Problem Chosen	2024 MCM/ICM Summary Sheet	Team Control Number
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Since the 1830s, the sea lamprey population entered the Great Lakes ecosystem as an invasive species, driven by the construction of canals and shipping lanes. Sea lampreys target the apex predator population in the Great Lakes, such as Lake Trout and Sturgeon. However, most interesting is their dynamic sex ratios. During times of low food density, larval Sea lampreys often can be upwards of 60-70 percent male due to higher nutrient demands of the female population. However, as larval density decreases and nutrient-rich environments increase, larval populations can reach up to 60 percent female. The oscillating and dynamic behavior has greatly affected the Great Lakes ecosystem.

We modeled in Great Lakes ecosystem in 2 parts. First, we create a **3-factor Lotka-Volterra** model to simulate the predator-prey relatonship between producers (e.g., algae and plankton), consumers (e.g., alewife), and apex predators (e.g. lake trout). This model is composed of 3 linear ODEs. We measure the impact of sea lampreys on the ecosystem by looking in a world with and without sea lampreys. Second, we create a model of the Sea lamprey's unique reproductive cycle using a 3 compartmental model. Inspired by pharmacodynamic models, we treat Sea lampreys' reproduction as a **chemical reaction** between two substrates, binding and subsequently forming children. We base our models off **Michaelis–Menten kinetics** using 3 nonlinear ODEs. We justify the fitting of around 25 parameters in our system using past data and Fermi estimations backed by literature. Furthermore, to better understand the long-term behavior of our models, we calculate various equilibrium points and measure the signs of the eigenvalues of its corresponding **Jacobian matrix**.

Ultimately, to test the presence of Sea lampreys in the Great Lakes, we simulate various regimes in the ecosystem, including an explosive **lamprey growth region** and a **lampricide treatment phase**. We show the changes in ecosystem as sea lampreys expand in the ecosystem and as they fall due to human intervention efforts. From our model, we ultimately conclude that the unique ability Sea lamprey's possess to alter its sex ratio serves to maximize **its equilibria population**. In turn, it actually negatively affects lamprey survival in the face of negative stimuli, both in the Great Lakes environment and in an adjusted habitat. However, the biggest impact of the adaptive sex ratio is the **stabilization of ecosystem populations, especially during introduction**. We find a **6% reduction** in the oscillation of apex predators during the lamprey introduction phase, and a **50 % reduction in oscillation** during apex predator recovery during lampricide treatment.

Finally, we simulate alternative lampricide treatments to identify the optimal treatment plan. We find that a biyearly treatment over six years serves to exterminate **90%** of the population in seven years. We also find that specifically killing female lampreys at a rate five times slower than lampricide was able to eliminate the entire lamprey community in 30 years.

Keywords: ODEs, Lotka-Volterra Model, Michaelis-Menten Kinetics, Jacobian Linearization

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1 Introduction

Sea lampreys are an invasive species of parasitic fish that have had significant impacts on the Great Lakes ecosystem. Native to the Atlantic Ocean, Sea lampreys were introduced to their new habitat via the construction of shipping canals in the early 20th century, where they found environments suitable for reproduction and survival. Identifiable by their distinctive appearances with oral disc of sharp teeth, they are known for feeding on the blood and bodily fluids of their hosts [8].


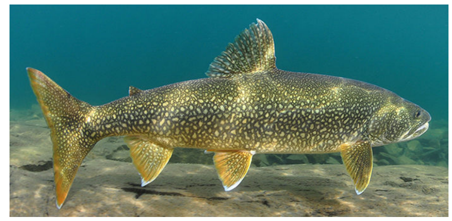

Figure 1: Sea lamprey and Lake trout

Sea lampreys primarily target apex predators such as the Lake Trout or Sturgeon. Due to their invasive nature, the apex predators of the Great Lakes have yet to evolve defensive mechanisms. Thus, instead of the parasitic niche they fill in their native environments, lamprey attacks are often lethal, with a mortality rates of 40 to 60 percent. These apex predator populations are critical not only for the fishery economy of the Great Lakes region, but also for the regulation of other fish species in the ecosystem. For example, the alewife, an invasive herring species, has had its population explode after the gutting of Lake Trout populations by sea lampreys. To alleviate this issue, the government has spent millions to disrupt the expansion of the Sea lamprey population through lambricides targeting the larval population [8] [4].

Within this context, the dynamic characteristics of the sex ratios within the sea lamprey population can provide a solution. A landmark 2017 study discovered that high-density and low-food environments resulted in highly biased male-denominated species, while more favorable conditions produced more efficient gender distributions. For example, prior to human intervention, scientists estimated the Sea lamprey distribution to be approximately 65 percent male in upper Great Lakes. However, after human intervention, adult sea lamprey populations became only 40 percent male, due to far less density. This suggests a self-regulating behavior, as more larva results in male-biased future generations which reduce the number of potential mates. Conversely, more sparse environments create favorable conditions for female larval sea lampreys, thus improving population growth in the future. Within the context of its interactions with others, this self regulation could majorly impact sea lamprey population dynamics and thus the apex predator population [7][12].

2 Model Overview

Our dynamic model is composed of 6 differential equations. We employ a compartmental model based on substrate-receptor mechanics to model the changing sex ratios of the sea lampreys. We base our model on enzyme kinetics, treating the population of sea lampreys are something similar to biochemical reactions involving substrates and enzymes. To model its interactions with other organisms in the Great

Lakes Ecosystem, we then embed our model of sea lamprey sex ratios to a greater ecological model. This ecological model will be based upon a 3-factor Lotka-Volterra model [2].

2.1 Model Assumptions

Both the sea lamprey life cycle and the Great Lakes ecosystem are incredibly complex systems. We show the relationship between various species in this simple diagram. Producers represent species like algae plankton, which provide an essential food source for secondary feeders. Consumers are fish species like the rainbow smelt and alewife which feed on producers. Apex predators include the species which feed on consumers and themselves are eaten by the adult sea lampreys. These include the rainbow trout, sturgeon, and lake trout [6] [10].

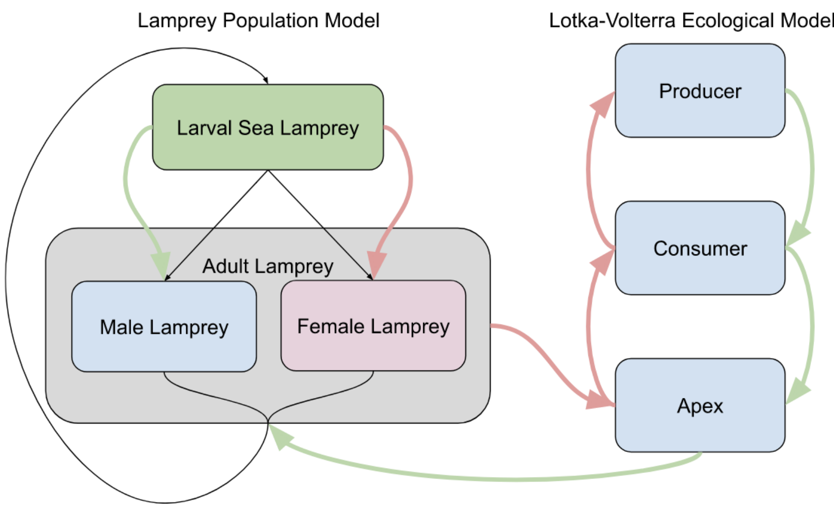

Figure 2: Simplistic Model Diagram

Thus, we make some simplifying assumptions with justification.

