Preliminary Results of a Population Viability Analysis Applied to Lake Erie Cisco

1 INTRODUCTION

On October 16th and October 30th of 2024, a panel of experts met to explore the available data for Lake Erie Cisco and review the population viability analysis (PVA) modeling efforts to date. Panelists were asked to work with the modeling team to make decisions on input parameters and modeling strategies. The PVA model was tweaked based on suggestions from the expert panelists and the initial results are presented here.

2 METHODS

2.1 Matrix Projection Model

Custom simulation models were used to assess the recovery potential of Cisco in Lake Erie under various scenarios. All models were based on a stochastic Leslie matrix modeling framework (Leslie 1945; Caswell 2001). The Leslie matrix models were age-structured, female-only, and assumed an annual time step. All model coding was performed in R (v4.4.2; R Core Team 2024).

Population dynamics from year *y* to *y* + 1 are governed by:

$$N_{y+1} = \mathbf{A}N_y$$

where *N* represents a vector of numbers at age at time *y* and **A** is the Leslie matrix that takes the form:

$$\mathbf{A} = \begin{bmatrix} f_1 & f_2 & f_3 & \cdots & f_{t-1} & f_{t+} \\ S_1 & 0 & 0 & \cdots & 0 & 0 \\ 0 & S_2 & 0 & \cdots & 0 & 0 \\ 0 & 0 & S_3 & \cdots & 0 & 0 \\ \vdots & \vdots & \vdots & \ddots & \vdots & \vdots \\ 0 & 0 & 0 & \cdots & S_{t-1} & S_{t+} \end{bmatrix}$$

where f_t and S_t are the fertility and survival for age class *t*, respectively. Here, the maximum age is 15 and is assumed to represent a plus-group, which accumulates all older individuals.

2.2 Survival

The sub-diagonal cells of the Leslie matrix show the probability of an individual surviving from one age class to the next. In the absence of survival estimates for Lake Erie Cisco, we opted to derive estimates from life history relationships. Specifically, we estimated survival at age based on the assumed relationship between natural mortality and weight (Lorenzen 1996). This required parameter values characterizing both the age-length and length-weight relationships in order to derive weight at age (alternatively, an age-weight relationship could be applied). The relationship between age and total length was described by the von Bertalanffy age-length function:

$$L_t = L_\infty\left[1 - e^{-K(t-t_0)}\right]$$

where L_t is total length (mm) at age *t*, L_∞ is the theoretical asymptotic average total length (if $K > 0$), *K* is growth rate at which the asymptote is approached, and t_0 is the hypothetical age at which length is zero. The age-length parameters were used to compute length at each age and each length was then converted to weight using a length-weight relationship. An allometric function was used to relate weight to total length and requires two parameters, a and b:

$$W_t = aL_t^b$$

where W_t is weight (g) at age t, L_t is total length (mm) at age t, and a and b are parameters of the length-weight relationship.

The estimated weights (at age) derived above were used to compute natural mortality based on the Lorenzen (1996) relationship between natural mortality and weight:

$$M_t = 3{W_t}^{-0.288}$$

where M_t is the instantaneous rate of natural mortality at age t and W_t is weight at age t. This gives estimates of age-specific M, which were then converted to survival rates (finite) at age:

$$S_t = e^{-M_t}$$

where S_t is the finite rate of survival at age t and M_t is the instantaneous rate of natural mortality at age t.

Data characterizing the life history of Cisco in Lake Erie are limited and were collected during a period of high commercial fishery exploitation (Clemens 1922) and when lake conditions were likely much different from what they are today. For this reason, we borrowed life history parameters from Cisco occurring in the other Great Lakes for the development of survival estimates (Tables 1 and 2; Figures 1 and 2). During each simulation, the model selects one set of age-length parameters and one set of weight-length parameters to derive survival at age.

In order to add additional realism to the models, the vector of age-specific survival rates were varied within each year of each simulation. This was accomplished by randomly selecting an error (+/- 30%) and adding that value to the entire vector of survival at age for the given year. This process effectively results in the inclusion of both process error (uncertainty in the expected natural mortality) as well as environmental uncertainty (some random noise on an expected value).

2.3 Reproduction

The top row of the Leslie matrix contains age-specific fertility rates (f_t) defined as the average number of offspring produced from an age class. These rates are calculated using data on sex ratios, maturity, fecundity and early juvenile survival:

$$f_t = P_t m_t F_t E$$

where P_t is the proportion of females at age t, m_t is the proportion of mature females at age t, F_t is the fecundity at age t, and E is the early juvenile survival (finite). For the Cisco Leslie matrix model, a 1:1 sex ratio was assumed for all ages. Estimates of female maturity at age were borrowed from the Green Bay model of Cisco published in Rook et al. (2024)—18% at age 2, 99% at age 3, and 100% at age 4–15. Maturity at age 1 was assumed to be 0.

A review of the primary literature yielded four fecundity equations for cisco—two based on relationships with weight and two based on relationships with length. The fecundity-weight relationships were based on data collected from the Wisconsin waters of Lake Superior (Yule et al. 2006a):

$$F_t = -86.5 + 46.5W_t$$

and the Ontario waters of Lake Superior (Yule et al. 2006b):

$$F_t = -440.35 + 44.48W_t$$

where F_t is fecundity (number of eggs) at age t and W_t is weight (g) at age t.

