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Recovery Potential Modelling of Pygmy Whitefish (*Prosopium coulterii*) in Canada (Great Lakes – Upper St. Lawrence populations)

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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 Great Lakes–Upper St. Lawrence populations (DU 5) of Pygmy Whitefish (PWF, *Prosopium coulterii*) in Canada as Threatened. Here population modelling is presented to assess the impacts of harm and determine abundance and habitat recovery targets in support of a recovery potential assessment (RPA). This analysis demonstrated that PWF populations were most sensitive to perturbations to juvenile survival. Population viability analysis was used to identify potential recovery targets. Demographic sustainability, (i.e., a self-sustaining population over the long term) can be achieved with adult female population sizes of ~ 430 to 4,000 or ~ 8.4 to 75 kg of whole population age-1+ biomass depending on catastrophe frequency and desired persistence probability. The population would require up to ~ 21 km² of habitat.

INTRODUCTION

Populations of Pygmy Whitefish (PWF, *Prosopium coulterii*) within designatable unit (DU) 5, Great Lakes–Upper St. Lawrence, have been assessed as Threatened by the Committee on the Status of Endangered Wildlife in Canada (COSEWIC). Six additional DUs are recognized for PWF, three were assessed as Data Deficient, two as Not At Risk, and one (Waterton Lake populations) was assessed as Special Concern (COSEWIC 2016). This report will only address DU 5 populations occupying Lake Superior.

The *Species at Risk Act* (SARA) mandates the development of strategies for the protection and recovery of species that are at risk of extinction or extirpation from Canada. In response, 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 the RPA through use of population modelling to assess the impact of anthropogenic harm to populations and identify recovery targets for abundance and habitat with associated uncertainties. This work is based on a demographic approach developed by Vélez-Espino and Koops (2009, 2012) and Vélez-Espino et al. (2010).

METHODS

Information on vital rates was compiled to build projection matrices that incorporate environmental stochasticity and density-dependence. The impact of anthropogenic harm to populations was quantified with use of elasticity and simulation analyses. Estimates of recovery targets for abundance and habitat were made with estimation of the minimum viable population (MVP) and the minimum area for population viability (MAPV).

SOURCES

Limited published information concerning Lake Superior populations of PWF is available. Eschmeyer and Bailey (1955) presented the first detailed description of PWF in Lake Superior providing information on distribution, growth, and reproductive biology. Stewart et al. (2016) provide the only other report specific to Lake Superior PWF life-history characteristics including information on length-at-age and the relationship between length and weight.

The United States Geological Survey (USGS) conducts annual bottom trawl surveys which capture PWF (USGS 2018). The annual survey began sampling locations on the Canadian side of Lake Superior in 1989. In 2011 the survey was extended to include offshore sites. Information from the annual trawls includes the number and biomass of PWF captured in each trawl, as well as the lengths of fish caught.

All analyses and simulations were conducted using the statistical program R 3.5.0 (R Core Team 2018). Parameter values incorporated into the population model are listed in Table 1.

LIFE HISTORY

Age and Growth

Maximum age differs between male and female PWF (Stewart et al. 2016). The oldest age observed for males was age-7 and age-9 for females. Growth also differs between sexes with females experiencing more rapid growth and achieving greater maximum size than males

(Stewart et al. 2016). Female length-at-age, in mm, can be described with the von Bertalanffy growth function (VBGF) as (Stewart et al. 2016):

$$L_t = 166.5(1 - e^{-0.219(t+1.06)}). \quad (1)$$

With male growth modelled as (Stewart et al. 2016):

$$L_t = 117.4(1 - e^{-0.376(t+1.02)}). \quad (2)$$

Stewart et al. (2016) also provided the relationship between length, in mm, and weight, in grams, for PWF where:

$$W_t = 10^{-5.626} L_t^{3.204}. \quad (3)$$

Table 1. Parameter definitions and values used in the population model describing female PWF.

	Symbol	Description	Value	Source
Age	t_{max}	Longevity	9	Stewart et al. (2016)
	t_{mat}	Age-at-maturity	3	Eschmeyer and Bailey (1955)
	ζ	Generation time	4.33	Estimated
Growth	L^∞	Asymptotic length (mm)	166.5	Stewart et al. (2016)
	k	von Bertalanffy growth coefficient	0.22	
	t_0	Age at 0 mm in length	-1.06	
Spawning	α_f	Fecundity allometric intercept	1.6×10^{-5}	Fitted / Eschmeyer and Bailey (1955)
	β_f	Fecundity allometric exponent	3.5	
	φ	Proportion female at hatch	0.5	COSEWIC (2016)
	T	Spawning periodicity	1	
Weight	α_W	Length-weight allometric intercept	2.4×10^{-6}	Stewart et al. (2016)
	β_W	Length-weight allometric exponent	3.20	
Mortality	σ_a	Adult (age-3+) annual survival rate	0.45	Fitted
	σ_2	Age-2 survival rate	0.42	
	σ_1	Age-1 survival rate	0.33	
	$\sigma_{0,1}$	Egg to age-1 survival rate with $\lambda = 1$	0.017	
	CV_M	Coefficient of variation of mortality	0.125	
Density-dependence	$\sigma_{0,max,bh}$	Beverton-Holt estimate of maximum egg to age-1 survival	0.076	Fitted
	$\beta_{d,bh}$	Beverton-Holt density-dependence parameter	3.40	
	$\sigma_{0,max,r}$	Ricker estimate of maximum egg to age-1 survival	0.053	
	$\beta_{d,r}$	Ricker density-dependence parameter	1.12	
	SD_d	Standard deviation of recruitment	0.34	

Reproduction

Information on the reproductive life-history of PWF comes from Eschmeyer and Bailey (1955). Egg counts were measured from 63 females ranging in size from 87–149 mm. A relationship between length and egg count was fit as a log-transformed linear model giving the relationship (Figure 1):

$$f_l = 0.000016L^{3.514} \quad (n = 63, SE = 0.1134, p < 0.001). \quad (4)$$

Maturity, similar to growth, differs between males and females. Males begin reaching maturity at age-1 (5%) and become 100% mature by age-2. Females, however, first mature at age-2 and

are not 100% mature until age-4 (Eschmeyer and Bailey 1955; Figure 2). The ages of fish used to calculate the maturity schedule were determined from scales. For PWF scale ages have been found to be biased towards younger ages when compared to otoliths (Stewart et al. 2016). Therefore, it is possible that the maturity schedule for females was skewed toward younger ages. The sex ratio is approximately 1:1 at birth but becomes skewed toward females with age (Eschmeyer and Bailey 1955; Figure 2).

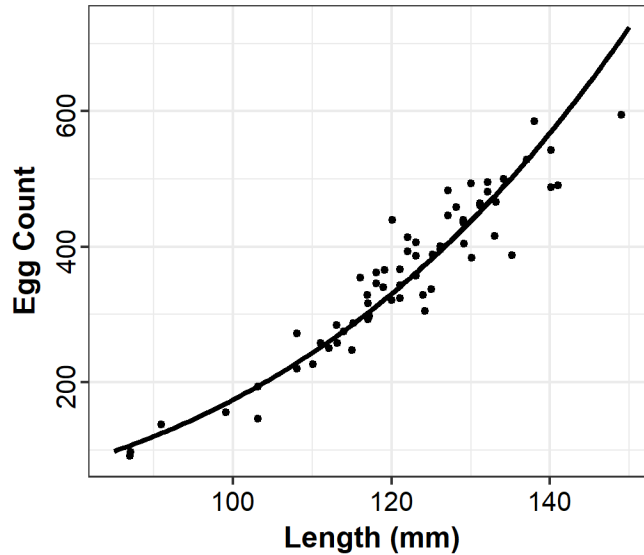


Figure 1. The relationship between body length and egg count for Lake Superior PWF (Equation 4). Data are from Eschmeyer and Bailey (1955).