2.1.1 Sea Lamprey Reproduction

S-1. We assume that Sea lamprey population can be divided into the following three categories: **larvae**, **male juvenile**, and **female juvenile**. We can justify the creation of a larval category because Sea lampreys spent the majority of their life cycle in the larval state. Also, there is evidence of delayed sexual differentiation in larvae, but sexes are generally fixed upon reaching the juvenile state [3].

S-2. We assume that **the major driver in food availability for lamprey larvae is the density of larvae in a given region**. Multiple studies have shown that when sea lamprey populations are abundant, the male to female ratio rise, while depleted populations cause the ratio to fall [7]. This can be explained by the fact that plankton, their primary food source, is extremely abundant and thus should hold fairly constant populations across the Great Lake ecosystem. Thus, more larvae means more competition for an unchanging food source. Since the availability of food and subsequently growth rate potentials are lower, this drives more males [7].

S-3. We assume that the primary driver of death in Sea lamprey juveniles is **food scarcity**. Furthermore, we assume that **males and females are impacted equally by food scarcity.** This is justified by the fact that they do not have natural predators in the Great Lakes. However, we do not account for factors such as disease.

S-4. Sea lampreys migrate up tributaries to reproduce. Females and males then pair up, with the male building a nest in the river bed [3]. We assume that **one male and one female form a male-female pair upon bumping into each other randomly in the tributary**. If the pair successfully complete the mating ritual, both parents die and create offspring. Although there is some polygyny displayed among sea lamprey populations, the mating process is generally monogamous [3].

S-5. Upon the female laying eggs in the nest, the male fertilizes the eggs, and both lampreys die.

S-6. The number of male and female lamprey pairs are in a **quasi-steady state equilibrium**. This is justified by the fact that the duration of a mating ritual is short relative to the lifespan of lampreys and the timescale at which their populations change.

S-7. Male and female lamprey exist in two states, either unpaired and searching for a mate, or in a current mating dance.

S-8. Given the numerous possible causes of death for lamprey, we aim to simplify our model by assuming a **first-order death function**, much like how drugs in the human body are processed.

S-9. Lampricide only affects the population of Sea lampreys. Although the main chemical of lampricide is deemed slightly to highly toxic to other fish, it does not accumulate in their systems and most communities show swift recovery [1].

2.1.2 Great Lakes Ecosystem

G-1. We assume that the Great Lakes Ecosystem has a constant rate of human impact. Thus, the fishing rate will be a constant factor. Likewise, other human effects like pollution will be captured in the parameter fitting of the model [6].

G-2. We assume that organisms of the Great Lakes can be classified into three trophic levels: producers, consumers, and apex predators. Producers would include autotrophic plankton and algae, Consumers would include small fish such as the Alewife, and Apex predators would include large fish with no natural predators such as the Lake Trout.

G-3. We assume that the Great Lakes food web is predominantly a chain with the following structure:

For model simplicity, we do not include the presence of decomposers or interactions between apex predators. Nevertheless, many Great Lakes ecosystems primarily exhibit this one-directional flow [site diagram]

G-4. We assume that apex predator growth is proportional to the consumer population, the consumer growth is proportional to the producer population, and that producers grow in a logistic fashion.

G-5. Along with G-4, we assume all of the predator-prey assumptions in the Lotka–Volterra predator-prey model.

3 Ecological Model

The focus of our analysis is on the impact of sea lamprey's on the Great lakes ecosystem. Thus, we first built an ecological model of the Great Lakes, stable without the presence of sea lamprey's. Afterwards, we measure the impact of the sea lampreys on the producer, consumer, and apex population. Through our initial estimates, we are able to look at an ecosystem with and without sea lampreys.

3.1 Parameters

Symbol	Description	Units
P	Producer Population	Tonnes
C	Consumer Population	100s
A	Apex Predator Population	100s
g_1	Primary Growth Rate	Annual Rate %
ψ	Rate of Competition	Annual Rate %
ϕ_p	Primary Rate of Consumption	Annual Rate %
d_s	Secondary Death Rate	Annual Rate %
c_p	Primary Contribution	Annual Rate %
ϕ_s	Secondary Rate of Consumption	Annual Rate %
d_p	Predator Death Rate	Annual Rate %
c_s	Secondary Contribution	Annual Rate %
h_f	Human Fishing Factor	Annual Rate %

Table 1: Symbols, Descriptions, and Units for the Ecological Model

3.2 Model Development

Due to the predator-prey interactions of the ecosystem, we implement a modified **Lotka-Volterra Predator-Prey Model**. With the food chain structure from G-3, we take inspiration from Hsu et al. and modify the equations to fit three categories of organisms. Below are the three differential equations of the Ecological Models.

$$\frac{dP}{dt} = [P](g_1 - \psi[P] - \phi_p[C]) \tag{1}$$
$$\frac{dC}{dt} = [C](-d_s + c_p[P] - \phi_s[A]) \tag{2}$$
$$\frac{dA}{dt} = [A](-d_p + c_s[C] - h_f) \tag{3}$$

We will start with the first equation:

$$\frac{dP}{dt} = [P](g_1 - \psi[P] - \phi_p[C])$$

This represents the growth of the producer population for species like plankton and algae. The first term (g_1) represents the natural growth of those species. In our example, we use a constant growth rate to model the producer population. The middle term (ψ) introduces the **carrying capacity** of the producer population. This ensures that there is slower growth as the producer population increases. Finally, the last term ϕ_p reveals interaction effects with the consumer population which feed on algae and plankton. Naturally, as there are more consumers, they feed on more of the producer population and thus reduce its size over time. Similarly,

$$\frac{dC}{dt} = [C](-d_s + c_p[P] - \psi_s[A])$$

The above equation reflects the consumer population, whose outcome is determined by their death rate, availability of food from the producer population, and the consumption from predators. We chose a constant death rate (d_s) to be measured by the lifespan of an average small fish. We look at c_p to estimate the capacity of the consumer population as a function of the availability of food. As there are more producers, there is greater availability for the consumer population. As they stand in the middle of the food chain, their numbers are affected by the apex population with the ϕ_p term.

$$\frac{dA}{dt} = [A](-d_p + c_s[C] - h_f)$$

Finally, our apex predator population has similar characteristics with the consumer population. Its growth is dependent on the death rate, availability of food like the consumer population. We introduce a fishing effect to factor in the constant consumption from humans in the Great Lakes. Overall, while our model is simple for simulating the interactions in our ecosystem, it is tried-and-tested in the predator-prey modeling literature, which provides a strong baseline for receiving simple results.

3.3 Parameter Search

Parameters are estimated through literature, available data, and related approximations. d_s and d_p model the death rate, and thus we estimate these values by using the life spans of the lake trout and alewife, and assuming that 95% die by their natural life expectancy [6]. Likewise, we obtain g_1 by approximating the time for autotrophs like plankton and algae to double in mass given unlimited resources. ψ is estimated by approximating that the carrying capacity of autotrophs should not exceed double our initial values. by We obtain h_f by literature estimates of the percent of Great lake biomass impacted by fisheries [11]. Finally, we approximate the remaining parameters ϕ_p, c_p, ϕ_s, and c_s by growth predictions and parameters of previous literature [2] [6] [11] [5].