The fecundity-length relationships were derived from data collected from Lake Superior (Yule et al. 2020):

$$\log_{10}(F_t) = 2.919 + 0.037L_t$$

and Michigan-Huron combined (Yule et al. 2020):

$$\log_{10}(F_t) = 2.978 + 0.037L_t$$

where F_t is fecundity (number of eggs) at age t and L_t is total length (cm; note that all other lengths are in mm) at age t. The model randomly selected one of these four parameter sets in each simulation to estimate fecundity. Weight and length at age were computed using the parameters and relationships described in section 2.2.

Early juvenile survival was the product of egg, fry, and age-0 survival and was assumed constant across ages of mature individuals (i.e., age-invariant). In each simulation, the values for egg, fry, and age-0 survival were drawn from beta distributions characterized by a mean and variance. The mean and variance for egg survival were taken from a Cisco egg survival study in Lake Ontario that evaluated egg survival at different depths for both control and experimental (exp.; enhanced substrate) habitat types. In our base model, we calculated the mean and variance of egg survival in the control habitat types based on a suggestion from the lead scientist for that study (B. Weidel, personal communication; Table 3). For fry and age-0 survival, the mean and variance values used in Fielder and McDonnell (2024) were applied.

2.4 Stocking

Stocking was used to initialize the numbers at age for the population projections and occurred in the first 10 years of each simulation. Based on the maximum potential production of the Lamar (S. Davis, personal communication) and Allegheny (B. Layton, personal communication) hatchery facilities, the model assumed stocking of 1,025,000 age-0 Cisco in the fall and 600,000 age-1 Cisco in the spring. To account for variation in the hatchery rearing and stocking process, the number of stocked individuals was varied by +/- 25% in each year of stocking for each simulation.

In their first year in the model, stocked individuals were subject to age-specific survival rates that were one half the rates computed for wild fish. Survival rates were age-specific and varied among years and simulations. Stocked individuals could not produce offspring in their first year in the model, even if considered mature. After the first year, hatchery fish were assumed to behave like wild fish in that the survival and reproductive rates assumed for wild fish were applied to hatchery fish. The offspring of stocked fish are considered wild. The model tracked hatchery and wild fish separately.

2.5 Population Growth Rate

The dominant eigenvalue, λ, of the projection matrix **A** defines the rate of growth of the population. Population growth is stationary when λ is 1 (exactly replaces itself from one time step to the next); the population is decreasing when λ is less than 1 and increasing when λ is greater than 1. We applied an alternative computation for the population growth rate:

$$\lambda_y = N_{wild,y+1}/N_{wild,y}$$

where λ_y represents the population growth rate for wild fish at time y. The post-stocking λ was computed as the geometric mean over post-stocking (*ps*) years and represented by $\lambda_{ps,wild}$. Although calculating λ_y in this manner is somewhat biased as compared to calculating λ_y directly from the Leslie matrix because of the persistence of hatchery fish for some years after stocking ends, it still represents a rate of population change given simulated management (i.e., stocking). Each model was projected forward for 50 years and a total of 10,000 simulations were run for each model scenario. Stocking occurred in the first 10 years of each simulation (see section 2.4). We computed the extinction probability for each model scenario as the number of simulations with less than one fish in the terminal year divided by the total number of simulations (10,000). We also computed summary statistics for the mature portion of the population over all simulations for each year of each model scenario.

2.6 Sensitivity Analyses

2.6.1 Egg Survival

The impact of egg survival on the predicted population growth was evaluated by considering an alternative estimate for the assumed value of egg survival in the calculation of fertility. The base model derived egg survival values from the control habitat in an experiment in Lake Ontario (see section 2.3; Table 3). A sensitivity analysis assumed egg survival values derived from the experimental habitat in that study (Model 2 or base* run; Models 3 through 6 are described in section 3.2.1).

2.6.2 Year-Class Strength

Ciscoes occurring in the Great Lakes are known to exhibit highly variable recruitment (Rudstam et al. 1993; Yule et al. 2006, 2008; Stockwell et al. 2009; Fisch et al. 2019; Fisch and Bence 2020; Brown et al. 2024; Fielder and McDonnell 2024). Here, we considered 2-, 4-, and 6-year frequency of large, or ‘boom’, recruitment years for both the control and experimental egg survival values (Models 7 through 12). The occurrence of a boom year was determined randomly and the probability of any year being defined as a boom year is the mean number of years between recruitment events. In boom years, the survival of the fry stage was increased by 600% (Fielder and McDonnell 2024).

2.6.3 Commercial Fishing

For those scenarios that produced a population with a lambda greater than or equal to 1.0, we explored the addition of fishing mortality, F. Specifically, we investigated the degree of fishing mortality the population could sustain before the calculated lambda, $\lambda_{ps,wild}$, dropped below 1.0. Assuming selectivity by the fishery was knife-edge with full selectivity at ages 3 and older, fishing mortality was added to the scenarios of interest starting with $F = 0.05$ and increasing by increments of 0.05 until $\lambda_{ps,wild}$ fell below 1.0 (Models 13 through 22).