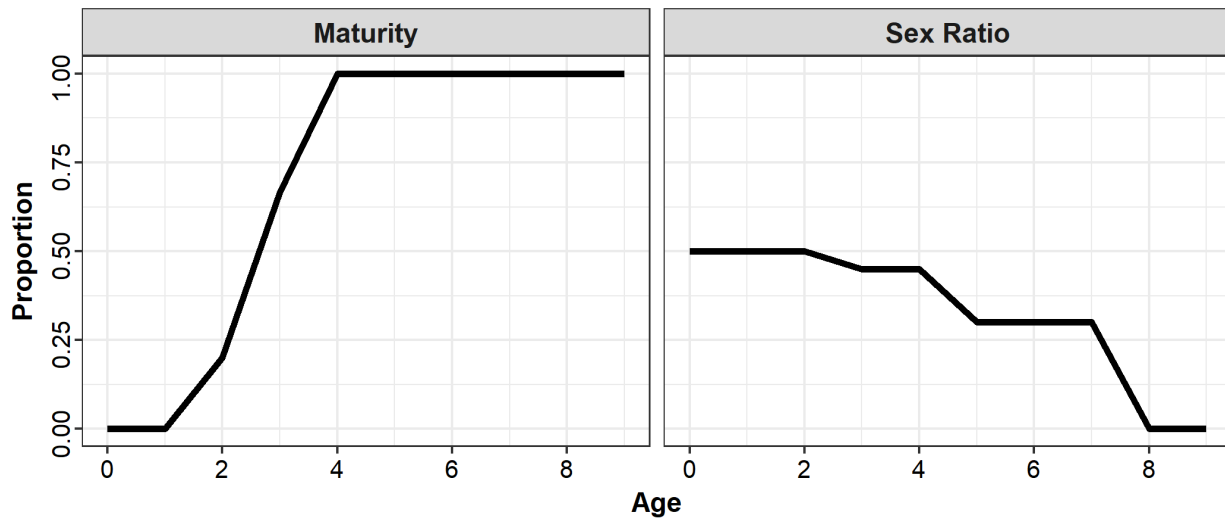


Figure 2. The proportion of females mature-at-age (left) and proportion of the population that is male-at-age (right) for Lake Superior PWF. Data are from Eschmeyer and Bailey (1955) with ages estimated from scales.

Mortality

Published estimates of mortality for PWF were not available. Adult mortality was estimated using the USGS trawl data (USGS 2018). Length measurements were available for every PWF

captured from the nearshore survey. Age- and sex-keys from Stewart et al. (2016) were utilized to assign sex and ages to each fish. Sex and ages were assigned stochastically based on binomial and multinomial distributions. Catch curves for each year were fit to give an annual estimate of instantaneous mortality (M) for female PWF in Lake Superior. This was repeated 5,000 times and the median estimate of M was taken for each year. The average M for female PWF across years was 0.79 with a SD of 0.19.

Juvenile mortality was assumed to be greater than that of adults and increased as an inverse function of body length (Lorenzen 2000). With PWF growth described by the VBGF the mean survival rate between ages (σ_t) can be estimated from:

$$\sigma_t = \left[\frac{L_t e^{-k}}{L_{t+1}} \right]^{M_r L_r / k L_\infty} \quad (5)$$

Where k and L_∞ are VBGF parameters and M_r and L_r are mortality and length at a reference size (i.e. at length-at-maturity).

Table 2. Fitted parameter values for stock-recruitment curves (Figure 3).

Parameter	Stock-Recruitment Curve	
	Beverton-Holt	Ricker
α	0.076	0.052
β	3.5×10^{-6}	1.1×10^{-5}
SE	0.69	0.69

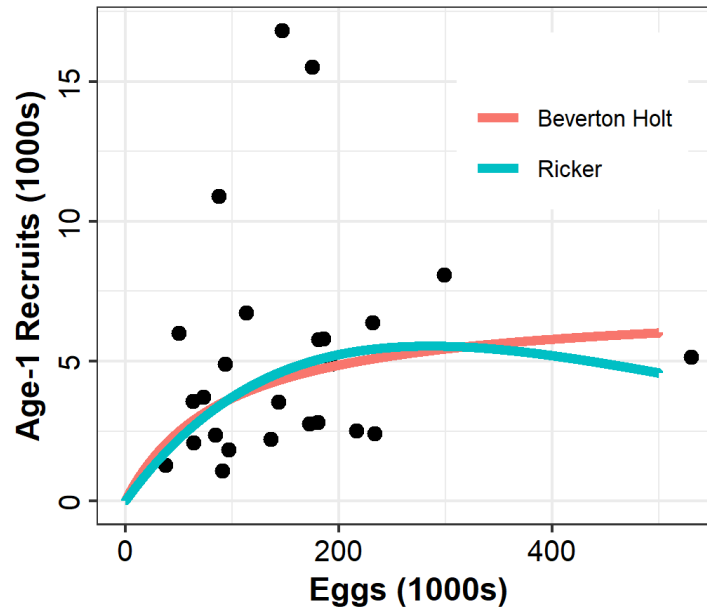


Figure 3. Fitted median stock recruitment curves (red – Beverton-Holt; blue – Ricker; Table 2). Data represent one stochastic iteration from replicates.

First year survival was estimated by fitting stock recruitment curves to the stochastically aged and sexed PWF length data. Recruits were represented by age-4 females; when full recruitment to the gear occurred. Spawners were represented by mature females in the catch. These values were converted to the number of age-1 females based on the above survival schedule and annual egg production based on Equation 4 such that the fitted relationship represents survival

from egg to age-1 for given levels of egg production. S-R curves were fit using both the Beverton-Holt:

$$R = \alpha S / (1 + \beta S), \quad (6)$$

and Ricker forms.

$$R = \alpha S e^{-\beta S}. \quad (7)$$

S-R curves were fit assuming a log-normal error structure and repeated 5,000 times with the median of parameter estimates taken (Table 2, Figure 3).

THE MODEL

The PWF life cycle was modeled using a female only, density-dependent, birth-pulse, pre-breeding, age-structured population matrix model with annual projection intervals (Caswell 2001, Figure 4).

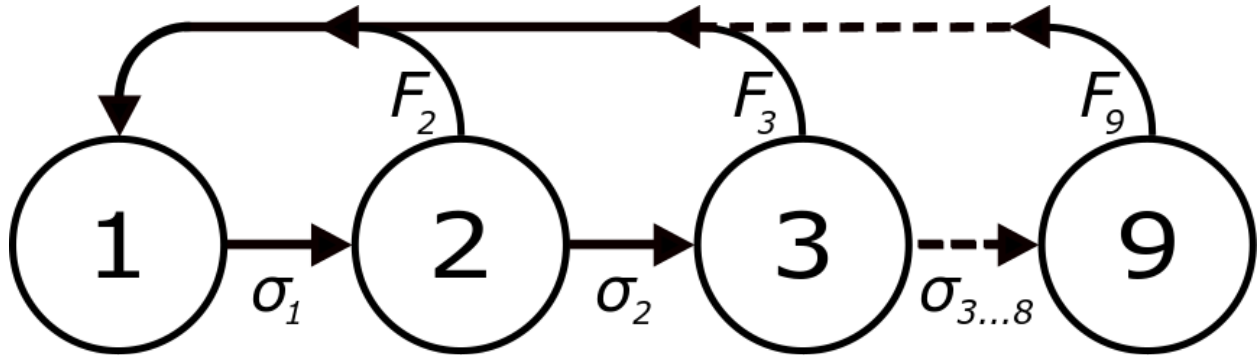


Figure 4. Generalized life cycle used to model the population dynamics of PWF. F_i represents stage-specific annual fertility and σ_i represents the survival from stage i to $i+1$.