We estimate the population of apex predators A by literature on fish biomass density in the Great Lakes. This approximation is further supported by data on lake trout in Lake Superior, which we can then extrapolate into apex predator data in the whole Great Lakes system [6]. C and P are estimated through an approximation of biomass transfer through trophic levels.

Parameter	**Value**	**Justification**
g_1	36	Chosen to make it so that the group of plankton double each week
ψ	$5 \cdot 10^{-6}$	Chosen from estimating carrying capacity of plankton
ϕ_p	$7.1 \cdot 10^{-10}$	Estimated from biomass models [2]
d_s	0.57	The lifespan of medium fish is 4 years, so 5 percent remain [6]
c_p	$5.3 \cdot 10^{-7}$	Based on estimates on how medium fish double on average [6]
ϕ_s	$1.0 \cdot 10^{-6}$	Historical estimates based on how fast they are consumed by secondary predators [11]
d_p	0.101	Estimates for how long big fish live [2]
c_s	$1.5 \cdot 10^{-10}$	Secondary Contribution estimates based on fish doubling in the future [5]
h_f	0.045	Estimates based on historical data [11]

Table 2: Parameter Selection Justification

3.4 Results

This baseline Ecological Model exhibits the expected oscillations that a Lotka-Volterra model generates. The producer levels stay fairly consistent. The consumer population oscillates against the apex population, where larger levels of apex predators reduce the consumer population, resulting in future food pressures in the apex predator population. The oscillations themselves show some form of stability with population cycles forming with a period of 8-9 years. Note that each of the populations are on different magnitudes, revealing the immense population differences between the consumers and apex predator population in the Great Lakes.

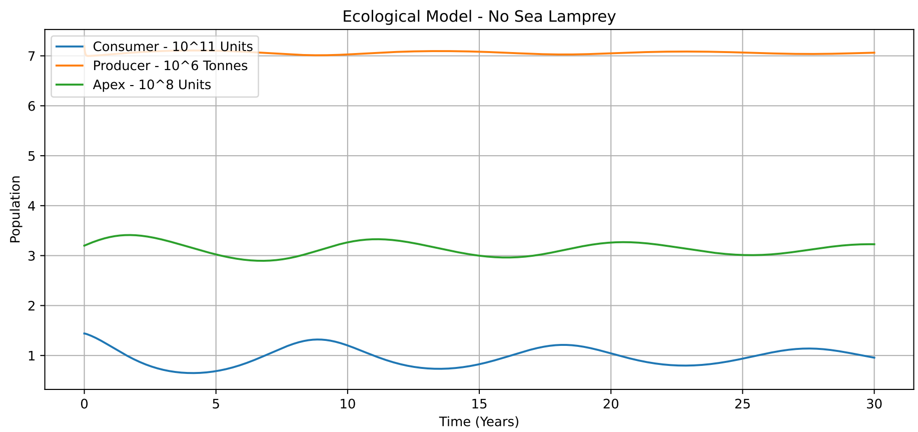

Figure 3: Ecological Model

3.5 Equilibrium Analysis

Figure 4 shows the existing phase diagram shift between the consumer population and the predator population across time. In the phase diagram, each point represents a specific combination of predator and prey population. As time progresses, the variations between the consumer and predator population reduces, revealing evidence of an reaching an eventual equilibrium point.

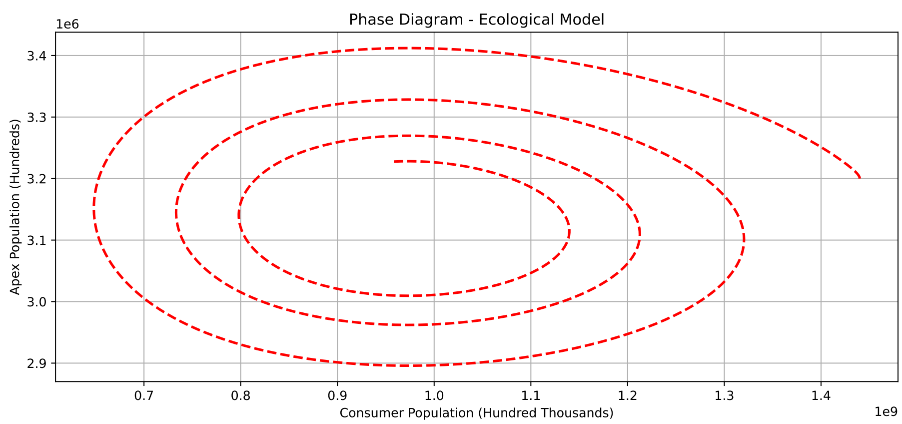

Figure 4: Ecological Model Phase Diagram

The spiral effect implies reaching convergence in the predator-prey population. To find examine the long-term stability of the modified **Lotka-Volterra Predator Prey Model**, we find various equilibrium points in the system of ODEs by finding the nullclines. Afterwards, we can measure the Jacobian matrix of the ODEs at the specified equilibrium point and calculate its eigenvalues to understand if the system reaches a stable point. According to the Hartman-Grobman theorem, if the real parts of the eigenvalues are all negative, then the system is considered to be robust and proof of eventual convergence. Using numerical solvers, we find one of the initial equilibrium points to be

$$y_{init} = \left[7.06 \cdot 10^{13}, \quad 4.67 \cdot 10^{8}, \quad 3.13 \cdot 10^{8}\right]$$

Afterwards, we numerically calculate the Jacobian matrix at this equilibrium point and find that all eigenvalues are negative, showing robustness of our system.

4 Lamprey Population Model

Our lamprey population model is a 3 compartment model that follows similar approaches to how pharmacokinetic/pharmacodynamic models would be developed. The model treats lamprey populations moving through life cycles as drugs moving through various compartments in the human body. Dynamic interactions between the ecosystem and the Lamprey are considered as relationships between how the human body reacts to drugs, frequently employing the use of Hill curves to mimic the asymptotic nature of different parameters. Reproduction of Lamprey is considered a chemical reaction between two substrates, binding and subsequently forming children.