3 RESULTS

A summary of all model scenarios with the computed lambda values and probabilities of extinction can be found in Table 4.

3.1 Base Run

The base run of the model resulted in a declining population. The median $\lambda_{ps,wild}$ was 0.695 and none of the simulations produced a $\lambda_{ps,wild}$ value greater than or equal to 1.0 (Table 4; Figure 3). The number of mature females in the population was less 3,000 fish throughout the projection time period (Figure 4). The number of mature hatchery fish peaked in year 10, the final year of stocking, and quickly declined to 0. Year 38 was the last year any fish were predicted to be present.

3.2 Sensitivity Analyses

3.2.1 Egg Survival

Increasing the assumed value for egg survival to the value derived from the experimental habitat in the Weidel study (see section 2.3) produced a $\lambda_{ps,wild}$ value larger than that was produced in the base run (Table 4; Figure 5); however, $\lambda_{ps,wild}$ was still below 1.0, suggesting a declining population. In light of this, we ran a series of model scenarios to determine the egg survival needed to result in $\lambda_{ps,wild}$ greater than or equal to 1.0. Starting with an assumed mean value of 0.10 for egg survival (using a beta distribution), we incremented egg survival by 0.01 until $\lambda_{ps,wild}$ equaled or exceeded 1.0. The variance for the assumed egg survival value was computed assuming a coefficient of variation of 0.20.

The exploration of egg survival values found that egg survival needed to be at least 0.13 to produce a $\lambda_{ps,wild}$ of 1.0 (Table 4; Figure 5). While assuming egg survival greater than used in the base run but less than 0.13 results in populations of wild fish that are larger than in the base run, the population began to decline after stocking ends in year 10 (Figure 6).

3.2.2 Year-Class Strength

The ability of intermittent boom recruitment years to produce a persisting population depended on the assumed value for egg survival. The presence of boom recruitment years with the baseline value of egg survival was not sufficient to generate an increasing or even persisting population (Table 4; Figure 7); however, when egg survival was increased to the value derived from the experimental habitat in the Weidel study and boom recruitment years occurred, on average, every 2 or 4 years, the resulting $\lambda_{ps,wild}$ exceeded 1.0 (Table 4; Figure 8).

3.2.3 Commercial Fishing

Three model scenarios resulted in $\lambda_{ps,wild}$ values greater than or equal to 1.0—models 6, 10, and 11 (Table 4). Fishing mortality was added to these model scenarios to determine how much fishing pressure the population could sustain without declining. In Model 6 (egg survival = 0.13), the population was not able to persist with the addition of a small amount (F = 0.05) of fishing mortality (Table 4). In the case of Model 10 (boom recruitment every 2 years and egg survival = 0.0865), the population was able to persist through moderate levels of F (Table 4; Figure 9). For Model 11 (boom recruitment every 4 years and egg survival = 0.0865), the population persisted until F reach a value of 0.10 (Table 4; Figure 10).

4 SUMMARY

The results suggest that, under the baseline assumptions, the population will not persist once stocking ends. Given the results of the sensitivity analyses, this is likely largely due to the low value assumed for egg survival in the base run (~0.3%). The sensitivity analyses indicate that in order for the population to persist or even grow post-stocking is completely dependent on the assumption of egg survival. For example, increasing the egg survival in the base model to 13% and leaving all other assumptions unchanged, produces a population growth rate that exceeds 1.0. The occurrence of intermittent recruitment booms alone did not yield an increasing or persisting population; however, assuming higher egg survival (~9%) in conjunction with boom recruitment that occurs every 2 to 4 years proved positive for population growth.

5 LITERATURE CITED

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6 TABLES

Table 1. Summary of von Bertalanffy age-length parameters that are used in the Leslie matrix model for Lake Erie Cisco where total length is measured in millimeters. $L_t = L_\infty\left[1 - e^{-K(t-t_0)}\right]$

Location	L_∞	K	t_0	**Source**
Lake Superior	404	0.227	-2.45	this study
Lake Huron	381	0.390	-1.49	this study
Lake Huron	451	0.261	-3.26	Yule et al. 2020
St. Mary's River	435	0.245	-1.82	this study

Table 2. Summary of length-weight parameters that are used in the Leslie matrix model for Lake Erie Cisco where weight is measured in grams and total length is measured in millimeters. $W_t = aL_t^b$

Location	a	b
Lake Superior	1.16E-06	3.33
Lake Michigan	1.13E-05	2.93
Lake Huron	1.28E-06	3.35
Lake Ontario	1.24E-06	3.34
St. Mary's River	4.91E-06	3.13

Table 3. Estimates of early juvenile survival considered in the Leslie matrix model scenarios for Lake Erie Cisco. Values were drawn from beta distributions characterized by the mean and variance values given in the table.

Stage	**Mean**	**Variance**
egg (control habitat)	0.00276	5.27E-06
egg (exp. habitat)	0.0865	0.00573
fry	0.0611	0.000149
age 0	0.0556	0.000121

Table 4. Summary of model scenarios and results for the Leslie matrix models applied to Lake Erie Cisco. P[extinction] refers to the probability of extinction over a 50-year time horizon.