The matrix consisted of 9 stages (Figure 4) representing ages 1 through 9. The projection matrix \mathbf{A} is the product of the transition matrix \mathbf{B} , consisting of the life-history characteristics, and the density-dependence matrix \mathbf{D} (see below) representing the density-dependence effects, where:

$$\mathbf{B} = \begin{bmatrix} 0 & F_2 & F_3 & F_4 & F_5 & F_6 & F_7 & F_8 & F_9 \\ \sigma_1 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & \sigma_2 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & \sigma_3 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & \sigma_4 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & \sigma_5 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & \sigma_6 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & \sigma_7 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & \sigma_8 & 0 \end{bmatrix} \quad (8)$$

and:

$$\mathbf{A} = \mathbf{B} \circ \mathbf{D}, \quad (9)$$

where the symbol \circ represents the Hadamard product or the element by element multiplication of the matrices.

Age-based matrix models incorporate parameters F_i , age-specific fertility, and σ_i , age-specific annual survival rate. Fertility, F_i , is the product of all reproductive parameters and as a pre-breeding matrix also incorporates the probability of surviving from the egg stage to age-1 (σ_0):

$$F_i = f_i \varphi \rho_i \sigma_{0,1} T, \quad (10)$$

Where f_i represents age-specific fecundity, φ represents the sex ratio at hatch, ρ_i presents the proportion of females mature at age- i , $\sigma_{0,1}$ represents survival from hatch to age-1 under stable population growth, and T represents spawning periodicity which was assumed to be 1 year (COSEWIC 2016).

Density-dependence

Density-dependence was assumed to act only during the first year of life. Density-dependence was incorporated using the Beverton-Holt (Equation 6) and Ricker (Equation 7) functions adapted for inclusion in the projection matrix:

$$d_0 = \frac{\sigma_{0,max}/\sigma_{0,1}}{1 + \beta_d \times N_e / K_e}, \quad (11)$$

$$d_0 = \sigma_{0,max}/\sigma_{0,1} e^{-\beta_d N_e / K_e}. \quad (12)$$

Where $\sigma_{0,max}$ and $\sigma_{0,1}$ represent maximum and equilibrium egg to age-1 survival rates respectively, β_d is the density-dependence parameter scaled to a single individual, N_e is the current annual egg production and K_e is carrying capacity or egg production that gives a stable adult population size, where $K_e = \sum_{t=1}^{i=1} K_i f_i \rho_i T$ with adult carrying capacity $K_a = \sum_{t=1}^{i=1} K_i \rho_i$, and K_i representing age-specific carrying capacities based on the stable age distribution.

Density-dependence matrix \mathbf{D} was structured as:

$$\mathbf{D} = \begin{bmatrix} 1 & d_0 & d_0 & d_0 & d_0 & d_0 & d_0 & d_0 & d_0 \\ 1 & 1 & 1 & 1 & 1 & 1 & 1 & 1 & 1 \\ 1 & 1 & 1 & 1 & 1 & 1 & 1 & 1 & 1 \\ 1 & 1 & 1 & 1 & 1 & 1 & 1 & 1 & 1 \\ 1 & 1 & 1 & 1 & 1 & 1 & 1 & 1 & 1 \\ 1 & 1 & 1 & 1 & 1 & 1 & 1 & 1 & 1 \\ 1 & 1 & 1 & 1 & 1 & 1 & 1 & 1 & 1 \\ 1 & 1 & 1 & 1 & 1 & 1 & 1 & 1 & 1 \\ 1 & 1 & 1 & 1 & 1 & 1 & 1 & 1 & 1 \end{bmatrix}. \quad (13)$$

Stochasticity

Recruitment and age-specific survival were varied annually to simulate environmental stochasticity in vital rates. The amount of variability included in the population model was based on half the residual standard deviation from fitting the functional relationships for recruitment and the variability in M estimates across years.

Recruitment (age-0 survival) was assumed to follow a lognormal distribution with a standard deviation of 0.35. Survival rate was varied as instantaneous mortality ($\sigma_i = e^{-M_i}$). It was assumed M varies following a normal distribution with a CV of 0.125. Stochasticity was executed using the stretched-beta distribution to remove the extreme tails of the normal distribution but maintain the mean and standard deviation (Morris and Doak 2002). It was assumed M was correlated intra-annually with an AR1 correlation structure (correlation diminishes as difference between ages increases) with a correlation value of 0.75.

This amount of stochasticity in vital rates resulted in adult population size varying with a CV of ~ 0.22 .

IMPACT OF HARM

The impact of anthropogenic harm to a PWF population was assessed with deterministic elasticity analyses of the projection matrix and stochastic simulations.

Two deterministic elasticity analyses were used: a density-independent analysis to determine the impact of changes to vital rates on population growth (ϵ_λ); and a density-dependent analysis to determine the impact of changes to vital rates on stable population density (ϵ_N).

Elasticity analysis of matrix elements provides a method to quantify the impact of changes to vital rates on a population. Specifically, elasticities measure the proportional change to population growth rate (λ) or equilibrium density (N) that results from a proportional change in a vital rate (v). For example, an elasticity of λ value of 0.2 for juvenile survival indicates that a 10% change in juvenile survival rate (e.g. $0.5 \times (1 + 0.1) = 0.55$) would cause a 2% increase in population growth rate (e.g. $1 \times (1 + 0.1 \times 0.2) = 1.02$). The elasticity of N functions the same way except acting on stage-specific densities; for example, an elasticity of N value for adult density of 0.15 for perturbations to egg carrying capacity (K_e) would indicate that a 20% decrease in K_e (e.g. $225,000 \times (1 - 0.20) = 180,000$) would cause a 3% decrease in adult equilibrium density (e.g. $1,000 \times (1 - 0.15 \times 0.20) = 970$).

Elasticities are useful as they allow for assessment of how impactful changes to vital rates and other model parameters are to a population. Because they represent proportional changes, their values are directly comparable. They are preferable to simulation analyses because of the speed they can be estimated, allowing for many more perturbations to be examined than simulations. Elasticities are limited, however, as they represent permanent changes and assume all other model parameters remain unchanged. As a result, simulation analysis was used to examine the effects of transient or periodic harm to a population.

Elasticity of λ

Elasticities of λ (ϵ_λ) are calculated by taking the scaled partial derivatives of λ with respect to a vital rate (v , Caswell 2001):

$$\epsilon_\lambda = \frac{v}{\lambda} \sum_{i,j} \frac{\partial \lambda}{\partial a_{i,j}} \frac{\partial a_{i,j}}{\partial v}, \quad (14)$$

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

Elasticity estimates are influenced by current conditions. Elasticity values are therefore provided for four population states: declining, stable, growing, and booming. A declining population was defined based on COSEWIC criterion A2 for Threatened species as a $\geq 30\%$ reduction in population size over 10 years or 3 generations, whichever is longer; resulting in $\lambda_{\min} = 0.973$. A stable population was defined as one with $\lambda_1 = 1$. A booming population was one with young of the year (YOY) survival set to the maximum value, i.e., when density is 0; resulting in $\lambda_{\max} =$

1.46 when assuming Beverton-Holt density-dependence and $\lambda_{\max} = 1.32$ when assuming Ricker density-dependence. Finally, a growing population was defined by setting vital rate values as if population size was at 50% of carrying capacity; resulting in $\lambda_{\text{mean}} = 1.12$ and 1.14 for Beverton-Holt and Ricker density-dependence, respectively.