4.1 Parameters

Symbol	Description	Units
Y	Young Larva Population	1,000s
M	Male Lamprey Population	1,000s
F	Female Lamprey Population	1,000s
k_2	Mating Rate	1/s
c	Offspring Per Mate	Unitless
K_M	Pseudo-Michaelis Constant (See 5.2.1)	1,000s
k_{yd}	Young Death Rate	1/s
k_l	Lampricide Effectiveness Rate	1,000 fish/s
l	Lampricde in Great Lakes Systems	lbs
EC_{l50}	Lampricide Needed for 50% Lampricide Effectiveness	lbs
c_m	Maturation Rate	1/s
Y_{50}	Amount of Young Needed for Even Sex Ratio	1000s
k_{ad}	Adult Death Rate	1/s
k_s	Starving Death Rate	1000 fish/s
EC_{50f}	Amount of Food Needed to Halve Starving Death Rate	10s Fish/Lamprey
a	Female Food Multiplier	Unitless
λ	Food Scarcity Constant Multiplier	Unitless

Table 3: Symbols, Descriptions, and Units for the Lamprey Population Model

4.2 Model Development

4.2.1 Reproduction of Young

Our lamprey reproduction function is based heavily on enzyme kinetic models, using the assumption that we can treat the mating ritual as a formation of a novel chemical compound, which then, if successful, results in the creation of young lamprey as the product. Our proposed reaction mechanism is provided below:

$$M_u \quad + \quad F_u \quad \underset{k_{-1}}{\overset{k_1}{\rightleftharpoons}} \quad MF \quad \xrightarrow{k_2} \quad cY$$

Where M_u and F_u represent unpaired male and female lamprey, MF represents Lamprey performing a mating ritual, Y represents new young, and c represents how many children each mating pair produces. Lamprey performing a mating ritual (MF) can either fail to mate successfully, returning to unpaired M and F, or mate successfully and produce offspring. Because successful mating results in parent Lamprey dying, as per assumption S-5 the production of Y from MF is irreversible, and results in the destruction of both parents. This reaction scheme forms the basis of the reproduction function of our Lamprey. As such, the rate of growth of the young population of lamprey, or our reproduction term, can be modeled by the rate of production of Y.

To find the rate of production of Y, or $\frac{dY}{dt}$ based on the total male and female population (M and F), we employ a similar strategy to the derivation of the Michaelis-Menten equations. We start by determining the rate of production and consumption of MF, which according to the reaction diagram, can be described by the following equations:

$$\text{Production of MF: } k_1 \cdot M_u \cdot F_u$$

$$\text{Breakdown of MF: } k_{-1} \cdot MF + k_2 \cdot MF$$

Using the quasi-steady state assumption from S-6, we know that the production of MF must be equal to the breakdown of MF, yielding

$$\frac{dMF}{dt} = k_1 \cdot M_u \cdot F_u - k_{-1} \cdot MF + k_2 \cdot MF = 0$$

Rearranging and grouping like terms yields

$$k_1 \cdot M_u \cdot F_u = (k_{-1} + k_2) \cdot MF$$

From here, Michaelis-Menten proofs commonly make the substitution of $K_M = \frac{k_{-1}+k_2}{k_1}$. In most contexts, K_M is frequently understood to represent the concentration of substrate needed to achieve 50% of maximum reaction rate. In our context, K_M can be understood as roughly the amount of male and female lamprey needed for 50% of lampreys to find a mating partner.

$$M_u \cdot F_u = K_m \cdot MF$$

Since our model takes in inputs of total male lamprey and total female lamprey, rather than unpaired male and female lamprey, we seek to replace M_u and F_u with M and F, where M and F represent total male and female lamprey respectively. Given assumption S-7, we can express M as $M_u + MF$ and F as $F_u + MF$. Using this relationship to eliminate M and F yields

$$(M - MF) \cdot (F - MF) = K_m \cdot MF$$

Expanding and combining like terms yields

$$MF^2 - (M + F + K_M) \cdot MF + M \cdot F = 0$$

Solving for the number of lampreys in a mating dance (MF) yields

$$MF = \frac{(M + F + K_M) \pm \sqrt{(M + F + K_M)^2 - 4 \cdot M \cdot F}}{2}$$

To determine whether we take the positive or negative discriminant, we consider the case where we have no males or no females in our population. By symmetry, we'll use the case where $M = 0$, which yields

$$MF = (F + K_M) \pm \sqrt{(F + K_M)^2} = (F + K_M) \pm (F + K_M)$$

From here, it is obvious we should take the negative discriminant since we expect there to be no mating pairs if we have no male lampreys! Finally, with the number of mating pairs, we can determine the growth rate of young (and also the death rate of males and females due to reproduction). From the reaction mechanism drawn, the production of young and death of males/females is simply

$$\frac{dY}{dt} = c \cdot k_2 \cdot MF = c \cdot k_2 \cdot \frac{(M + F + K_M) - \sqrt{(M + F + K_M)^2 - 4 \cdot M \cdot F}}{2}$$

$$\frac{dM}{dt} = -k_2 \cdot MF = -k_2 \cdot \frac{(M + F + K_M) - \sqrt{(M + F + K_M)^2 - 4 \cdot M \cdot F}}{2}$$

$$\frac{dF}{dt} = -k_2 \cdot MF = -k_2 \cdot \frac{(M + F + K_M) - \sqrt{(M + F + K_M)^2 - 4 \cdot M \cdot F}}{2}$$

A plot of the reproduction function is provided below:

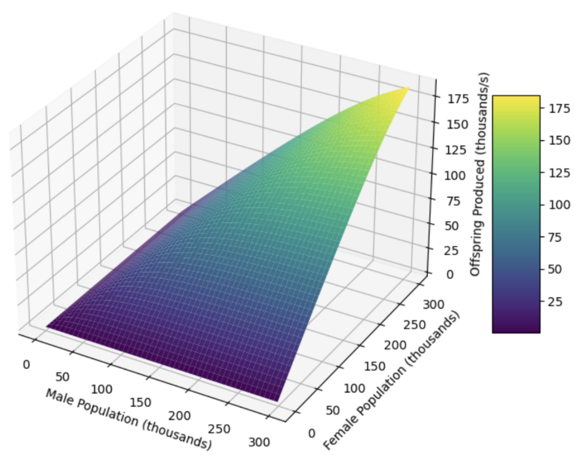

Figure 5: Michaelis-Menten Birth Rate Function

As shown in the above, the birth rate of larval lamprey increase most significantly when both the male and female populations, and remains at 0 if either the male or female population remains at 0. This is the main strength of using our kinetic approach. We observe that at a constant female population, we approach an asymptotic limit for how many offspring can be produced. This corresponds to the female population approaching full saturation - that is, all females are already in a mating pair, and thus adding more males does not further increase the rate of offspring being produced. This is contrary to a simple linear relationship, which would imply infinite offspring production if we had infinite male population, even if we only had a finite female population

4.2.2 Death of Young

Lamprey are r-selected species [7], implying both large reproductive capabilities but also high mortality rates for children. As such, our model must account for the death of larva. Our function modeling the death of young takes into account two factors, natural death function as per assumption S-8, which can be further augmented by lampricide use, which particularly targets larva.

Since lampricides are essentially poisons, we model the effectiveness of lampricides as hill functions to accurately capture both the concept that there must be a minimum dosage before the poison can take effect and the concept that there is an asymptotic maximum effectiveness.

Hill functions commonly take the form of

$$\frac{k \cdot [X]^n}{EC_{50}^n + [X]^n}$$

so combining a hill function with the first order death rate of larva yields:

$$\frac{dY}{dt} = -Y \cdot (k_{yd} + \frac{k_l \cdot l^n}{EC_{l50}^n + l^n})$$

where k_{yd} is the natural death rate, k_l is a scaling factor for lampricide effectiveness, l is concentration of lampricide, n is the hill coefficient, and EC_{l50} is the concentration of lampricide needed for 50% maximum effectiveness.