Model No.	Scenario	Egg Survival	Boom Frequency	Fishing Mortality	Median Lambda	P[extinction]
1	base	0.00276	none	0.0	0.695	0.952
2	base*	0.0865	none	0.0	0.898	0.158
3	egg*S*=0.10	0.10	none	0.0	0.964	0.120
4	egg*S*=0.11	0.11	none	0.0	0.982	0.070
5	egg*S*=0.12	0.12	none	0.0	0.999	0.040
6	egg*S*=0.13	0.13	none	0.0	1.015	0.020
7	boom2	0.00276	2 years	0.0	0.729	0.711
8	boom4	0.00276	4 years	0.0	0.715	0.830
9	boom6	0.00276	6 years	0.0	0.709	0.873
10	boom2*	0.0865	2 years	0.0	1.167	0.043
11	boom4*	0.0865	4 years	0.0	1.041	0.072
12	boom6*	0.0865	6 years	0.0	0.994	0.090
13	egg*S*=0.13,*F*=0.05	0.13	none	0.05	0.987	0.001
14	boom2*,*F*=0.05	0.0865	2 years	0.05	1.138	0.058
15	boom2*,*F*=0.10	0.0865	2 years	0.10	1.110	0.076
16	boom2*,*F*=0.15	0.0865	2 years	0.15	1.084	0.096
17	boom2*,*F*=0.20	0.0865	2 years	0.20	1.058	0.115
18	boom2*,*F*=0.25	0.0865	2 years	0.25	1.034	0.133
19	boom2*,*F*=0.30	0.0865	2 years	0.30	1.010	0.153
20	boom2*,*F*=0.35	0.0865	2 years	0.35	0.987	0.173
21	boom4*,*F*=0.05	0.0865	4 years	0.05	1.012	0.098
22	boom4*,*F*=0.10	0.0865	4 years	0.10	0.986	0.125

7 FIGURES

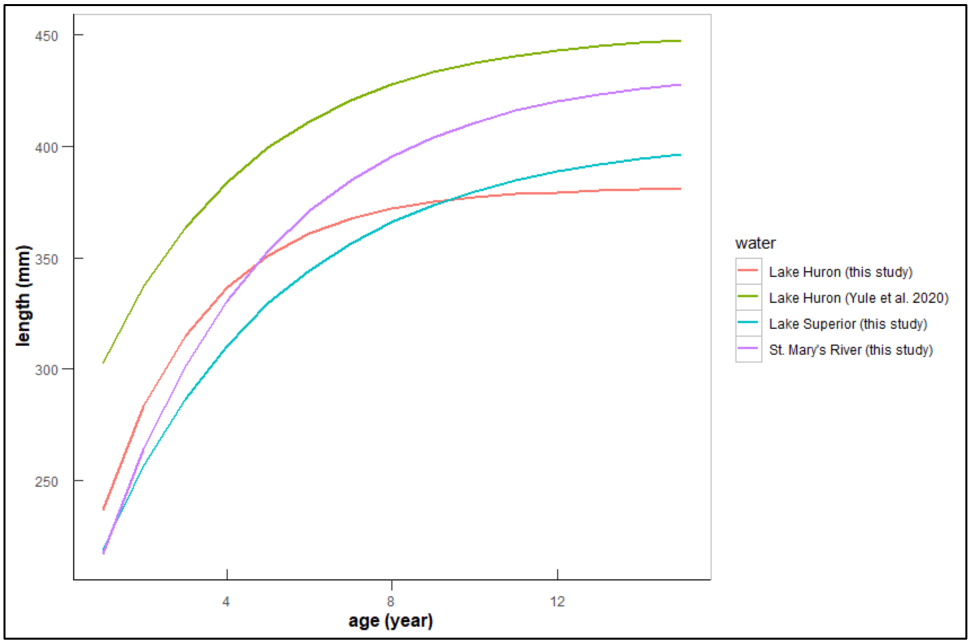

Figure 1. von Bertalanffy age-length relationships considered in the Leslie matrix models for Lake Erie Cisco.

