrophe probability of 0.15/generation and risk of extinction of 1% over 100 years; however, the extent of intra-annual correlation among life history parameters is uncertain and MVP estimates ranged from 6,302 to 383,291 from variation in the level of intra-annual correlation alone. This variation is likely due to the increased range of λ values that result from choice of intra-annual parameter correlation (Figure 5). This increases the probability of population decline resulting from environmental stochasticity (i.e., ‘bad’ years) and therefore increases the risk of population extinction. The level of correlation among parameters is unknown for Warmouth populations and must be further explored with future research.

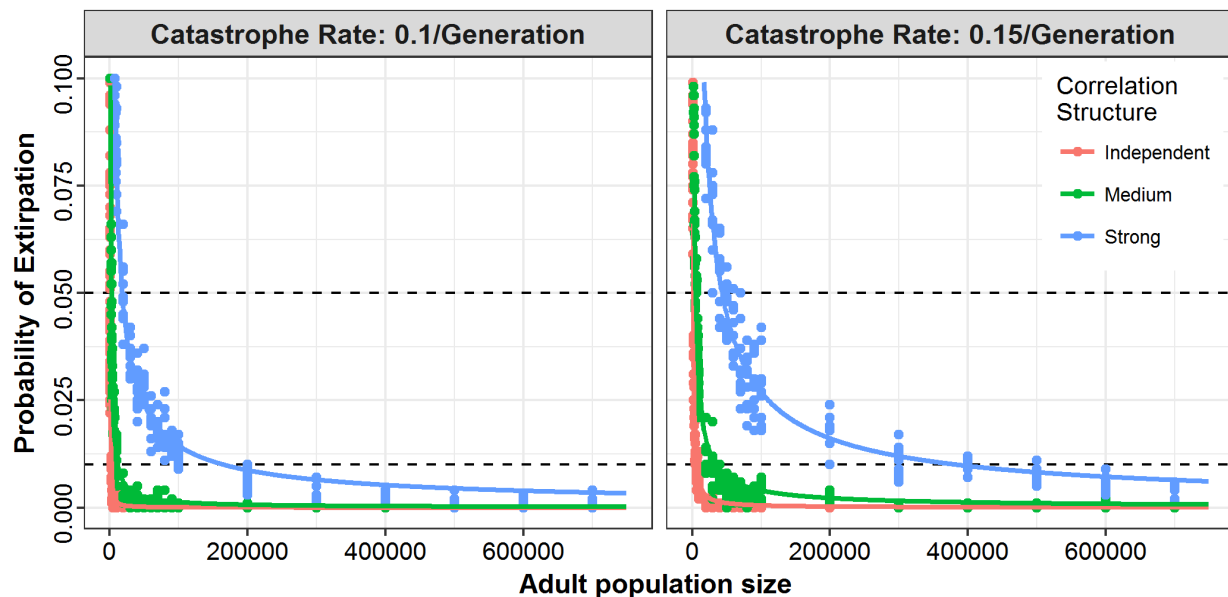


Figure 10. The probability of extirpation from recovery target simulations. Results are presented for MVP scenarios with a probability of catastrophe of 0.1 and 0.15/generation and a quasi-extinction threshold of 50 adults using three levels of intra-annual correlation among stochastic parameters.

Table 6. Estimates of the stage-specific minimum viable population (MVP) for Warmouth for two extinction probabilities ($P[ext.]$). Results are presented for MVP simulation scenarios using a quasi-extinction threshold of 50 adults, a catastrophe probability of 0.1 and 0.15/generation and three levels of intra-annual correlation among stochastic parameters.

Catastrophe Rate	Correlation Structure	Stage	MVP	
			$P[ext.] = 5\%$	$P[ext.] = 1\%$
0.10	Independent	YOY	1,912,136	6,549,606
		Juvenile	2,880	9,866
		Adult	651	2,231
	Medium	YOY	6,519,591	34,774,140
		Juvenile	9,821	52,384
		Adult	2,221	11,846
	Strong	YOY	53,551,810	486,471,350
		Juvenile	80,671	732,829
		Adult	18,242	165,717
0.15	Independent	YOY	4,177,508	18,498,704
		Juvenile	6,293	27,867
		Adult	1,423	6,302
	Medium	YOY	15,224,284	100,229,918
		Juvenile	22,934	150,988
		Adult	5,186	34,143
	Strong	YOY	126,881,420	1,125,172,287
		Juvenile	191,136	1,694,978
		Adult	43,222	383,291

Habitat: Minimum Area for Population Viability (MAPV)

Space requirements of a cohort increase until age 2.06 and decrease thereafter (Figure 11). Daily trends in stage-specific space-requirements differ among stages (Figure 12). Space-requirements of YOY and juvenile exclusive habitat are maximized at the end of the year while that of adult exclusive habitat is maximized at the beginning of the year (Table 7). Assuming juveniles and adults (age-1+) share habitat, space requirements peak at the start of the year. Finally assuming shared habitat among all age classes results in maximum space requirements on day 215.