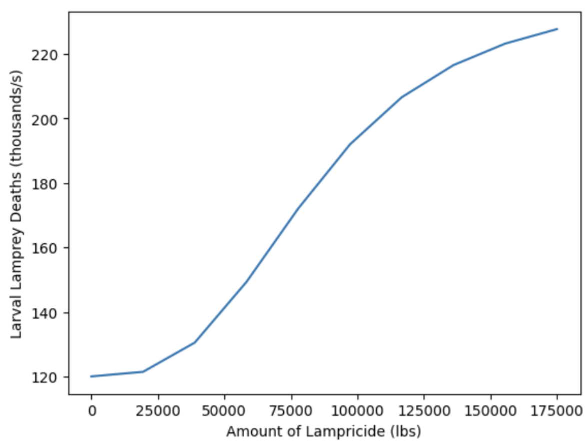

Figure 6: Death rate of Larval Lamprey Based on Amount of Lampricides Used

4.2.3 Maturation of Young

Overall, we expect the maturation rate of larva to be first order relative to the young population. Additionally, according to assumptions S-1 and S-2, the maturation of the larva to the adult phase is where gender differentiation occur. As such, our maturation of young functions will account for the variable sex ratios present in the lamprey population.

Given that lamprey population in resource rich environments do not go below a 40%/60% male to female split, and even in the worst conditions, only approach an 80%/20% male to female split, we found a hill model to be the best away to accommodate this dual-asymptotic behavior [11][7]. The following set of hill equations effectively capture the proportion of males and females depending on the density of young, which according to assumption S-2 is how we model resource levels.

$$\text{Male Fraction} = 0.4 + \frac{0.4 \cdot Y^n}{a^n + Y^n}$$

$$\text{Female Fraction} = 0.6 - \frac{0.4 \cdot Y^n}{a^n + Y^n}$$

Where Y represent the amount of young, a represents the number of young needed for a roughly 50%/50% sex ratio, and n is an arbitrary hill constant. Below is a plot demonstrating how the sex ratio varies relative to quantity of young larval lamprey.

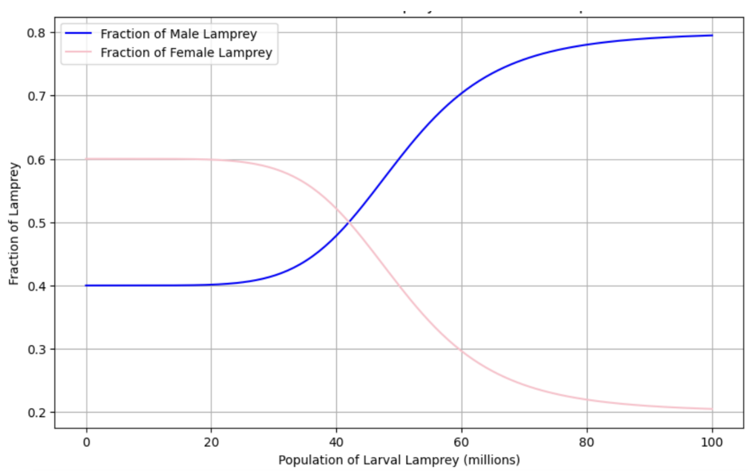

Figure 7: Male and female ratios based off density of larva

As such, the overall male and female maturation rates can be expressed as

$$\frac{dM}{dt} = c_m \cdot Y \cdot (0.4 + \frac{0.4 \cdot Y^n}{a^n + Y^n})$$

$$\frac{dF}{dt} = c_m \cdot Y \cdot (0.6 - \frac{0.4 \cdot Y^n}{a^n + Y^n})$$

and the decline of young due to maturation to be

$$\frac{dY}{dt} = -c_m \cdot Y$$

where c_m represents the rate of maturation, which can be determined based on k_{yd} by comparing the number of lamprey that reach maturation and the number that die before maturing.

4.2.4 Death of Adults

The last function to complete the lamprey population model is a death function of adults, which we complete with a similar approach to the death of young. That is, we incorporate a baseline death rate due to natural causes.

However, because we particularly care about the impact of lamprey on apex populations, we further include a term to quantify death due to starvation. Since we don't excess food availability to allow lamprey to live significantly longer, we expect to see an asymptote in our starvation function where further increasing food does not further reduce the death rate. These restrictions, along with the if we consider food to be a substrate for lamprey feeding, leads us to consider the hill function once again.

Since the most important consideration for starving is the amount of food available per lamprey, we consider the term that varies in our hill function to be food density, which can be expressed as:

$$FD = \frac{A}{(1-a)M + aF}$$

Where A is the number of apex predators, our lamprey's primary food source, $M + F$ represents the total lamprey population, and a is a factor that represents how female lamprey consume more food than males to foster their young [7]. Additionally, since we expect the lack of food to cause the effect on death, we use the repressor form of the hill function, which takes the form of

$$\frac{k \cdot EC_{50}^n}{EC_{50}^n + [X]^n}$$

where $[X]$ is the variable of interest, resulting in a curve where maximum effect occurs at low concentrations of $[X]$, and approaches 0 as $[X]$ approaches infinity. Once again, EC_{50} represents the amount of $[X]$ needed for 50% effectiveness, n is the hill coefficient, and k represents the maximum drug effectiveness.

Combining these elements together yields an effective death function described below, whereby

$$\frac{d(M/F)}{dt} = -(M/F) \cdot \lambda(k_{ad} + \frac{k_{ad} \cdot EC_{50f}^n}{EC_{50f}^n + (FD)^n})$$

where k_{ad} represents the natural death rate, k_s represents the maximum starving effect, and the remaining variables are as specified from the generic hill function.

4.2.5 Overall Lamprey Population Equations

Combining the functions established from the previous sections yields the following set of equations

$$\frac{dY}{dt} = c \cdot \text{reproduction} - \text{young death} - \text{maturation}$$

$$\frac{dM}{dt} = \text{male maturation} - \text{reproduction} - M \cdot \text{adult death}$$

$$\frac{dF}{dt} = \text{female maturation} - \text{reproduction} - F \cdot \text{adult death}$$

where

$$\text{reproduction} = k_2 \cdot \frac{(M_T + F_T + K_M) - \sqrt{(M_T + F_T + K_M)^2 - 4 \cdot M_T \cdot F_T}}{2}$$

$$\text{young death} = Y \cdot (k_{yd} + \frac{k_l \cdot l^n}{EC_{l50}^n + l^n})$$

$$\text{maturation} = \text{male maturation} + \text{female maturation} = c_m \cdot Y$$

$$\text{male maturation} = c_m \cdot Y \cdot (0.4 + \frac{0.4 \cdot Y^n}{a^n + Y^n})$$

$$\text{female maturation} = c_m \cdot Y \cdot (0.6 - \frac{0.4 \cdot Y^n}{a^n + Y^n})$$

$$\text{adult death} = \lambda(k_{ad} + \frac{k_s \cdot EC_{50f}^n}{EC_{50f}^n + (\frac{A}{(1-a)M+aF})^n})$$

4.3 Parameter Search

Because kinetic data on the maturation rates or pseudo-Michaelis constants don't exist, many parameters are chosen to most reasonably capture the known life cycle of lamprey populations. Instead, we provide a justification below for our parameter estimates. [7][3][11][12]