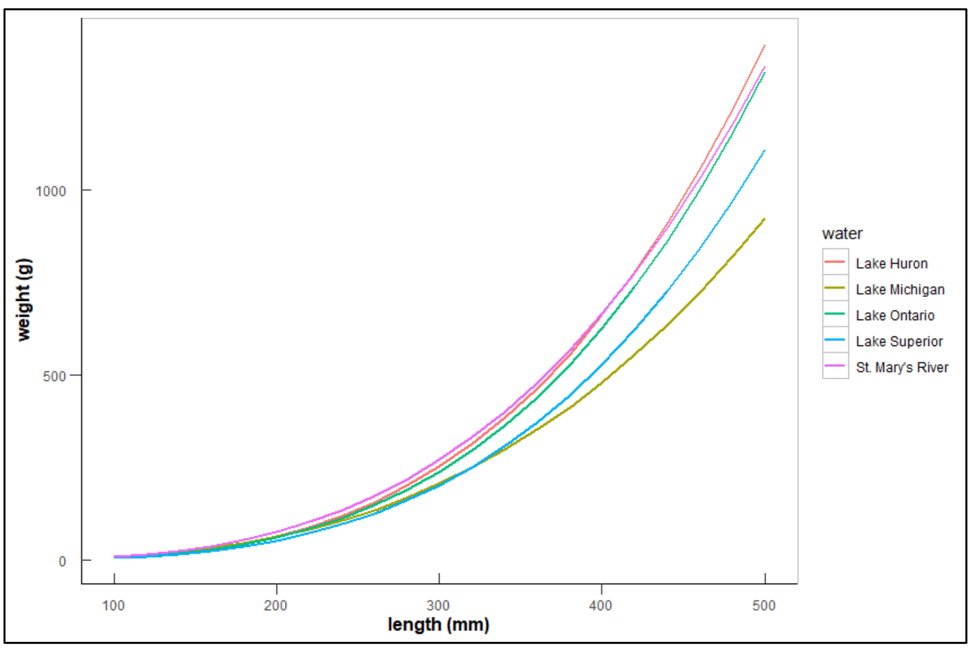

Figure 2. Length-weight relationships considered in the Leslie matrix models for Lake Erie Cisco.

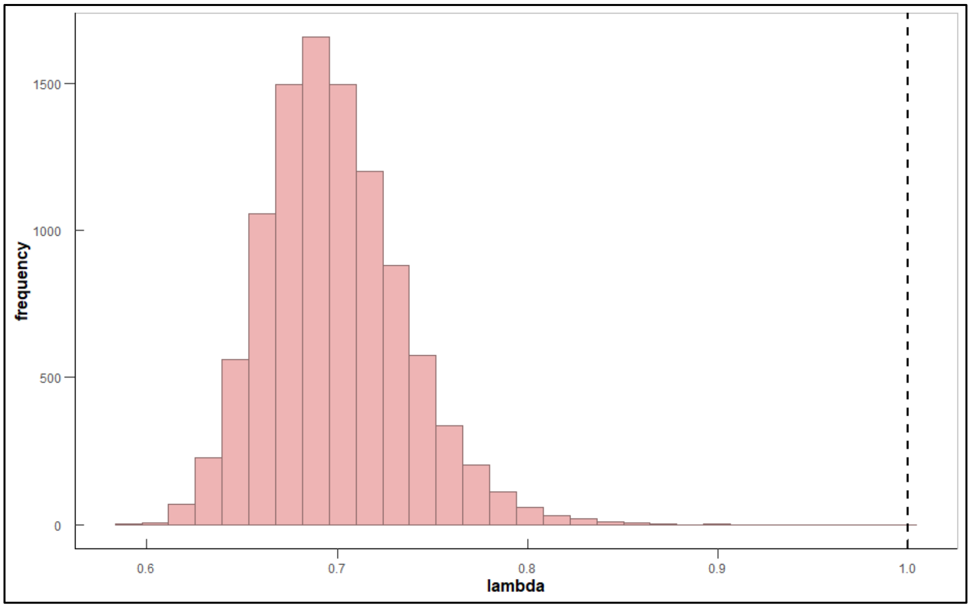

Figure 3. Distribution of post-stocking lambda for wild fish, $\lambda_{ps,wild}$, from the base run of the Leslie matrix model for Lake Erie Cisco. The vertical dashed line represents a lambda equal to 1.0.

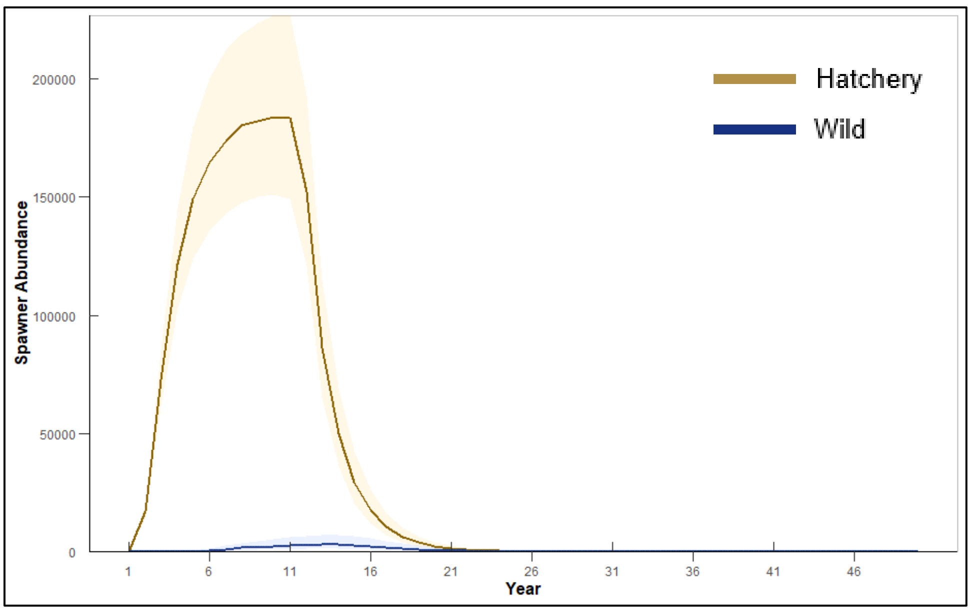

Figure 4. Simulated population trajectories for Lake Erie Cisco from the base run of the Leslie matrix model. The lines represent the median values over all simulations while the shaded areas depict the inner-quartile ranges.

