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Dynamical Modeling of Sea Lamprey Populations: Adaptive Sex Ratios and Ecological Interactions

Sea lampreys are a blood-sucking marine parasite that latch on to host fish and drink their blood for sustenance. Sea lampreys exhibit a unique trait in that their population ratios correlate with their larval growth rate. As such, changes in the ecosystem altering the amount of sustenance sea lamprey larvae are able to consume can affect the sex ratio of sea lampreys.

To understand the impacts of the variable sex ratio of sea lampreys, we created 5 interdependent differential equations to model the ecosystem and the holistic impacts of sea lampreys' adaptive sex ratio. The 5 population groups that we modeled were the sea lamprey host fish population, male lamprey population, female lamprey population, lamprey predator population, and non-lamprey parasite populations. We modeled the interaction on our dynamical system inspired by the commonly used Lotka-Volterra model to understand the interspecies relationships between these populations.

Our model showed highly unstable dynamics in ecosystems containing sea lampreys. Our model in all scenarios had severe ecosystem collapse in which at least one population in the ecosystem went extinct or nearly extinct, indicating to us that the adaptive sex ratio of sea lampreys had little to no effect on the overall stability of the ecosystem, as there were no stable equilibria both with and without the adaptive sex ratio. Based off our model, we determined that the adaptive sex ratio provided little to no advantage and primarily disadvantaged the sea lampreys since it restricted the reproductive ability of sea lampreys, as a 50:50 sex ratio allows for the maximum reproduction of sea lampreys given a fixed population. Our model showed that the primary effects of the adaptive sex ratio of sea lampreys was that the adaptive sex ratio made it so that the success of different population groups correlated with the prevalence of plankton and detritus in the environment. Higher plankton and detritus concentrations saw greater success for lamprey predators, whereas lower plankton and detritus concentrations saw more success for lamprey host fish populations. We also found that the adaptive sex ratio of sea lampreys limits the success of many other populations within our model, such as non-lamprey aquatic parasites which would benefit greatly if sea lampreys had a 50:50 sex ratio.

To analyze the sensitivity of the parameters we then used a Naive Monte-Carlo Simulation to quantifying sensitivity, and conducting range analyses. We observed that the variables that were most sensitive to initial condition were the predation and reproduction rates. Using this information we are able to link that the sharp delta in rates is likely coincided with ecosystem unsuitability. This follows research showing that invasive lampreys can cause ecosystem degradation.

Overall, we found that the adaptive sex ratio of sea lampreys helped keep populations within the ecosystem in check, but also that the adaptive sex ratio made the ecosystem highly sensitive to changing plankton and detritus concentration, as that would affect not only the total population of lampreys but also their sex ratio, causing large changes that cascaded up to higher trophic levels within the ecosystem.

Contents

1 Introduction

Petromyzon Marinus, more commonly known as the sea lamprey, is a blood-sucking marine parasitic organism. They are most commonly known for their strange mouth, which is filled with teeth and is primarily used for latching onto organisms.

Sea lampreys have two primary stages in their life cycle: a larval stage and an adult stage (a juvenile stage also exists but is ignored here for the sake of simplicity, and due to the fact that the juvenile stage is highly similar to the adult stage in terms of lamprey interactions and behavior). Sea lampreys start off their life as an egg which hatches into a sea lamprey larvae. These larvae embed themselves into the sand in a riverbed and filter feed off plankton and detritus for multiple years [5]. Eventually, sea larvae grow to their adult stage, where they develop their distinctive mouth used for latching onto hosts and go out into ocean or lake environments. Sea lampreys primarily feed by latching onto a host fish and sucking blood from the host to feed themselves. While larger fish are often able to survive being a host for sea lampreys, smaller fish tend to die of blood loss to the sea lamprey [2]. After spending some time as an adult, sea lampreys travel to streams to reproduce. A sea lamprey pair that mate die after making eggs [12].

Of particular interest is sexual differentiation of sea lampreys. Sea lampreys become a specific sex based primarily off their success in feeding during their larval stage, with faster growing larvae being more likely to become female, and slower growing ones more likely to become male [10]. This makes it so that sea lampreys have an adaptive sex ratio that is dependent on the concentration of plankton and detritus within their environment, a unique attribute of sea lampreys that starkly contrasts the 50:50 split found in most sexually reproducing species. Sea lampreys are typically male-dominated, with studied populations ranging from almost 50:50 male to female to having a higher than 3:1 male to female ratio [10].