Elasticity of N

Elasticities of N (ε_N) are calculated from the sensitivities of N ($\frac{d\hat{N}}{dv^i}$) where (Caswell 2019):

$$\frac{d\hat{N}}{dv^i} = \left(\mathbf{I}_i - \mathbf{A} - (\hat{\mathbf{N}}^\top \otimes \mathbf{I}_i) \frac{\partial \text{vec} \mathbf{A}}{\partial \mathbf{N}^\top} \right)^{-1} (\hat{\mathbf{N}}^\top \otimes \mathbf{I}_i) \frac{\partial \text{vec} \mathbf{A}}{\partial v^i}, \quad (15)$$

and:

$$\varepsilon_N = \text{diag}(\hat{\mathbf{N}})^{-1} \frac{d\hat{N}}{dv^i} \text{diag}(\mathbf{v}). \quad (16)$$

\mathbf{A} is the projection matrix of dimension $i \times i$, \mathbf{I}_i is an identity matrix of dimension $i \times i$, $\hat{\mathbf{N}}$ is a vector of equilibrium densities, $\frac{\partial \text{vec} \mathbf{A}}{\partial \mathbf{N}^\top}$ is the partial derivatives of matrix \mathbf{A} with respect to stage densities, $\frac{\partial \text{vec} \mathbf{A}}{\partial v^i}$ is the partial derivatives of matrix \mathbf{A} with respect to the vital rates or the model parameters of interest, \top is the transpose operator and \otimes represents the Kronecker product. $\text{diag}(\hat{\mathbf{N}})$ and $\text{diag}(\mathbf{v})$ represent diagonal matrices with the equilibrium densities and parameter values on the diagonal, respectively, and 0s on the off diagonal entries. See Caswell (2019) for more details.

Estimates of ε_N are provided with respect to perturbations of fecundity, life stage-specific survival rate, and density-dependence parameters for the Beverton-Holt and Ricker models.

Simulation

Simulation analysis was used to investigate the impacts of stage-specific harm on adult population density. Stage-specific survival rates were reduced by some level of harm, ranging from 0 to 99%, at different frequencies: 1, 2, 5, and 10 years, over a 100 year simulation. The initial carrying capacity was then compared to the mean population size over the final 15 years of simulation to determine the effect of the harm, quantified as the proportion of initial K_a . The frequency indicates how often harm was applied to the population. A frequency of 1 indicates that harm is constant and applied every year, where a frequency of 10 indicates that harm is periodic and applied once every 10 years. As a density-dependent model it is assumed that the population is able to recover in between applications of harm as conditions are returned to the initial state and since this is a single-species model, no competitors exist.

RECOVERY TARGETS

Abundance: Minimum Viable Population (MVP)

The concept of demographic sustainability was used to identify potential minimum recovery targets for PWF. 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 (~ 23 PWF generations), where 'adult' correspond to mature females. MVP was estimated using simulation analysis which incorporated environmental stochasticity and density-dependence.

Important elements incorporated in population viability analysis include: the choice of time frame over which persistence is determined, the severity and frequency of catastrophic events, 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 within PWF populations is unknown. Based on a meta-analysis, Reed et al. (2003) determined that among vertebrate populations, catastrophic die-offs that resulted in a one-year decrease in population size > 50% occurred at a rate of 14%/generation on average. This result was used to guide the MVP simulations and three levels of catastrophe rate were used to allow for uncertainty: 5%/generation, 10%/generation and 15%/generation. These rates correspond to an average catastrophe frequency of one catastrophe every 87, 43 and 29 years, respectively. The impact of catastrophes affect all life-stages simultaneously and was drawn randomly from a beta distribution scaled between 0.5 and 1 with shape parameters of 0.762 and 1.5 (Reed et al. 2003; Figure 5), representing the probability of a 50 to 100% decline in population size. Catastrophes represent any temporary and reversible large-scale disturbance to the population and may be from natural or anthropogenic causes.

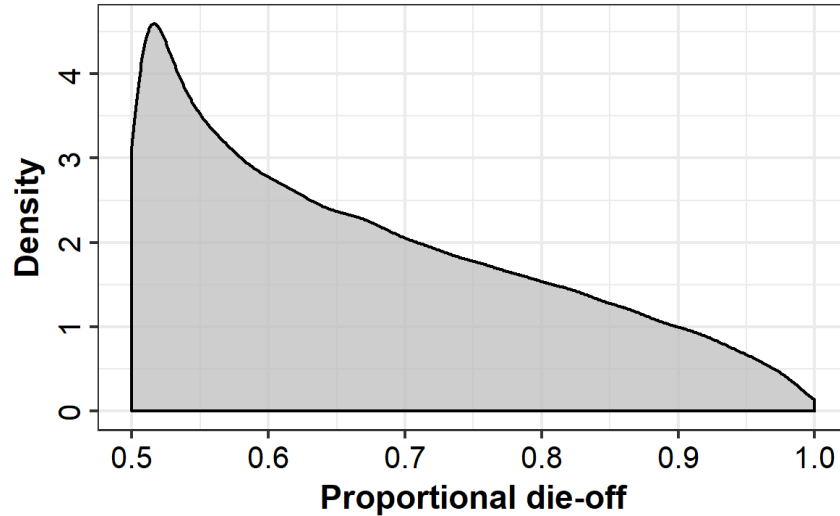


Figure 5. Beta distribution (scaled between 0.5 and 1) used in stochastic draws of catastrophic impacts. This represents the proportional decrease in population size following a catastrophic event. Shape parameters were 0.762 and 1.5 (Reed et al. 2003).

Quasi-extinction accounts for the compounding effects of Allee effects, demographic stochasticity, and inbreeding depression (Lande 1988) leading a population to extinction once the threshold is crossed. The value of the quasi-extinction threshold cannot be empirically measured; therefore, 25 adult females was used as a reasonable approximation (Morris and Doak 2002).

Density-dependent, stochastic simulations were conducted for populations of various initial densities (initial density represented adult female carrying capacity, K_a , where $\lambda = 1$). Simulations were run for 100 years. Independent simulations incorporated three rates of catastrophes (0.05, 0.1, and 0.15/generation). Each simulation was replicated 5,000 times and the number of quasi-extinctions were counted. The probability of extinction ($P[ext.]$) was modelled as a logistic regression, such that:

$$P[ext.] = \frac{1}{1 + e^{-(b_{MVP} \log_{10}(N_a) + a_{MVP})}} \quad (17)$$

where a_{MVP} and b_{MVP} represent the fitted intercept and slope from the logistic regression. Equation 17 can be rearranged to estimate the adult population size required to give a desired level of population persistence (MVP):

$$MVP = 10^{\frac{\log(1/P_{[ext.]})^{-1} + a_{MVP}}{b_{MVP}}}. \quad (18)$$

MVP estimates are presented for quasi-extinction probabilities of 5% and 1%.

Habitat: Minimum Area for Population Viability (MAPV)

Minimum area for population viability (MAPV) is defined as the quantity of habitat required to support a population of MVP size (Velez-Espino et al. 2010). MAPV is estimated simply as MVP divided by mean population density. Population density (kg biomass/ha) was estimated using a spatial hurdle model estimated from annual bottom trawl data collected by USGS (van der Lee and Koops 2020). The predicted estimate for biomass was 0.036 kg/ha for 2018 accounting for depth, likelihood of occurrence, and spatial dependency.

RESULTS

IMPACT OF HARM

Various analyses were used to assess the impact of harm to PWF populations: deterministic elasticity analysis on population growth rate (Figure 6) and life-stage density (Figure 7) and simulation analysis (Figure 8).