MAPV values were estimated for MVP simulations using a quasi-extinction threshold of 50 adult fish, a 0.1 or 0.15/generation probability of catastrophe and a risk of extinction of 5 or 1% over 100 years assuming three levels of intra-annual correlation among age-specific parameters (Table 8).



Figure 11. Area occupied by a cohort over time.

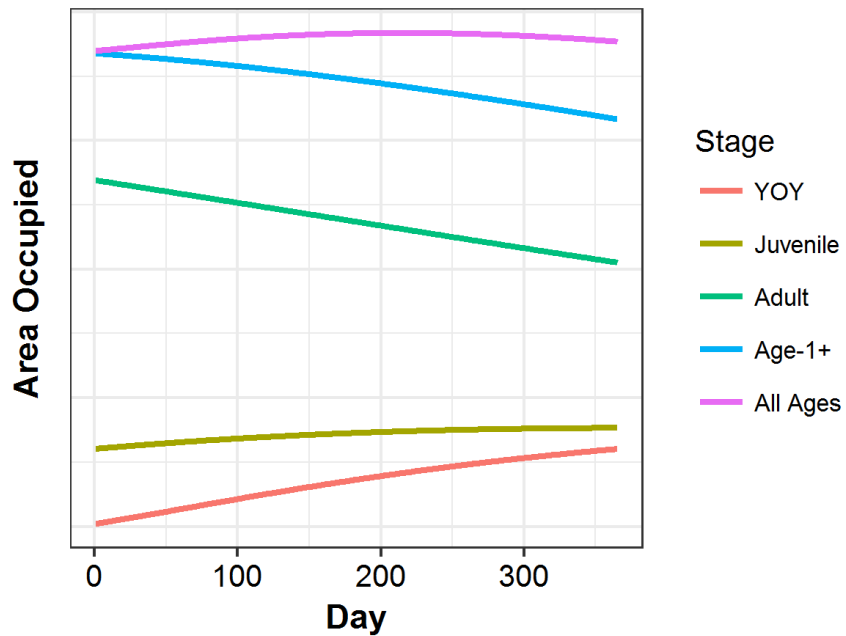


Figure 12. Daily area occupied by a stage over 1 year.

DISCUSSION

ELEMENTS

Element 3: Estimate the current or recent life-history parameters for Warmouth

The best available data were assembled to provide life-history parameters for Warmouth. The value for each life-history parameter used in modelling is presented in Table 1. Details regarding

how the parameters were estimated and source data used are outlined in the Methods section of this report.

Table 7. Stage-specific average area per individuals (API; m²) on the day of maximum MAPV (Table 8). API is estimated from three densities measures: using an allometry from the literature (Randall et al. 1995); using high (upper 90% confidence interval) density estimates (maximum) and mean density estimate from Florida Warmouth populations (Willis et al. 2009).

Stage	Day	Mean API		
		Randall	Maximum	Mean
YOY	365	1.19	0.80	2.56
Juvenile	365	7.32	4.92	15.76
Adult	1	15.51	10.42	33.38
1+	1	5.43	3.65	11.70
All Ages	215	2.14	1.44	4.61

Element 12: Propose candidate abundance and distribution target(s) for recovery

Estimates of minimum viable population (MVP) were made for a variety of simulation criteria: using a quasi-extinction threshold of 50 adults; a catastrophe rate of 10% or 15% per generation; and extinction risk of 5% or 1% over 100 years; and with three levels of intra-annual correlation among stochastic parameters. Over all simulation criteria MVP values ranged from 651 to 383,291 adults. The more conservative approach utilized an extinction risk of 1% per 100 years and a catastrophe rate of 15% per generation with MVP estimates ranging from 6,302 to 383,291. Including intra-annual correlations among stochastic variables significantly affected MVP estimates. MVP estimates incorporating the independent correlation structure are consistent with previous RPA models. Use of the strong correlation structure resulted in MVP estimates greater than 60 times that of estimates made with the independent correlation structure. The likely driving force behind the difference in MVP estimates that resulted from differing correlation structures was the difference in the annual and long term distributions in population growth rate (Figure 5). Further work in determining long term population abundances and inter-annual variability in population growth rate will help to inform the probability distribution of λ and reduce uncertainty in MVP analysis.