Parameter	Value	Justification
k_2	$2.8 \cdot 10^-7$	Chosen based on average time mating cycles last for [7]
c	65,000	65,000 eggs are laid per nest [11]
K_M	10	Estimated from reproduction rate of lampreys [12]
k_{yd}	140	Chosen from lifespan of lamprey larva [7]
k_l	140	Estimated from population responses to lampricide usage
EC_{l50}	175,000	Estimated from population responses to lampricide usage
c_m	0.0186	Chosen from percentage of larva that reach adulthood relative to death
Y_{50}	50,000	Estimated from existing lamprey counts [7]
k_{ad}	1.997	Calculated from lifespan of adult lamprey [7]
k_s	35.3	Estimated from death rate of lamprey in food-poor regions
EC_{50f}	7200	Estimated from current lamprey food availability
a	1.4	Females demand roughly twice as many nutrients to harbor eggs
λ	1.997	Food Scarcity Constant is measured from lifespan of adult [7]

Table 4: Symbols, Descriptions, and Units for the Lamprey Population Model

5 Final Combined Model and Discussion

5.1 Key Results

For our key results, we combined our Lotka-Volterra Ecosystem model with our lamprey population model. Using the steady-state initial conditions obtained from our Ecological model, we began the simulation with a small population of lampreys, which took around 10 years to grow into a stable steady-state population. We allowed the simulation to run for 20 more years to observe the long-term impacts on the balance of the Great Lakes ecosystem, before beginning a highly intensive lampricide dosage treatment.

5.1.1 Ecosystem

As anticipated, we see apex predator populations initially plummet as the lamprey begin feasting on them, dropping down to roughly half of their initial population. Soon after, the consumer populations skyrocket up to 4 times the steady-state population, as their major form of population control is damaged. Likewise, producer populations drop roughly 10% as the drastic rise in consumers significantly curb their population. These results align with what actually occurred [3].

For the first 10 years, there are major population rebounds and collapses as the system tries to reach a new steady-state. Interestingly, the huge uptick in consumer population upon lamprey introduction causes the apex predator to briefly exceed healthy ecosystem levels around year five. Between years 10 and 30, we see mild oscillations as remnants of the Lotka-Volterra model, but they are significantly dampened due to the negative feedback loops provided by the lamprey. After the lampricide is introduced, populations stabilize to their healthy levels over ten years.

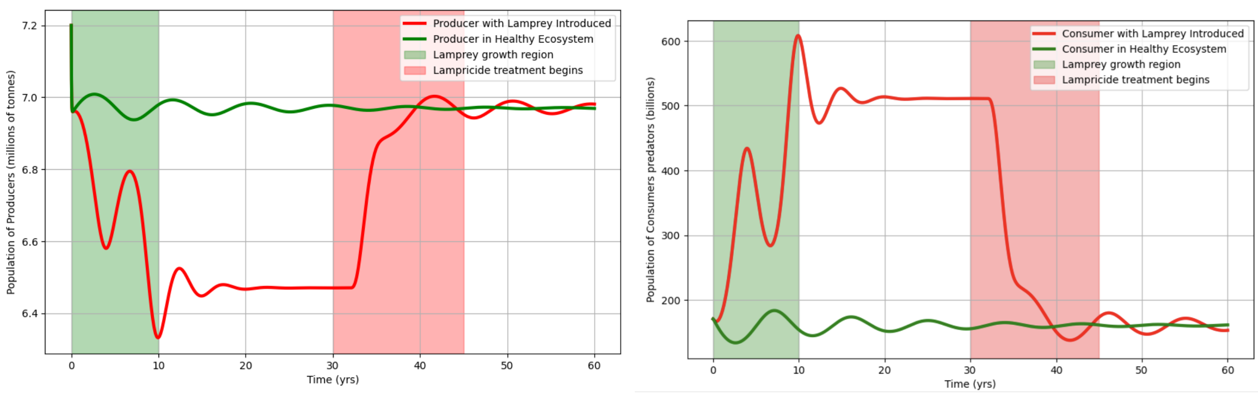

Figure 8: Consumer (Left) and Producer (Right) Populations in Final Model

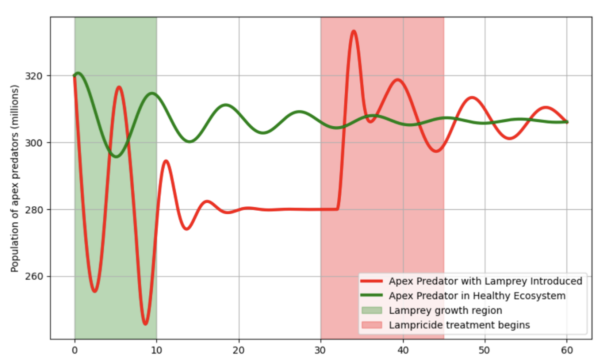

Figure 9: Apex Predator Populations in Final Model

5.1.2 Lamprey Reproduction

Sea lamprey populations explode upon introduction. Even with a 60/40 ratio of females to males introduced, by year 7 they quickly reach their equilibrium sex ratio of 60/40 males and females, consistent with literature [9]. Once lampricide is introduced, we see that the ratio of lamprey females increases during dire times. As male populations decline following a few years of lampricide, female populations remain stable and even surpass the male population briefly. This is consistent with the events that occurred during high lampricide usage [7].

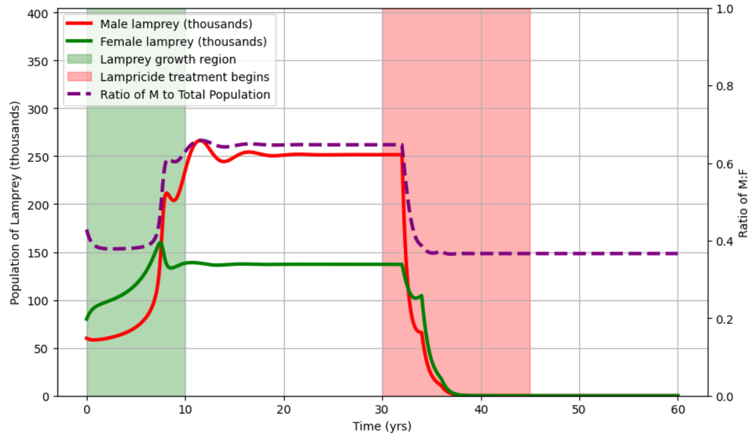

Figure 10: Male and Female Sea Lamprey Populations in Final Model

5.2 Sex Differentiation

When lampricide was introduced to the system, the male-female ratio approached 40/60, a far-cry from its 60/40 equilibrium. The fast nature of this shift indicated that the sex ratio shifts could serve as a rebalancing tool in the face of negative pressures. Thus, we hypothesized that the adaptive sex ratio, although slightly inefficient during times of plenty, helps the sea lampreys adapt to sudden negative forces. However, our model demonstrates the exact opposite result!