Elasticity of λ

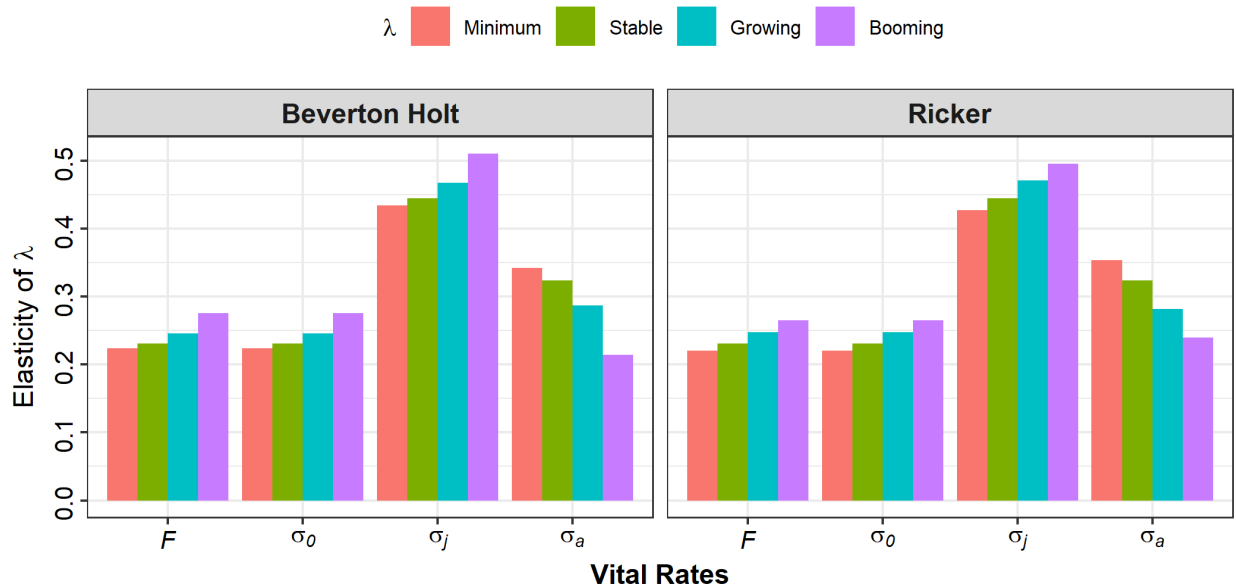


Figure 6. Elasticity of λ analysis results for Beverton-Holt and Ricker population models under four population states: declining, stable, growing and booming. F represents fertility indicating the effects of independent perturbations to all parameters that contribute to fertility (Equation 10) and σ represents survival for the YOY (0), juvenile (j) and adult (a) stages.

The elasticity to λ to perturbations of vital rates (Figure 6) gives an indication of how the population may respond to changes in vital rates; where positive values indicate that population growth rate will increase if the vital rate is increased. Elasticity estimates are presented for fertility (F) which encompasses all parameters contributing to Equation 10 and survival rates (σ) for the YOY, juvenile, and adult stage.

The results were nearly identical when parameterized with Beverton-Holt or Ricker density-dependence parameters and were similar across different rates of population growth. Generally, population growth rate was most sensitive to perturbations to juvenile survival with elasticity values ~ 0.46 . This was greater than the sensitivity of λ to adult survival (~ 0.29) or fertility/YOY survival (~ 0.24). This indicates that a population of PWF would be most affected by mortality to the juvenile stage (assuming density-independence). For example, a mortality rate of 5% on top of natural mortality would cause a stable population ($\lambda = 1$) to experience a 2.3% decline in population size annually ($1 \times (1 - 0.05 \times 0.46)$).

Elasticity of N

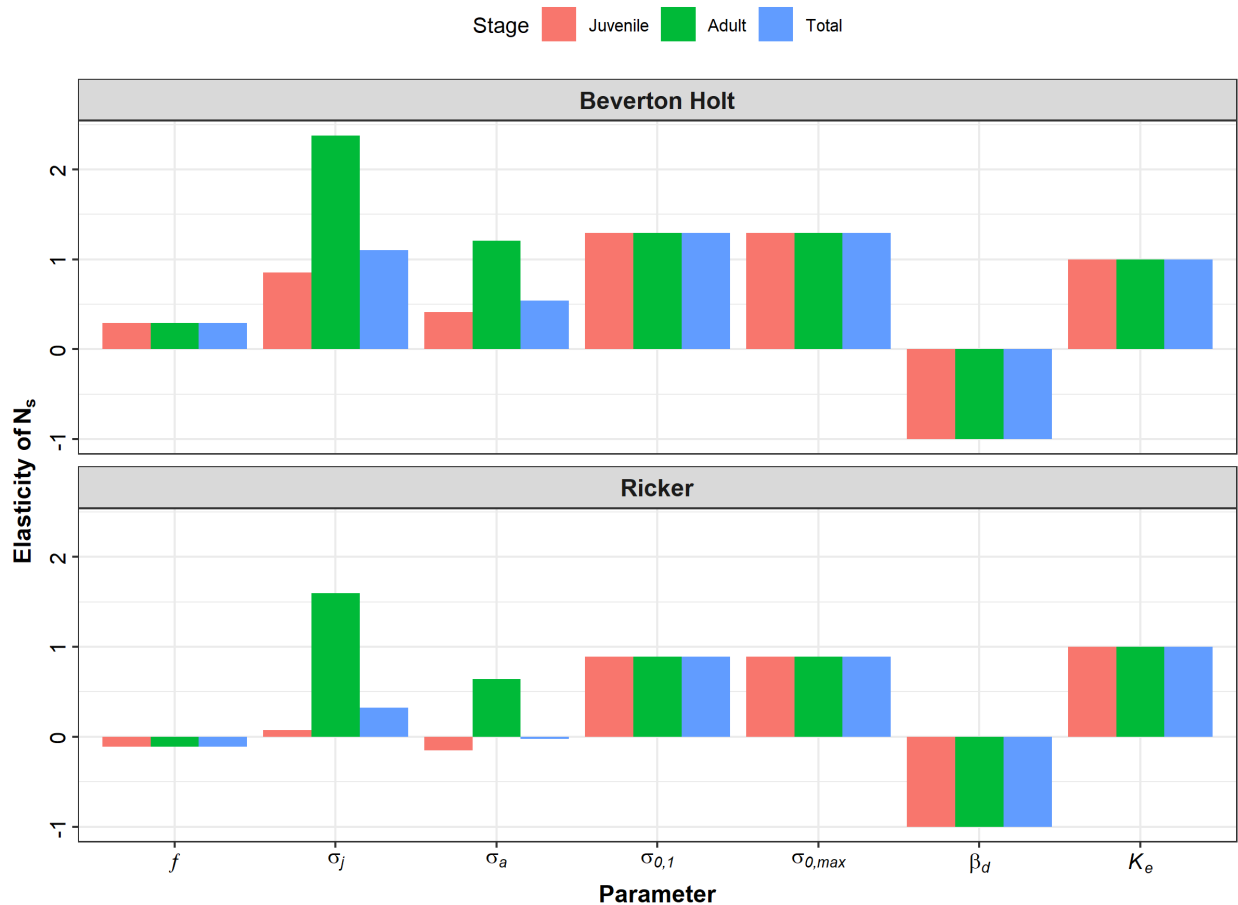


Figure 7. Elasticity of N_s analysis results for Beverton-Holt and Ricker models. The x-axis represents the model parameter that is perturbed; the y-axis represents the resultant proportional change to life-stage-specific density. f represents total fecundity, and σ_s represents life-stage-specific survival, β_d is the density-dependent parameter and K_e represents egg carrying capacity.

The above analysis of elasticities of λ assumes density-independence but if density-dependence acts on the populations the results may not hold. Therefore an analysis of the elasticity of life-stage-specific density (N_s) to changes in vital rates was applied accounting for the effects of density-dependent recruitment.

Density-dependence was assumed to act only in the first year of life but could follow either the Beverton-Holt or Ricker forms (Figure 7). Perturbations to density-dependence parameters were similar for the two models with ubiquitous increases in density across life-stages with increases in carrying capacity (K_e), and equilibrium ($\sigma_{0,r}$) or maximum ($\sigma_{0,max}$) YOY survival, and decreased in density if the density-dependence parameter (β_d) was increased.