The choice of recovery target is not limited to the scenarios presented. MVP estimates with additional persistence probabilities can be made using the parameter values listed in Table 5.

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. It is uncertain at what frequency catastrophic events occur for Warmouth populations. Modelling of recovery targets was done assuming a stable population with the most conservative catastrophe scenario, based on Reed et al. (2003), of 15%.

As well, recovery targets based on MVP can be easily misinterpreted as a reference point for exploitation or allowable harm. A recovery target based on MVP 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. Importantly, these MVP targets refer to adult numbers only. If juveniles are being included in abundance estimates, then the MVP must include these age classes as well.

Additionally, MVP estimates for Warmouth were made using a post-breeding matrix model. This means that abundance estimates were made directly after spawning has occurred and before

age-specific mortality has acted. Therefore abundance estimates from MVP analysis represent maximum annual abundances for a given population. When compared to field observations of abundance sampling date relative to spawning date should be considered and the expected mortality rate over this time period accounted for.

Table 8. Estimates of Warmouth stage-specific minimum area for population viability (MAPV), in hectares, for two extinction probabilities (P[ext.]). Results are presented with MVP simulation scenarios using a quasi-extinction threshold of 50 adults, a catastrophe probability of 0.1 and 0.15/generation and three levels intra-annual of correlation among stochastic parameters. MAPV was estimated using three estimates of fish density (API): using an allometry from the literature (Randall et al. 1995), based on mean and high (upper 95% confidence interval) of Warmouth densities in 60 Florida lakes (Willis et al. 2009).

Catastrophe Rate	Correlation Structure	Stage	MAPV					
			Randall Density		Maximum Density		Mean Density	
			5%	1%	5%	1%	5%	1%
0.10	Independent	YOY	0.31	1.05	0.21	0.71	0.66	2.26
		Juvenile	0.39	1.34	0.26	0.90	0.84	2.88
		Adult	1.37	4.70	0.92	3.16	2.95	10.11
		1+	1.87	6.42	1.26	4.31	4.03	13.82
		All Ages	1.96	6.70	1.31	4.50	4.21	14.42
	Medium	YOY	1.05	5.58	0.70	3.75	2.25	12.02
		Juvenile	1.33	7.10	0.89	4.77	2.86	15.28
		Adult	4.68	24.94	3.14	16.76	10.07	53.69
		1+	6.39	34.08	4.29	22.90	13.76	73.37
		All Ages	6.67	35.56	4.48	23.89	14.35	76.56
	Strong	YOY	8.59	78.08	5.78	52.46	18.50	168.10
		Juvenile	10.93	99.27	7.34	66.70	23.53	213.73
		Adult	38.41	348.88	25.81	234.43	82.69	751.14
		1+	52.48	476.73	35.26	320.33	112.99	1,026.37
		All Ages	54.76	497.46	36.80	334.26	117.90	1,071.01
0.15	Independent	YOY	0.67	2.97	0.45	1.99	1.44	6.39
		Juvenile	0.85	3.77	0.57	2.54	1.84	8.13
		Adult	3.00	13.27	2.01	8.91	6.45	28.56
		1+	4.09	18.13	2.75	12.18	8.81	39.03
		All Ages	4.27	18.92	2.87	12.71	9.20	40.73
	Medium	YOY	2.44	16.09	1.64	10.81	5.26	34.63
		Juvenile	3.11	20.45	2.09	13.74	6.69	44.04
		Adult	10.92	71.88	7.34	48.30	23.51	154.76
		1+	14.92	98.22	10.02	66.00	32.12	211.47
		All Ages	15.57	102.49	10.46	68.87	33.52	220.66
	Strong	YOY	20.36	180.59	13.68	121.34	43.84	388.80
		Juvenile	25.89	229.61	17.40	154.28	55.74	494.33
		Adult	91.00	806.94	61.14	542.22	195.91	1,737.33
		1+	124.34	1,102.63	83.55	740.91	267.70	2,373.93
		All Ages	129.75	1,150.58	87.18	773.12	279.34	2,477.16

Element 13: *Project expected population trajectories over a scientifically reasonable time frame (minimum 10 years), and trajectories over to the potential recovery target(s), given current Warmouth population dynamics parameters.*

Current population abundances of Warmouth in Canada are unknown and population trajectories are thought to be stable (BurrIDGE et al. 2020). Under current population dynamics it seems likely the population will remain unchanged. Improvements in population size will potentially require management action to improve vital rates or increase the available of suitable habitat.