This adaptive sex ratio attribute of sea lampreys raises many questions about how their imbalanced sex ratio affects not only sea lampreys, but also their ecosystem as a whole. To understand the effects of their adaptive sex ratio on their ecosystem as a whole, we created a dynamical system model to allow us to understand how their unique trait of having a variable sex ratio can affect both the sea lampreys themselves and the ecosystems they live in as a whole.

2 Assumptions

To model the ecosystems in which sea lampreys live in, we made the following assumptions:

1. **Both maturation rate and sex ratio are reliant on only the plankton and detritus density.** To the best of our knowledge, it is unknown specifically when in the life cycle of sea lampreys do they sexually differentiate [9]. Current research supports the idea that larval growth rate influences sexual determination, as faster larval growth rates correlate to a greater number of females [10]. However, we are uncertain about whether or not the juvenile stage of the sea lamprey affects sexual determination. In our model we assume that growth during the juvenile sea lamprey stage does not affect its future sex, or that sexual determination occurs before the juvenile stage of the sea lamprey.

2. **Sea lamprey larvae cannot meaningfully impact the concentration of plankton and detritus within their ecosystem.** Since plankton serve as sustenance for countless many species in marine

ecosystems, we assume that lampreys play too small of a role in an ecosystem to be able to create meaningful change in the concentration of plankton or detritus.

3. **Parasite-host relationships resemble predator-prey relationships.** Our model uses a modified version of the Lotka-Volterra predator-prey model and assumes that parasites and their hosts have a similar relationship to that of predator and prey. Parasites, when they infect a host, absorb the host's energy, aiding in their reproduction and increasing the likelihood of the host to die. This is similar to a predator-prey relationship, where the predator coming into contact with the prey aids in the predator's reproduction and kills the prey (due to the predator killing the prey and gaining energy from eating the prey).

4. **The proportion of sea lamprey larvae that become male always exceeds the proportion that become female.** Literature on the adaptive sex ratio of sea lampreys suggests that even in resource-dense environments, sea lampreys do not have populations with a greater amount of females than males [10].

5. **Host fish are in ample enough concentration and the duration for which a lamprey is latched onto its host is long enough for concentration of host fish to not significantly impact lamprey growth rate.** There is a large range for the duration for which a sea lamprey can stay attached to its prey, ranging from days to weeks. While smaller fish tend to die quickly, larger fish can last longer and are more likely to survive [2]. Due to the relatively large size of the species that serve as hosts for sea lampreys [ADD A BUNCH OF CITATIONS HERE], we assume that hosts are plentiful for sea lampreys and that, as such, the concentration does not significantly impact reproductive rate. In addition, human intervention, such as in the Great Lakes, tends to seek to control sea lamprey populations when they grow too large relative to population of host fish due to commercial fishing interests [5].

6. **Natural death is insignificant compared to other factors causing death for host fish and adult sea lampreys.** We assume that the primary causes of death for host fish and sea lampreys are predation, parasitism for host fish, and spawning death for adult sea lampreys. (Death of sea lamprey larvae is a very common occurence that can occur by a variety of methods, including predation. This is taken into account through an adjustment of the lamprey reproduction rate to account for death of sea lampreys during their larval stage.)

3 Notation

A table giving variables and parameters present in our model are shown below.

Table 1: Notation Table for Population Categories

Variable	**Definition**
h	Host fish population in millions
m	Male adult lamprey population in thousands
f	Female adult lamprey population in thousands
A	Adult lamprey predator population in thousands
p	Non-lamprey parasite population in tens of millions

Table 2: Notation Table for Model Parameters

Parameter	Definition
α	Reproductive rate of host fish
β	Rate of host fish death by lampreys
θ	Rate of host fish death by non-lamprey parasites
λ	Proportion of population killed by external factors (fishing, other predators, etc.)
γ	Lamprey reproduction and survival until adulthood rate
μ	Plankton and detritus concentration in the ecosystem
ρ	Plankton and detritus density correction term
ω	Rate of adult lamprey death by predators
η	Lamprey spawning death rate
ψ	Adult lamprey predator reproduction rate
ϕ	Natural death rate of adult lamprey predators
ζ	Rate of adult lamprey predator death by non-lamprey parasites
χ	Parasite reproduction rate
ν	Parasite natural death rate

For stability analysis, we denote an equilibria for a population with $*$. For example, an equilibrium value for the population of male adult lampreys would be denoted m^*.

4 Model

We modeled the interactions in an ecosystem between different species and both male and female sea lampreys through the dynamical system shown below.

$$\frac{dh}{dt} = \alpha h - \beta h(m+f) - \theta p h - \lambda h$$
$$\frac{df}{dt} = \gamma m f \mu^2 - \omega f A - \eta m f$$
$$\frac{dm}{dt} = \gamma m f(\rho - \mu)\mu - \omega m A - \eta m f$$
$$\frac{dA}{dt} = \psi A(m+f) - \phi A - \zeta p A - \lambda A$$
$$\frac{dp}{dt} = \chi p(h+A) - \nu p$$

To explain the motivation behind our model, we will explore each differential equation individually.