The effects of changes to other vital rates, however, were more varied and differed somewhat between the density-dependence forms. The Beverton-Holt model represents compensatory density-dependence and therefore increases in vital rates caused an increase in density. Similar to the elasticity of λ analysis, the greatest increase in adult density resulted from increases in juvenile survival rate. The Ricker model, however, is over-compensatory resulting in counteracting effects on different life-stages with perturbations to vital rates. Again the greatest increase in population density resulted from increases in juvenile survival rate; however, to a lesser degree than the Beverton-Holt model. Increases in fecundity resulted in a net decrease in population size. This result differs from the Beverton-Holt model and elasticity of λ analysis (Figure 6), where increases in fecundity/fertility had a positive effect on the population. Finally, with the Ricker form of density-dependence, increases in adult survival allowed for an increase in the number of adults in the population but led to a decrease in recruitment. This results from an increase in mean age of adult females due to greater adult survival leading to an increase in annual egg production resulting in decreased YOY survival.

As an example, with the Beverton-Holt density-dependence form the elasticity values from changes in adult survival were 1.2 for adult density and 0.41 for juvenile density. Therefore a 10% increase in adult survival (i.e., $0.45 \times (1 + 0.1) = 0.495$) would lead to a 12% increase in the number of adults and a 4.1% increase in the number of juveniles in the population. Alternatively, with the Ricker density-dependence form the elasticity values were 0.64 and -0.15, respectively. This indicates that the same 10% increase in adult survival would coincide with a 6.4% increase in the number of adults but a 1.5% reduction in the number of juveniles.

Simulation

The above elasticity analyses assume that any change to a vital rate is permanent. Therefore, simulation analysis was used to investigate how adult population size may respond to periodic perturbations occurring annually (for comparison to elasticity analysis), every second year, fifth year, and tenth year (Figure 8). A reference line is included at the point where adult density reduces to 75% of initial carrying capacity which was arbitrarily chosen.

The results were similar between the two density-dependence models and consistent with the elasticity analyses with harm to juvenile stage (increases in annual mortality) having the greatest impact on adult density of the stage-specific harm. The impacts of harm, however, were slightly less when the Ricker density-dependence form was assumed compared to the Beverton-Holt form. The Ricker model required slightly greater harm values to result in a 25% reduction from initial adult density.

For the Beverton-Holt and Ricker density-dependence forms, the lower confidence interval for juvenile survival crossed the 75% threshold when harm equalled 0.03 and 0.07, respectively, indicating that an additional mortality of 3% or 7% on juveniles could cause adult density to decrease 25% from initial pre-harm densities. The lower confidence values for YOY and adult stages were 0.5/0.11 and 0.5/0.14, respectively.

As the frequency of harm decreased, the effects of harm decreased fairly linearly. The lower confidence interval from biennial harm simulations crossed the 75% threshold at approximately twice the harm value of annual harm. This trend continuing at 5 and 10 year harm intervals. For the Ricker model simulations, harm to the YOY or adult stage at a 10 year periodic frequency did not have a large effect on adult density.

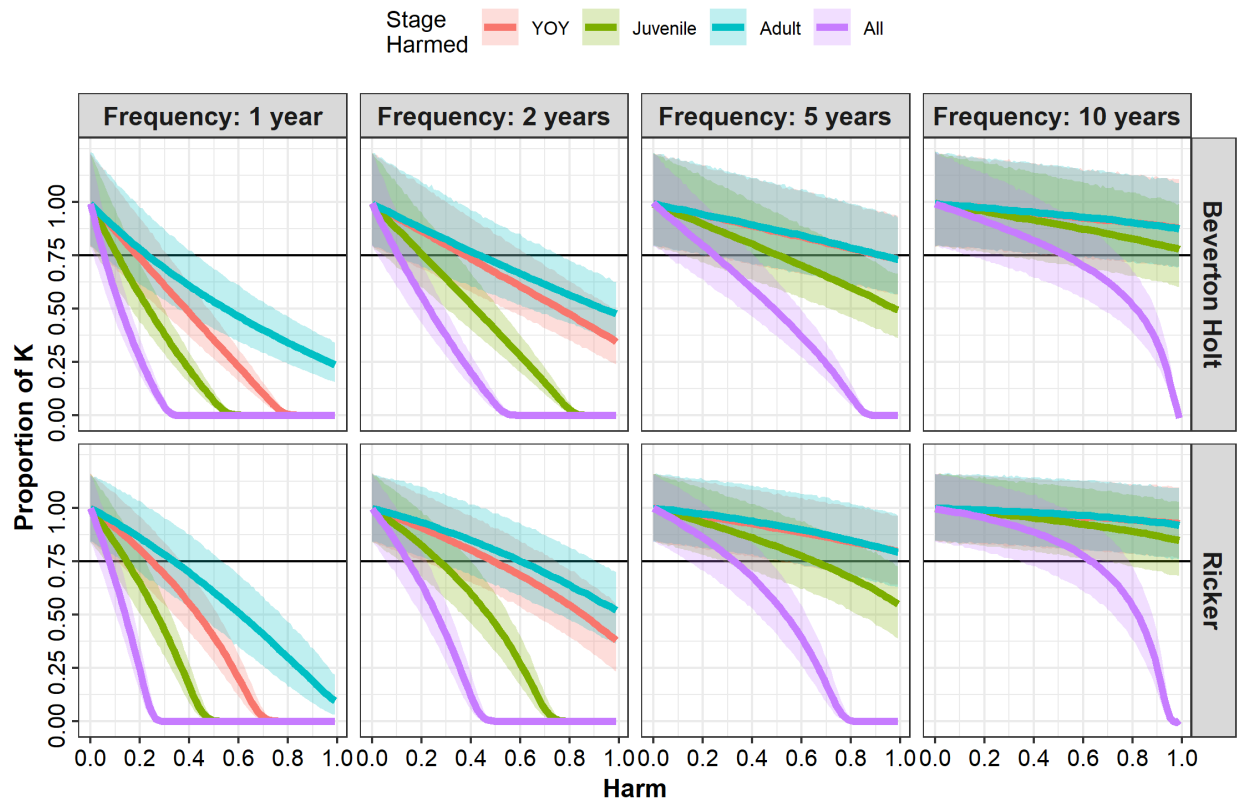


Figure 8. Results from harm simulation analysis where harm is applied at different frequencies to specific life-stages. The x-axis represent the proportional harm (e.g. annual mortality) applied to the life-stage and the y-axis represents the proportional decrease in adult density over a 100 year simulation. The solid lines represent the mean impact and the surrounding polygons represent confidence intervals. The reference line indicates a 25% decline from initial density.

RECOVERY TARGETS

Abundance: Minimum Viable Population (MVP)

Demographic sustainability was assessed using stochastic, density-dependent population simulations. Simulation outputs, binomial quasi-extinctions (1: extinct; 0: extant), were fitted using a logistic regression (Table 3; Figure 9).

Recovery target abundances that provide a 5% and 1% probability of quasi-extinction over 100 years are presented (Table 4). Additional targets, those with different extinction risks, can be estimated with use of Equation 18 and parameter values from Table 3. Simulation outputs applied solely to adult females in the population.

Table 3. Parameter values from logistic regression of extinction probability and adult female population size for PWF populations using Beverton-Holt and Ricker density-dependence at three rates of catastrophe.