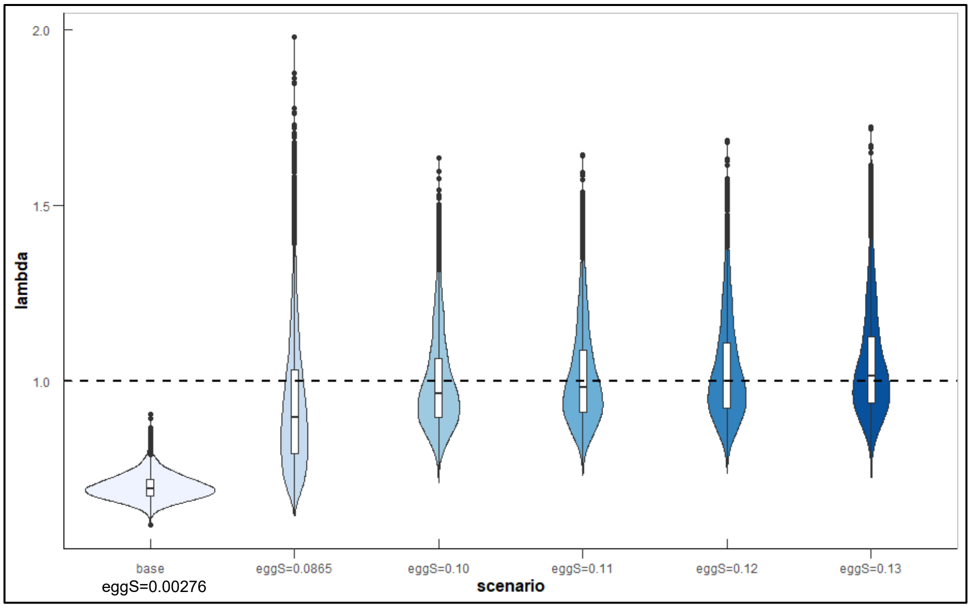

Figure 5. Violin plots depicting the post-stocking lambda for wild fish, $\lambda_{ps,wild}$, from the runs exploring the assumption for early juvenile egg survival. The horizontal dashed line represents a lambda equal to 1.0.