Element 14: *Provide advice on the degree to which supply of suitable habitat meets the demands of the species both at present and when the species reaches the potential recovery target(s) identified in element 12.*

Warmouth has a limited distribution in Canada and is present at only 3 locations which are considered to be isolated populations (COSEWIC 2015). The total amount of suitable Warmouth habitat in each location has not been quantified, as well, current estimate of population abundance are not available. As a result, is it unknown if the supply of habitat meets the current demand. However, estimates of the quantity of habitat required to sustain a minimum viable population are provided.

MAPV estimates were made for each MVP value presented (Table 8). In addition, MAPV estimates were made for multiple stage-specific habitat usage assumption (i.e., which age classes share habitat; Figure 12). The quantity of habitat required to support a population of MVP size was dependent on which age classes were assumed to share habitat. For Warmouth juvenile habitat requirements are thought to be similar to that of adults (BurrIDGE et al. 2020); therefore the estimate of age-1+ habitat may be most appropriate. The total amount of habitat required by the population would then be the summation of age-1+ and YOY habitat.

MAPV estimates from three different estimates of population density are provided. A density allometry from the literature (Randall et al. 1995) was utilized which described the relationship between community density and average weight. This allometry, when applied to Warmouth habitat estimates, provides a value of Warmouth exclusive habitat (independent of other species in the fish community) and is consistent with previous RPA models.

Additional estimates of Warmouth habitat requirements are provided based on measurement of Warmouth density in Florida lakes (Willis et al. 2009). Using the upper 90% confidence interval of density provides an estimate of the minimum habitat requirements of a dense population. It is possible that these values underestimate the minimum habitat requirements because the long term trajectories of the dense population were not available and therefore it is possible that they were above carrying capacity. Also MAPV estimated are provided based on the mean density of Florida Warmouth populations which represent average habitat requirements. As lake production is expected to decrease with latitude (Schlesinger and Regier 1982) mean habitat requirements of Great Lakes populations of Warmouth may be greater than those in Florida.

Element 15: *Assess the probability that the potential recovery target(s) can be achieved under the current rates of population dynamics, and how that probability would vary with different mortality (especially lower) and productivity (especially higher) parameters.*

The current population trajectory of Warmouth is thought to be stable (i.e., $\lambda = 1$; BurrIDGE et al. 2020). It is not known what factors may be limiting Warmouth population growth (e.g., habitat supply, resources, mortality rate, etc.). Therefore it is not clear what factors will lead to improved population growth and recovery. Under current conditions the population may remain stable and improvements in current conditions will likely be required for population recovery. Any deterioration from current conditions will likely lead to population decline.

Element 19: *Estimate the reduction in mortality rate expected by each of the mitigation measures or alternatives in element 16 and the increase in productivity or survivorship associated with each measure in element 17.*

No clear links have been identified between the mitigation measures and Warmouth mortality rates or productivity.

Element 20: *Project expected population trajectory (and uncertainties) over a scientifically reasonable time frame and to the time of reaching recovery targets, given mortality rates and productivities associated with the specific measures identified for exploration in element 19. Include those that provide as high a probability of survivorship and recovery as possible for biologically realistic parameter values.*

Without a direct link between mitigation measures and Warmouth mortality rates or productivity, this information cannot be provided.

Element 21: *Recommend parameter values for population productivity and starting mortality rates and, where necessary, specialized features of population models that would be required to allow exploration of additional scenarios as part of the assessment of economic, social, and cultural impacts in support of the listing process.*

The parameter values presented in Table 1 are based on the best available data for this population and should be used for any future population modelling.

Element 22: *Evaluate maximum human-induced mortality and habitat destruction that the species can sustain without jeopardizing its survival or recovery.*

Allowable harm analysis was conducted assuming average population growth rates of 1.15 and 1.67. Stage-specific estimates of allowable harm (Table 4) are provided for individual stages (YOY, juvenile and adult) and combined stages (age-1+ and all age classes). Chronic allowable harm was least when survival of all age classes was decreased simultaneously with an allowable decrease of only 12.2% and 40.1% and mean population growth rates of 1.15 and 1.67, respectively. Allowable harms was next lowest for age-1+ survival, followed by adult survival, then juvenile survival, with YOY survival and fecundity resilient to the most proportional harm.