- $\frac{dh}{dt}$: There are four factors that affect the population of host fish. The first is their ability to reproduce, modeled by a reproduction rate α and proportional to their population. Host fish die due to parasitism from lampreys and non-lamprey parasites, and we model this interaction in a way similar to Lotka-Volterra, with host fish deaths to each group being proportional to the population of host fish and also the population of the group parasitizing it. Lastly, we have a λh term to denote host fish deaths due to various external factors, such as natural death, fishing, death by other predators, etc.

- $\frac{df}{dt}$: Change in the population of female sea lampreys is determined by a reproduction term, a predation term, and a spawning death term. Firstly, lampreys breed when a male and female come into contact, thus making it so that reproduction is proportional to the male and female populations. Next, this is adjusted by a lamprey reproduction and survival until adulthood rate, γ, a wide-encompassing parameter that factors in the number of larvae that a male and female lamprey pair produces as well as the huge attrition rate that lamprey larvae suffer early in their life [6] [4], whether it be due to predators or human efforts to control sea lamprey populations [5]. To account for the fact that higher concentrations of lamprey larvae food leads to increases in larval growth rate [18], leading to faster maturation into adulthood, we have a μ parameter which describes the concentration of microorganisms in the environment. This represents the total reproduction of lampreys. We then scale this by μ to get the proportion of the total lamprey reproduction that ends up as females, as the higher the concentration of larvae food, the more likely larvae are to end up female. In addition to reproduction, we have two terms; $\omega f A$ represents the predation on female adult lampreys while $\eta m f$ represents how after spawning, both parents die [5].

- $\frac{dm}{dt}$: The motivation behind our expression for the change in the male adult lamprey population is almost identical to the motivation for the female adult lamprey population. Most significantly, we multiply the total reproduction of sea lampreys by a factor of $(1-\mu)$, since we multiplied the other by a factor of μ.

- $\frac{dA}{dt}$: The change in the population of adult lamprey predators is highly reminiscent of terms in the Lotka-Volterra model. Reproduction is represented by a reproduction rate, ψ, and is also proportional to both the number of adult lamprey predators and the total number of adult lampreys. Adult lamprey predators also suffer from natural death at a rate of ϕ and die as a result of parasitism with rate ζ, with this parasitism rate being proportional to their population and parasite population. Lastly, there is a λA term to account for external factors, similar to the λh term in the first differential equation.

- $\frac{dp}{dt}$: The change in the population of parasites is based off their parasitism (or "predation" in terms of Lotka-Volterra) of both host fish and adult lamprey predators and occurs at a rate of χ. They also suffer from natural death which occurs at a rate of ν.