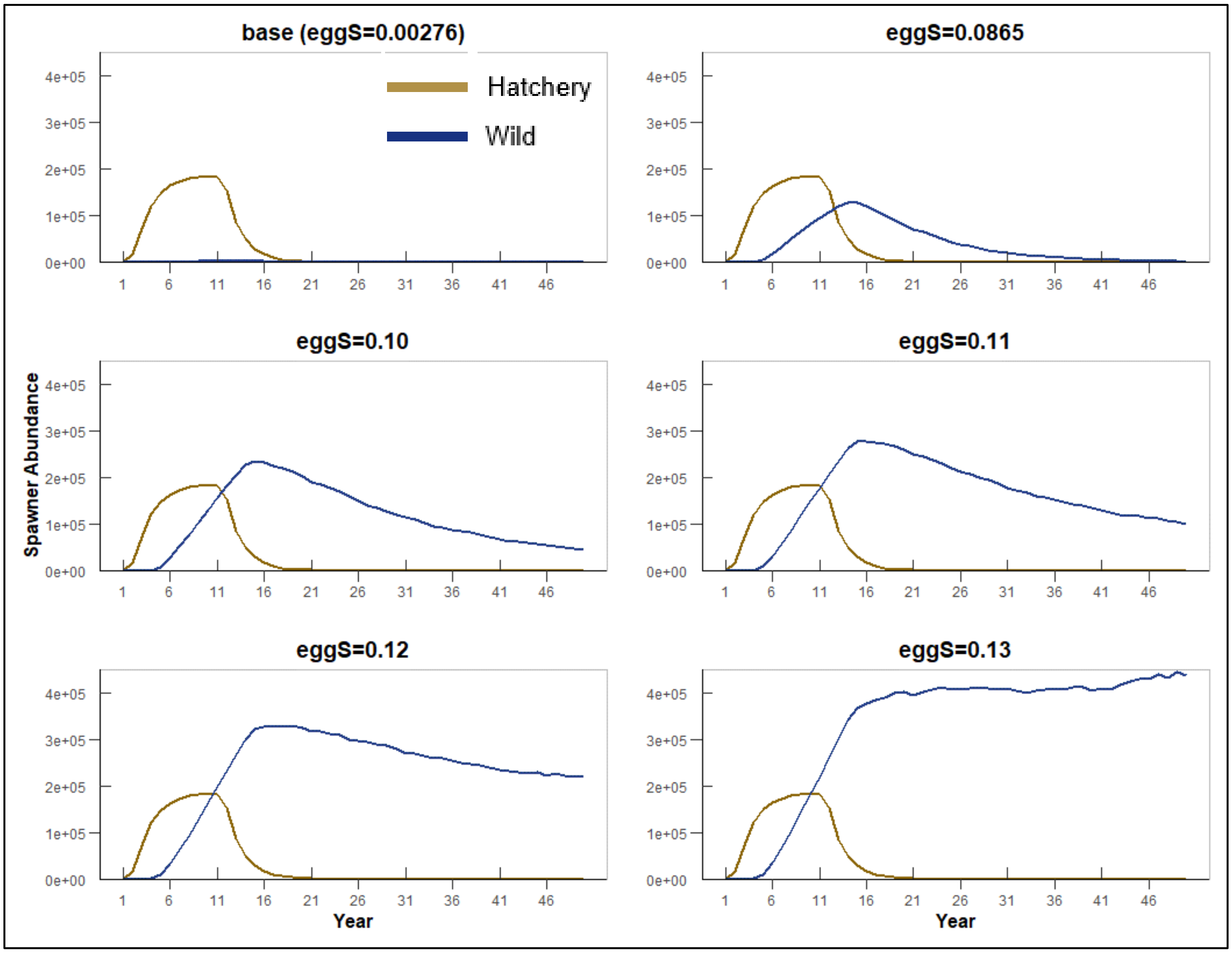

Figure 6. Simulated population trajectories for Lake Erie Cisco from the runs exploring the assumption for early juvenile egg survival. The lines represent the median values over all simulations.

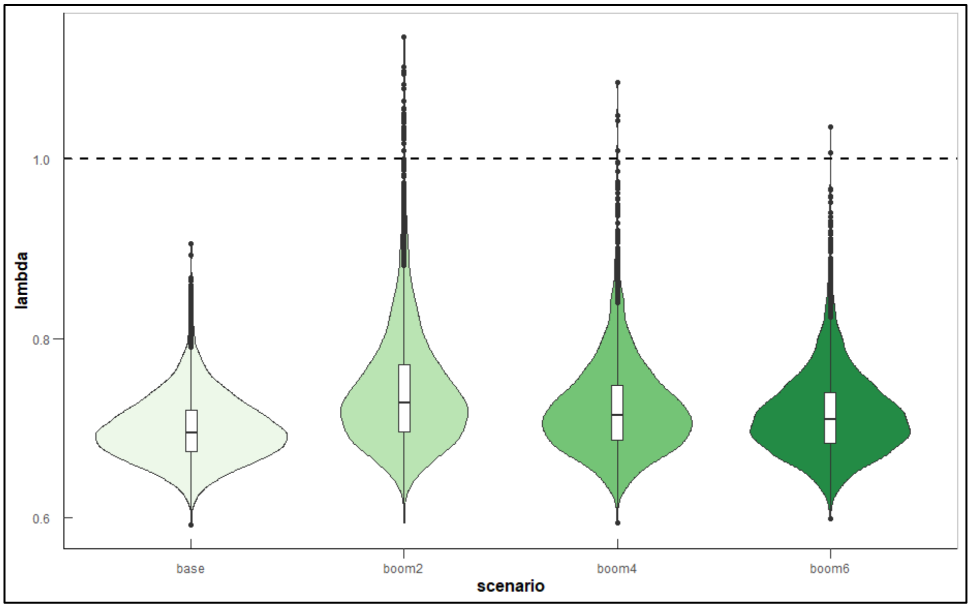

Figure 7. Violin plots depicting the post-stocking lambda for wild fish, $\lambda_{ps,wild}$, from the runs exploring the intermittent recruitment booms assuming egg survival equal to 0.00276 (control habitat from Weidel study). The horizontal dashed line represents a lambda equal to 1.0.

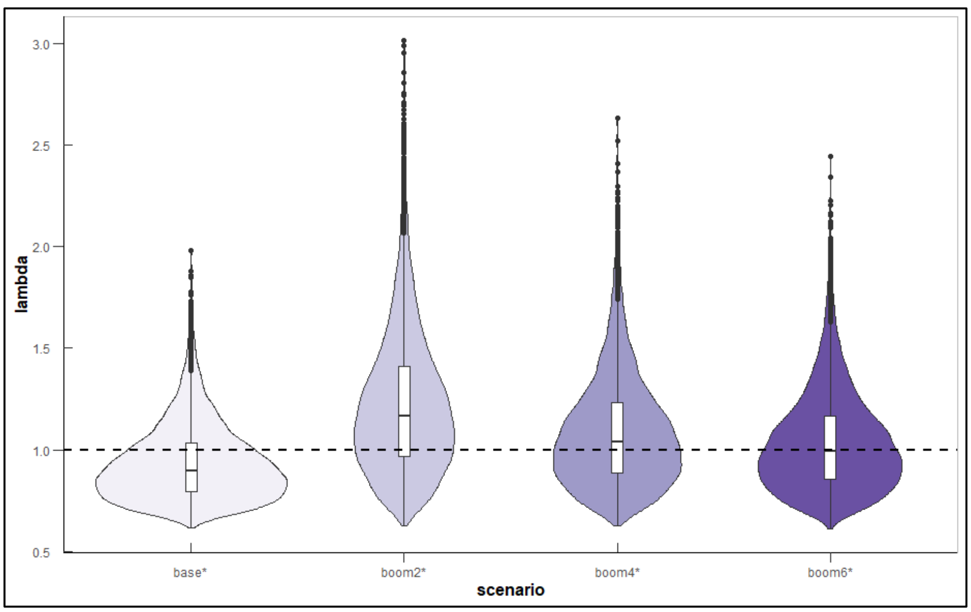

Figure 8. Violin plots depicting the post-stocking lambda for wild fish, $\lambda_{ps,wild}$, from the runs exploring the intermittent recruitment booms assuming egg survival equal to 0.0865 (experimental habitat from Weidel study). The horizontal dashed line represents a lambda equal to 1.0.