Simulation analysis was used to explore the effects of chronic harm (deaths per 100 individuals per year) on the probability of observing annual and long term (100 years) declines in population size (Figures 7 and 8) with an assumed initial average population growth rate of 1.15. Initially, a growing population (average $\lambda = 1.15$) had an ~ 33% chance of annual population decline and a 0% chance of long term decline. Additional annual stage-specific mortalities (YOY, age-1+ and all age classes were examined) caused the risk of population decline to increase. At levels of estimated stage-specific allowable harm (Table 4) there was an ~ 50% probability of observing an annual population decline and an ~ 40% probability of observing a long term population decline. Therefore a substantial risk to population growth remains at conservatively estimated levels of allowable harm. The exact level of risk will depend on the mean population growth rate and distribution of inter-annual population growth.

Transient harm may be applied without jeopardizing survival or recovery if the population is not in decline. Assuming a one-time removal of ~ 40% of the total population will result in a ~ 5% decline in population growth rate if the population is growing at $\lambda = 1.15$. The population would experience population decline, on average, if greater than ~ 75% of the population were removed. A lower average population growth rate would increase the impact of transient harm.

UNCERTAINTIES

Data related to Warmouth life history and population dynamics were very limited. Foremost, there was no information relating to Warmouth population trends. As a result, all calculations where population growth rate was required (e.g., allowable harm) were based on assumed population trajectories. More information relating to population trajectories at multiple sites, which would require abundance time series, would help refine estimates of λ for use in estimation of allowable harm/recovery effort. Additionally, estimates of inter-annual population growth would inform the probability distribution of λ values which proved to be highly influential on estimates of minimum viable population size. Here, the distribution of λ was influenced by the extent of intra-annual correlation among vital rates. As the correlation increased so did the distribution of λ leading to increases in MVP and MAPV (MVP with a strong intra-annual correlation was > 60 times that of uncorrelated vital rates). The distribution of λ values is also influenced by other factors such as vital rate variability (especially YOY mortality) which can greatly impact MVP estimates (Vélez-Espino and Koops 2012).

There were no empirical data relating to important model parameters such as density, growth, survival and fecundity for Canadian populations of Warmouth. Where available, data were taken from American populations. Parameter values for Canadian populations of Warmouth may differ from those in the United States due to the unique biotic and abiotic characteristics of the Great Lakes. Other species in the *Lepomis* genus, such as Bluegill (*L. macrochirus*) and Pumpkinseed (*L. gibbosus*), have shown significant plasticity in life-history characteristics relating to environmental variability. Significant changes in growth have resulted from changes in rearing density (Osenberg et al. 1988) and temperature (Villeneuve et al. 2005, Masson et al. 2015). Greater size can cause changes in age-at-maturity and reproductive investment (Fox 1994). As well, the presence of competitors or predators has been shown to impact growth and maturation (Fox 1994, Belk 1995, 1998). As a related species, Warmouth may experience similar plasticity in life-history traits. Growth and reproduction characteristics of Canadian populations of Warmouth may differ from those in more southern populations. As well, functional relationships between life-history traits and the environment (i.e., density effects) may influence within population variation in a manner not incorporated into the Warmouth model. Further research on Warmouth in Canada is needed to refine Warmouth population parameters to the location-specific level.

The estimates of MVP from the viability analysis may have been influenced by the incorporated population structure which was limited by data availability. Warmouth was modelled as a single population with density-independent population growth. Both of these assumptions can inflate estimates of MVP when compared to a meta-population structure (van der Lee et al. 2020) and density-dependent population growth (Roberts et al. 2016). van der Lee et al. (2020) conducted population viability analysis for Redside Dace (*Clintostomus elongatus*) and found the results were highly dependent on the assumed meta-population structure. MVP estimates assuming a single randomly mating population structure were up to more than 5 times that of a defined meta-population, depending on impacts of catastrophic die-offs, with all other life history characteristics held constant. Roberts et al. (2016) estimated MVP values for Roanoke Logperch (*Percina rex*) with inclusion of density-dependent and density-independent population growth. MVP estimates with density-dependence ranged from 200 to 4,200 adults while with density-independence greatly exceeded 1 million adults. Both of these analyses incorporated data that were not available for Warmouth populations. van der Lee et al. (2020) incorporated movement data between defined sub-populations and Roberts et al. (2016) had access to long (17 year) population size time series from which population growth rate and density-dependence effects could be estimated. Further research into population size and structure of

Warmouth populations will allow for refinement of model structure and improvement of population viability analysis.

Finally, the frequency and impacts of catastrophic events for Warmouth were unknown. Simulations were conducted with two different frequencies (0.10 and 0.15/generation). The choice of catastrophe frequency had a large impact on MVP estimates. Research that identifies the magnitude and frequency of catastrophic events at the population level would greatly reduce uncertainty in estimates of MVP size, and in recommendation for the conservation of Warmouth.

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