Catastrophe rate	Beverton-Holt		Ricker	
	a_{MVP}	b_{MVP}	a_{MVP}	b_{MVP}
0.05	6.51	-3.59	6.20	-3.47
0.10	7.20	-3.47	7.40	-3.56
0.15	7.90	-3.49	7.76	-3.43

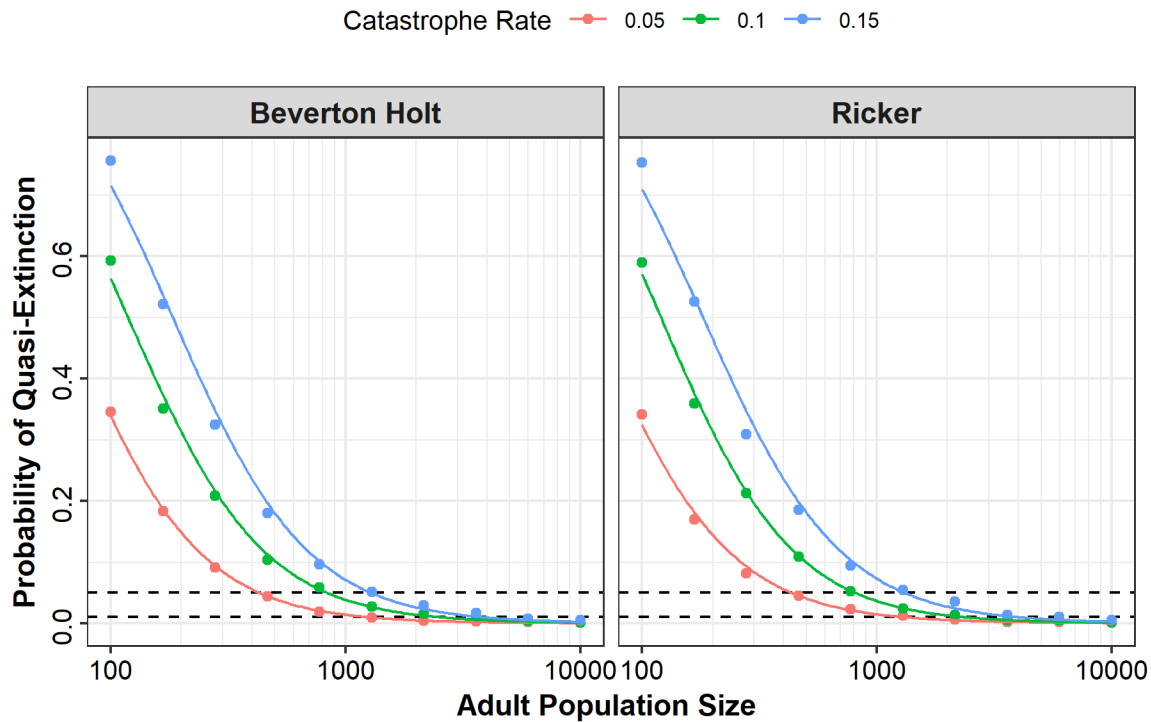


Figure 9. The probability of quasi-extinction at various adult densities for two density-dependence models and three rates of catastrophe. The points represent mean simulation values and the lines represent fitted logistic regressions for catastrophe rates 0.05, 0.10, and 0.15, respectively.

Table 4. Recovery targets for populations size (MVP) for PWF using Beverton-Holt and Ricker models under three rates of catastrophe. Values are reported for adult females, adult males, and whole populations (age-1+) biomass.

Catastrophe Rate	Adult Females		Adult Males		Biomass (kg)	
	P[ext] = 5%	P[ext] = 1%	P[ext] = 5%	P[ext] = 1%	P[ext] = 5%	P[ext] = 1%
Beverton-Holt						
0.05	430	1,240	987	2,847	8.34	24.05
0.10	834	2,493	1,915	5,725	16.18	48.36
0.15	1,282	3,812	2,944	8,754	24.87	73.94
Ricker						
0.05	434	1,299	997	2,983	8.42	25.20
0.10	809	2,354	1,858	5,406	15.69	45.66
0.15	1,312	3,971	3,013	9,119	25.45	77.02

The corresponding number of adult males in the population was estimated by back-calculating age-specific female densities using the stable-age structure from the matrix model, the sex ratio (Figure 2) to estimate the number of males, and the male maturity schedule to calculate the number of mature males. The number of mature males exceeded the number of female as they mature earlier; however, because they live for a shorter period and reach a smaller maximum size, male biomass is less than female biomass. As well, estimates of total population (age-1+) biomass are provided by using Equations 1, 2, and 3 to convert age- and sex-specific densities to whole population biomass.

The required population size of adult female PWF for sustainability were very similar with either Beverton-Holt or Ricker density-dependence forms assumed but depended greatly on the assumed frequency of catastrophic perturbations to the populations. To achieve a 99% likelihood of persistence over 100 years PWF adult female population sizes of ~ 1,300, 2,500, and 4,000 were required for catastrophe rates of 5, 10 and 15% per generation. This corresponds to whole population biomass of ~ 25, 50, and 75 kg.

Habitat: Minimum Area for Population Viability (MAPV)

The quantity of habitat required to support an MVP sized population of PWF can be estimated by dividing the MVP estimate by the mean population density. Mean PWF biomass density was estimated to be 0.036 kg/ha. Therefore, the maximum habitat quantity required to support an MVP sized population (1% extinction probability, 15%/generation catastrophe rate, and Ricker type density-dependence) is estimated to be ~ 21 km².

The spatial model was used to project population size (kg/ha) across Lake Superior and locations where densities were > 0.036 kg/ha (i.e. greater than lake-wide mean) were identified (Figure 10). With this projection all areas of approximately 21 km² represent potential MVP sized populations of PWF. Within Lake Superior there are many (> 7) spatially distinct areas that are likely to contain populations, potentially multiple populations, that exceed MVP. If these populations are entirely uncorrelated the extinction probability of PWF in Lake Superior as a whole would decrease to $0.01^7 = 1.0 \times 10^{-14}$.

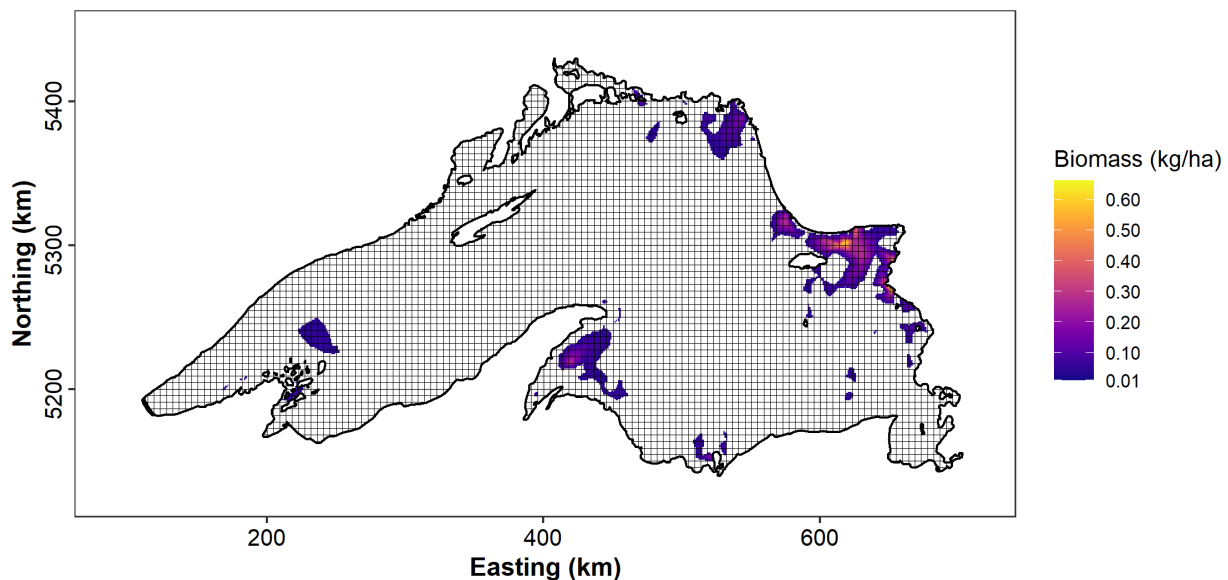


Figure 10. Locations with predicted PWF densities > 0.036 kg/ha (i.e. above average densities) from the spatial hurdle model (van der Lee and Koops 2020). The grid represents ~ 21 km² squares therefore any coloured grid square represents a potential MVP population.

DISCUSSION

A population model for PWF was created to make predictions on how a population may respond to anthropogenic harm and estimate recovery targets for abundance and habitat. Limited information on Lake Superior PWF life-history characteristics has been published. What information was available was compiled and additional parameters estimated, such as adult mortality and stock-recruitment relationships, making use of USGS's long term bottom trawl survey data.