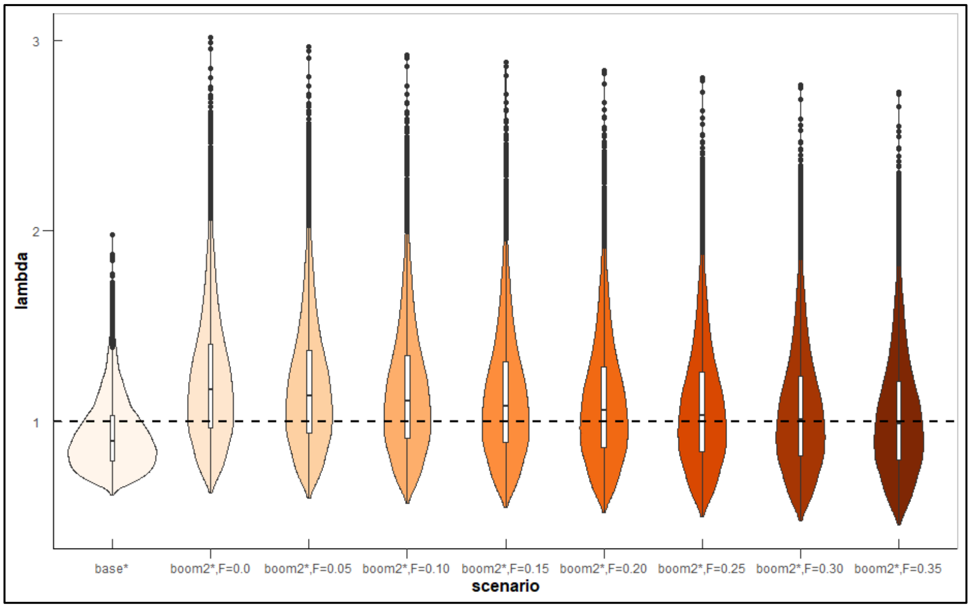

Figure 9. Violin plots depicting the post-stocking lambda for wild fish, $\lambda_{ps,wild}$, from the runs applying fishing mortality to a population that has intermittent recruitment booms every 2 years and assuming egg survival equal to 0.0865 (experimental habitat from Weidel study). The horizontal dashed line represents a lambda equal to 1.0.

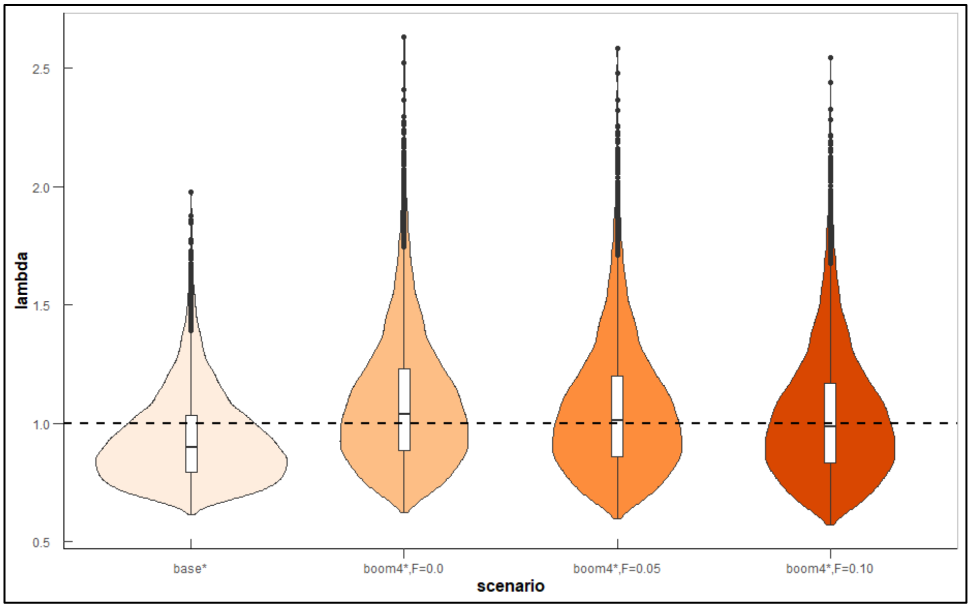

Figure 10. Violin plots depicting the post-stocking lambda for wild fish, $\lambda_{ps,wild}$, from the runs applying fishing mortality to a population that has intermittent recruitment booms every 4 years and assuming egg survival equal to 0.0865 (experimental habitat from Weidel study). The horizontal dashed line represents a lambda equal to 1.0.