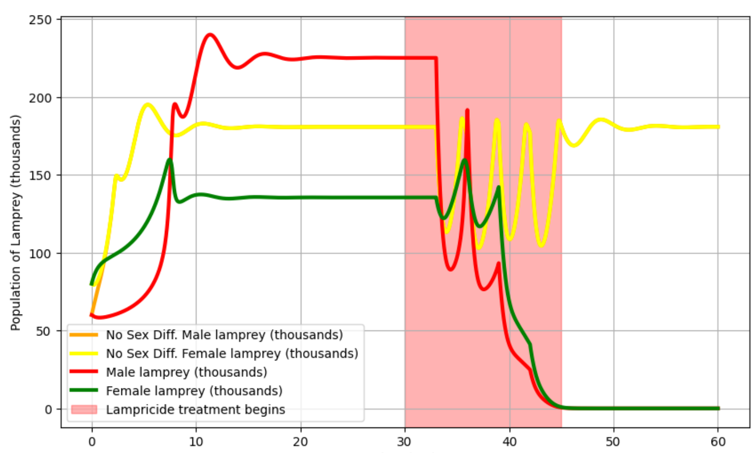

Figure 11: Male and Female Sea Lamprey Populations in Final Model

When we introduced a lampricide dosage of approximately 75% of our initial estimated parameter, we found that a **sea lamprey population with balanced sex ratios can recover its population, while the adaptive sex ratios do not.** At equilibrium, the adaptive sex ratio allows for the maintenance of a greater sea lamprey population. Another factor we considered was the invasive nature of the sea lamprey. Because they are supposed to be parasitic in their environment, they should kill their prey at much lower levels. Furthermore, they would have natural predators that curb their growth. We simulate sea lamprey growth, given the same lampricide dosage as the above graph, with the mortality rate of sea lampreys on apex predators reduced by 90% along with a natural predation rate that halves their population every 20 years.

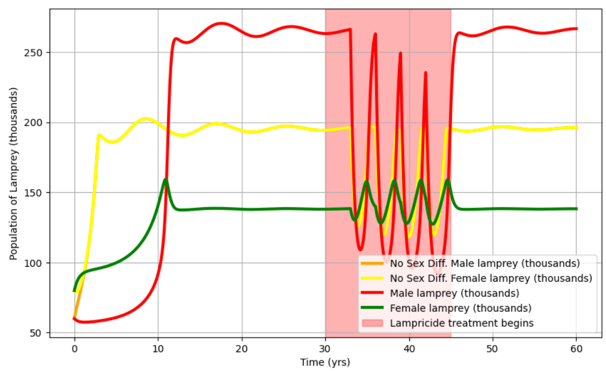

Figure 12: Adaptive vs. Non-Adaptive Sex Ratio in Natural Environment

The adaptive sex ratio can maintain a higher equilibrium population, but struggles mightily in the face of negative stimuli. Thus, we conclude that the **adaptive sex ratio of the sea lamprey generates a more plentiful equilibrium point, but makes it more difficult to adjust to negative stimuli**. This is likely a reason why 50/50 ratios are seen so commonly in the animal kingdom.

5.3 Sex Ratio Impact

Now, we examine how the adaptive sex ratio of the sea lamprey impacts the Great Lakes ecosystem. In the face of stressors, the adaptive sex ratio did not contribute to improved survival. Instead, perhaps these sex ratios could have resulted from evolutionary pressures to stabilize prey sources of the community. Thus, we analyze the populations of the producers, consumers, and apex predators in the face of a sea lamprey population without the adaptive sex ratio.

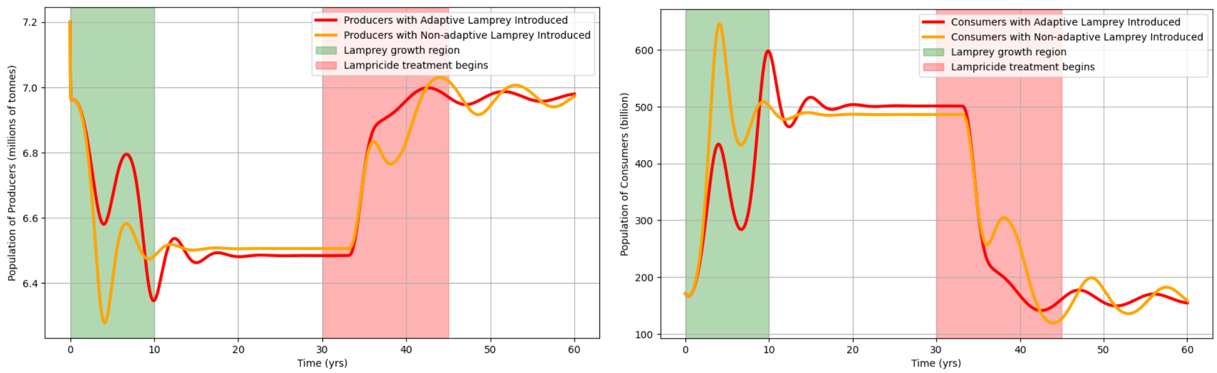

Figure 13: Consumer and Producer Populations in Adaptive vs. Non-Adaptive Sea Lampreys

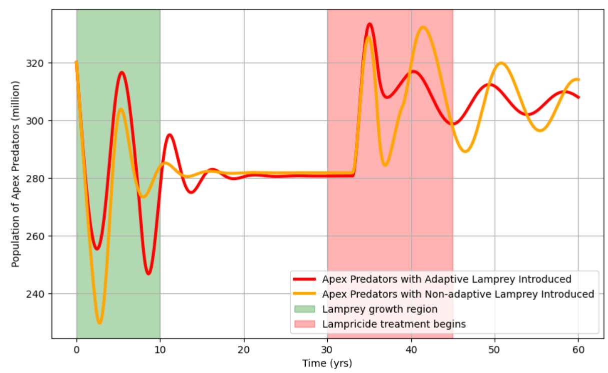

Figure 14: Apex Predator Populations in Adaptive vs. Non-Adaptive Sea Lampreys

The results here look significant. The adaptive sex ratio of the sea lampreys seems to **reduce the oscillation of the various populations**. In particular, when the lamprey are first introduced, the shifts in populations are more gradual for all three populations. These results seem to indicate that the adaptive sex ratio of the Sea lamprey could perhaps **serve to buffer prey populations when the lamprey migrate to new areas**. For the Great Lakes ecosystem, the adaptive sex ratio has served to ease the transition of native populations back to their steady state.

5.4 Treatment Plans

5.4.1 Lampricide Dosaging

Since the 1950s, the US government has aimed to control the invasive sea lamprey in the Great Lakes using lampricide, aimed at poisoning many larval sea lampreys. In our simulation, we aimed to test various treatment plans to find an optimal duration and interval to kill over 90 percent of the sea lamprey population while minimizing resources usage. We define duration as the length of treatment period and interval as how often the government would disperse the lampricide.

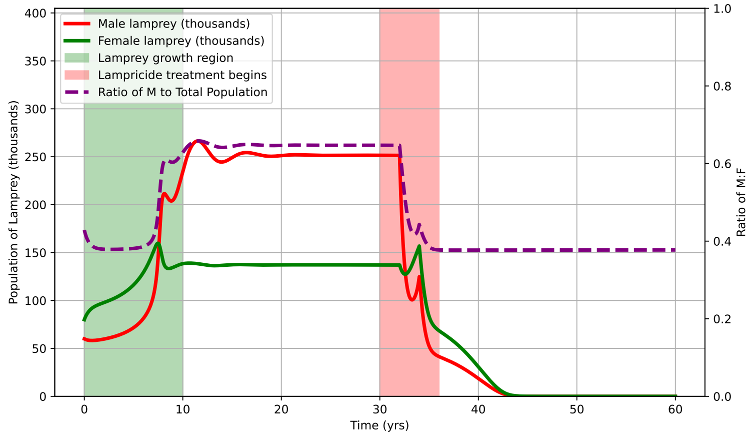

Figure 15: Potential Optimal Treatment

In the above graph, we noted that one of the more efficient plans included **selecting a duration of 6 years with lampricide treatment being dispersed every 2 years**. Within our parameters, we set the lampricide concentration / effectiveness rate to 0.9985, based on laboratory data [1]. Other configurations we found that did equally well include a duration of 3 years with lampricide treatment being dispersed every year. Overall, we found that short intervals per lampricide dispersion improved the effectiveness of the treatment, by preventing the sea lamprey population from growing back. Moreover, we find that around 3 treatments with the existing data was strong enough to kill most of the population. This has an important implication for the government, by showing in our models what can be done to further crack down on the sea lamprey population.