Multiple methods were used to assess the impacts of harm to PWF populations. Across the various methods it became apparent that PWF are most impacted by perturbations to the juvenile stage. This result holds for assumptions of density-independence and -dependence and periodic harm.

Elasticity analysis of N (Figure 7) demonstrates the impact of changes to vital rates on stage-specific population densities incorporating the effects of density-dependence. With Beverton-Holt and Ricker type density-dependence, respectively, annual mortalities acting on juveniles in addition to natural mortality greater than ~ 10 and 15% would cause the population to decline to 75% of initial carrying capacity. This is similar to results from simulations with annual harm (Figure 8) where mortalities of $\sim 11\%$ or 14% to the juvenile stage (based on median) would cause a 25% decline in adult abundance. The YOY stage was the next most sensitive stage with harms of 19 or 28% causing a 25% decline in N_a , followed by the adult stage with 21 or 39% mortalities. The effects of harm to spawning (fecundity) differed between the density-dependence types. With Beverton-Holt density-dependence, harm to spawning would cause a slight decrease in abundance but required 85% reduction before adult abundance declined to 75% of carrying capacity. With Ricker density-dependence, however, harm to spawning did not cause a decline in abundance.

Simulation analysis was required to investigate the impacts of harm occurring periodically (at greater than one year intervals) as sensitivity analysis assumes all perturbations are permanent. The impact of harm decreased relatively linearly with decreased frequency, where the amount of harm that resulted in a 25% decline in N_a at different harm frequencies was approximately equal to the impact of annual harm divided by frequency. This indicates that the more recovery time allowed following periodic harm, the smaller the impact of each incidence of harm.

Estimates of recovery targets for abundance were made using simulation analysis to determine population sizes required for demographic stability through estimates of minimum viable population size (MVP). The results were similar regardless of the density-dependence function; depending mostly on persistence probability and rate of catastrophe. To achieve a 99% probability of persistence, populations in very stable environments (5% /generation catastrophe rate) achieve demographic stability with adult female populations sizes of $\sim 1,300$ fish. This corresponds to $\sim 3,000$ adult males and an age-1+ biomass of 25 kg. Populations that experience more frequent large scale disturbances (15% /generation catastrophe rate) required abundances of $\sim 4,000$ adult females, $9,000$ adult males, or 75 kg of age-1+ biomass. Lake-wide PWF abundance in 2018 was projected with a spatial hurdle model from trawl survey captures (van der Lee and Koops 2020). The projection is based on Gaussian spatial fields derived from the bottom trawl data and bathymetry information to define likely habitat. Lake-wide population biomass was estimated to be $68,707$ kg, although with broad confidence intervals ($2,465 - 1,357,612$). Therefore, it is likely that individual PWF populations in Lake Superior are currently larger than MVP.

Estimates of MVP were converted into habitat requirements by dividing MVP by mean estimates of density (0.036 kg/ha, van der Lee and Koops 2020) giving an estimate of ~ 21 km² required to support a population of PWF. Again using the spatial hurdle model, the quantity of usable

habitat available for PWF in Lake Superior was estimated. Two methods were used: quantifying the habitat where there is expected to be > 0 kg biomass; and quantifying the habitat where PWF occurrence is likely to be > 50%. The first method produced a median estimate of 18,850 (CI: 1,468 – 43,319) and the second method gave an estimate of 9,774 (CI: 712 – 26,014). Based on this result, it is likely that there is sufficient habitat in Lake Superior to support PWF populations.

UNCERTAINTIES

Few reports exist describing the life history characteristics of PWF (Eshmeier and Bailey 1955, Stewart et al. 2016). As a result, there is uncertainty in the parameterization of the population model. Most reproductive characteristics (i.e. fecundity, maturity, and sex ratio) were taken from an older report (Eshmeier and Bailey 1955) and others (such as growth) were based on small sample size (n = 53, Stewart et al. 2016). Additionally, recruitment and mortality functions were fit to long term trawl data, however, this required individuals to be aged and sexed based on length keys, adding potential error to estimates.

In fitting model parameters and conducting analyses, Lake Superior PWF was considered to be a single population with common life-history characteristics across the lake and no immigration. This is likely not appropriate for Lake Superior populations. PWF occupy multiple spatially disparate locations in Lake Superior and sub-populations may differ in some life-history characteristics, such as growth (Eshmeier and Bailey 1955). As well, if PWF sub-populations are subject to uncorrelated stochastic events but with migration among them, persistence probability would likely increase. Small populations structured as meta-populations, with migration among them, can see drastic increases in persistence probability compared to isolated populations of the same size. van der Lee et al. (2020) found a 4-fold decrease in MVP for Redside Dace (*Clinostomus elongatus*) when complex population structure was included in modelling. As well, Hilderbrand (2003) showed significant effects on persistence probability with only 2 sub-populations exchanging individuals for Cutthroat Trout (*Oncorhynchus clarkii*).

Finally, the frequency of catastrophic events for PWF was unknown and had significant impacts on estimates of MVP. Results are presented for multiple rates of catastrophes, however, which is most appropriate is not clear. Best practices may be to use the most conservative estimate (15%/generation) as this is close to the cross taxa average for vertebrates (Reed et al. 2003) and to buffer against uncertainty.

ELEMENTS

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

The best available data were assembled to provide life-history parameters for PWF. The value for each life-history parameter used in modelling is presented in Table 1, Figures 1:3 and throughout the Methods section.

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

Abundance targets were estimated using population viability analysis and estimates of minimum viable population (MVP). Simulations incorporated density-dependence, environmental stochasticity, and random catastrophes. Targets varied depending on the desired persistence probability and catastrophe rate (Table 4).

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 PWF population dynamics parameters

Lake-wide biomass (kg/ha) has been in decline since 2013 (~ 1 generation) and may be at the lowest mean biomass since 1989 (van der Lee and Koop 2020). Prior to 2013, PWF biomass appeared to follow periodic fluctuations suggesting the population could rebound following successful recruitment. As well there has been a decline in the occurrence of large (> 3 kg/ha) survey catches. Six sampling locations have produced catches > 3 kg/ha in the past; two of which are no longer sampled and the other have experienced similar periodic fluctuations with current low biomass.

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

The quantity of habitat required to support an MPV size population of PWF with a 1% extinction probability and a catastrophe frequency of 15%/generation was estimated to be ~ 21 km². The supply of habitat in Lake Superior far exceeds this. It was estimated that Lake Superior contains 9,774 km² of habitat with a > 50% probability of containing PWF. Locations where populations likely exceed MVP are depicted in Figure 10.

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

Population estimates indicate that current Lake Superior populations likely exceed MVP.

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

The impacts of harm to populations of PWF were evaluated through estimates of the elasticity of λ (Figure 6), the elasticity of N (Figure 7), and simulations (Figure 8). Across each analysis, perturbations to the juvenile stage had the greatest impact to the population.

Estimates of maximum human-induced harm can be estimated from the analysis but depend on the initial condition of the population and what final state of the population is considered allowable. Maximum harm, which is defined here as an additional mortality or proportional reduction in habitat, can be estimated as:

$$\text{Maximum Harm} = \frac{\text{final state} - \text{initial state}}{\text{initial state}} \times \frac{1}{\varepsilon \times \text{frequency}}, \quad (23)$$

Where ε , is the estimate of elasticity for the vital rate being perturbed, frequency is the number of times per year harm is applied (i.e., 0.2 represents a 5 year periodic cycle), and state is the population parameter being measured (λ or N). For example, the elasticity of N_a for adult survival (σ_a) was ~ 1.2 (Beverton-Holt) or 0.64 (Ricker), and if initial adult population size was 5,000 and managers wish to remain above 4,500, then the adult population could sustain an additional annual mortality of 8.3 or 15.6%.

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