5.4.2 Sex-Specific Treatment

So far, we have found that female populations remain stable in times of crisis and thus balance the population. Therefore, an effective treatment method could involve the targeting of female Sea lamprey. Even a minuscule negative pressure on female populations could be fatal for the entire community. To test this, we applied a slight negative force to female sea lamprey juveniles that would halve the female population in 10 years (roughly 1.5 generations of lamprey).

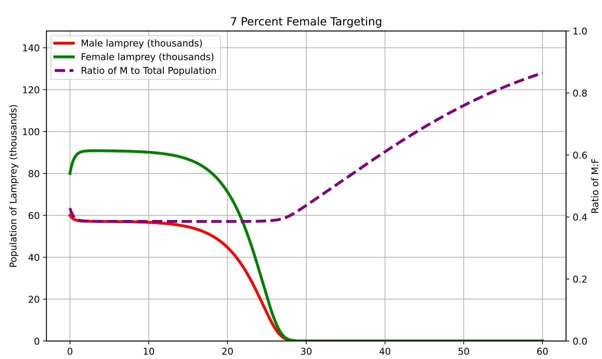

Figure 16: Female Targeting Population Impact

As this figure shows, even this slight negative force can eliminate the entire population. Thus, we conclude that **targetting female populations to disrupt the self-regulation of the adaptive sex ratio** is an effective method of Sea lamprey population control. As mentioned by Johnson et al., effective avenues of approach could include "Trojan" sex gene carriers and daughterless technology [7].

5.5 Stability Analysis

To understand the robustness of our model, we wanted to measure the long-term stability of our system of ordinary differential equations. Specifically, we wanted to examine the initial starting conditions of producers, consumers, apex predators, male lamprey, female lamprey, and the larval sea lamprey population. Because we are only looking at the environment, we ignore the presence of the lampricide to study a single non-changing linear system of ODEs. To do so, we employ numerical packages like scipy to find non-trivial nullclines, by setting each differential equation each to zero and solving for the values. We obtain one of the following equilibrium points

$$y_{init} = \left[6.78 \cdot 10^6, \quad 2.89 \cdot 10^{11}, \quad 2.97 \cdot 10^8, \quad 5.35 \cdot 10^4, \quad 8.82 \cdot 10^4, \quad 1.78 \cdot 10^7\right]$$

Note that there are various potential equilibrium points within the system. This was one of the potential solutions from the numerical nullcline solver. Afterwards, we need to find the eigenvalues of the Jacobian matrix from the system evaluated at the equilibrium point. Our analysis returned a 6 by 6 matrix, whose real eigenvalues were all non-positive, suggesting asymptotic stability within the model. We test for various levels of days, including 1 - 20 years, but it did not change the results. This validates the existence of a steady state within our model, as the ecosystem lives on.

6 Sensitivity Analysis

To test confidence in our model, we mainly look at varying two parameters in the simulation model and measure its impact on 3 factors: male lamprey, female lamprey, and the apex predator population. While we could test the sensitivity of the 23 other factors, we chose to analyze the food scarcity constant and the EC50 Maturation Rate. These factors could dramatically impact the outcome of the sea lamprey population and used the most assumptions compared to the historical data we took from the 23 other factors. Moreover, in our simulation, we removed the lampricide factor to purely test the changes of equilibrium in the simulation.

Male Lamprey Population

ec50_maturation / food_constant	40000.000000	45000.000000	50000.000000	55000.000000	60000.000000
1.800000	273.450771	275.022781	263.508332	248.321031	231.077728
1.850000	262.193431	270.693132	261.041120	246.497861	229.521821
1.900000	249.590182	265.319463	258.269976	244.542063	227.889365
1.950000	236.744282	258.466562	255.092452	242.420057	226.163349
2.000000	224.207059	249.729362	251.358275	240.086995	224.322410

Female Lamprey Population

ec50_maturation / food_constant	40000.000000	45000.000000	50000.000000	55000.000000	60000.000000
1.800000	116.083371	127.597783	138.014949	148.083462	158.171032
1.850000	115.298058	127.286927	137.837648	147.960891	158.091329
1.900000	114.425700	126.902623	137.639560	147.830755	158.010042
1.950000	113.548904	126.415587	137.413933	147.691237	157.926825
2.000000	112.712382	125.801158	137.151078	147.539992	157.841319

Figure 17: Final Male and Female Population

Iterating through the parameters shows relatively stable equilibrium for each of the male and female lamprey populations. Most notably, we found that the EC50 Maturation Rate had the most impact on the final outcome of the lamprey population. Increasing EC50 Maturation Rate increases the female lamprey population, while there is a more parabolic relationship for the male lamprey population. Finally, decreasing the food scarcity impact mainly impacted the male lamprey population which fits with our assumptions. Lower food scarcity results in a greater proportion of female lampreys compared to male lampreys, showing that bounce back effect mentioned in the results section. Overall, testing other parameters, we find that the majority of parameters did not result in a large shift in the equilibrium point, which shows the stability of our estimates. While reducing important factors like the food scarcity estimate and EC50 Maturation Rate shifted the dynamics of the environment, it still produced a stable result at the end of the simulation.

7 Strengths and Weaknesses

Our strengths include the following:

1. Our models are based on successful models from biology and biochemistry. The modified Lotka-Volterra model is used commonly to model predator-prey relationships, while the Substrate Model based on enzyme kinematics is commonly used for modeling chemical reactions.

2. Our model produces results which agree with intuition and show a clear pattern which stabilizes across time. Specifically, it mirrors the cyclical pattern of sea lamprey population across time and its impact on the apex, consumer, and producer populations.

3. Our model has a stable equilibrium from our intensive parameter selection, which enables us to perform more accurate and specific analysis for the entire ecosystem.

Our weaknesses include the following:

1. Our model uses various Fermi estimations to measure the number of total fish in the Great Lakes ecosystem, which could be off the mark (due to lack of measurements found publicly). We also estimate various pseudo-Michaelis constants which cannot be measured in the real world.

2. We provide a simplistic view of the Great Lakes ecosystem which is only made up of the producer population, consumer population, apex population, and sea lampreys. In reality, the relationship between these species are not as clear cut. We also mainly look at the large species in the Great Lakes ecosystem.

3. By modeling our relationships with Michaelis kinematics, we simplify the reproduction behavior of the sea lampreys. In reality, many of the sea lampreys reproduce during mating seasons and in tributaries, which are separate from the current ecosystem. These specific relationships were considered in the model creation but ultimately simplified for the sake of time.

8 Appendix

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