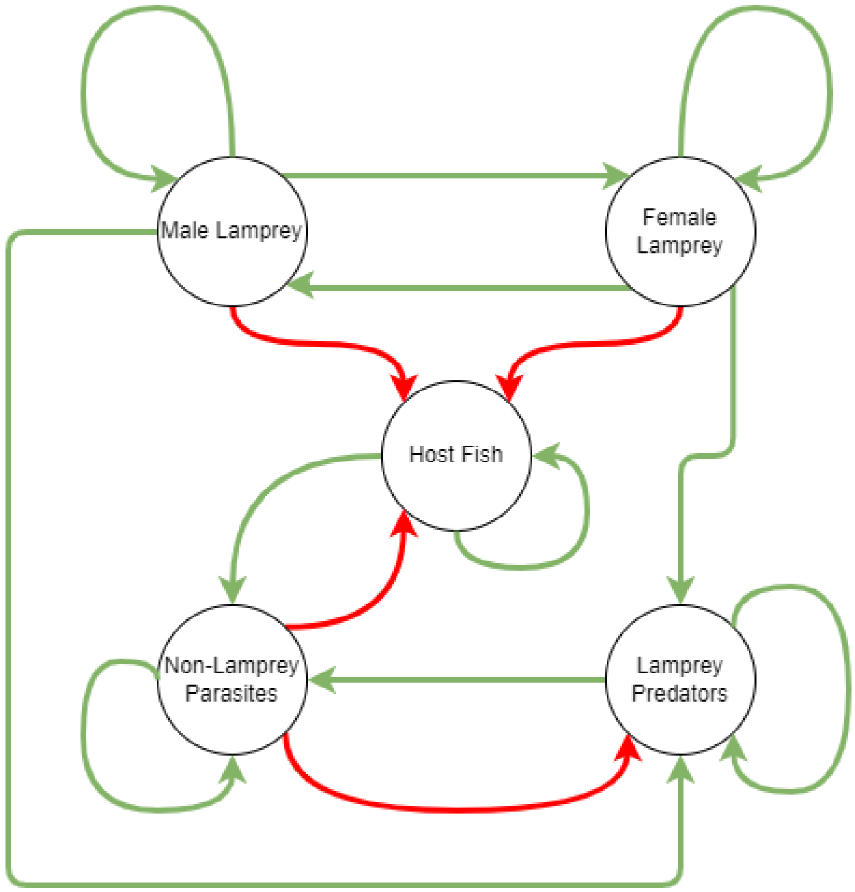


Figure 1: Graph showing effects of populations on other populations. Green arrows indicate a positive correlation and red indicates a negative correlation.

To analyze both a model in which lampreys do exhibit an adaptive sex ratio and one in which they do not, we create two cases. When lampreys do have an adaptive sex ratio, we will bound the value of μ to be in the range $(0, 0.5\rho)$. Here our ρ term is used to help control the impact of changing μ on the reproductive rate and gender ratio, as halving the concentration of plankton and detritus in the environment will not necessarily lead to an identical change in gender ratio. Since sea lamprey populations in literature almost always exhibit a greater number of males than females [10], we know that the rate at which female sea lampreys are produced should not exceed the rate at which males are produced. For the 50:50 sex ratio case, we will set μ to be exactly 0.5ρ.

5 Parameter Estimation

To determine values for parameters in our model, we used a combination of parameters determined from literature, as well as parameters determined through experimentation with our model through numerical simulations. We first determined feasible ranges for our parameters which are detailed below.

The final values we ended up using as our parameters are shown below.

Table 3: Boundary Values For Parameters

Parameter	Boundary	Value Obtainment
α	$0.4 \leq \alpha \leq 0.6$	Determined from literature [1]
β	$.04 \leq \beta \leq .06$	Determined from literature (manipulated) [7]
θ	$0.11 \leq \theta \leq 0.14$	Determined from literature [13]
γ	$0.2 \leq \gamma \leq 0.93$	Obtained from testing model
μ	$0.2 \leq \mu \leq 0.5$	Obtained from testing model
ω	$0.07 \leq \omega \leq 0.2$	Obtained from testing model
η	$.10 \leq \eta \leq .16$	Determined from literature [8] [15]
ψ	$.108 \leq \psi \leq .356$	Determined from literature [21]
ϕ	$.10 \leq \phi \leq .21$	Determined from literature [19]
ζ	$0.008 \leq \zeta \leq 0.01188$	Determined from literature [16]
χ	$0.002981 \leq \chi \leq 0.003112$	Determined from literature [3]
ν	$0.738 \leq \nu \leq 0.902$	Determined from literature [16]

Table 4: Final Parameter Values

Parameter	Value
α	0.5
β	0.0424
θ	0.13
γ	0.9
μ	0.3 for adaptive ratio, 0.5 for 50:50 ratio
ρ	1
ω	0.1
η	0.05
ψ	.115
ϕ	.125
ζ	0.008
χ	0.003
ν	0.8

6 Equilibria and Stability

6.1 Adaptive Sex Ratio Model

To reduce the complexity of our expressions for the equilibria, we define κ and τ as follows:

$$\kappa = \gamma\mu^2 - \eta$$
$$\tau = (\gamma(\rho - \mu)\mu - \eta).$$

We found the equilibrium values to be

$$m^* = \frac{\alpha\zeta + \theta(\phi+\lambda) - \lambda\zeta}{\beta\zeta + \frac{\beta\zeta\kappa}{\tau} + \theta\psi\left(1+\frac{\kappa}{\tau}\right)}$$
$$f^* = \frac{\kappa(\alpha\zeta + \theta(\phi+\lambda) - \lambda\zeta)}{\tau(\beta\zeta + \frac{\beta\zeta\kappa}{\tau} + \theta\psi\left(1+\frac{\kappa}{\tau}\right))}$$
$$A^* = \frac{\kappa(\alpha\zeta + \theta(\phi+\lambda) - \lambda\zeta)}{\omega(\beta\zeta + \frac{\beta\zeta\kappa}{\tau} + \theta\psi\left(1+\frac{\kappa}{\tau}\right))}$$
$$p^* = \frac{\psi\left(\frac{\alpha-\lambda}{\beta}\right) - \phi - \lambda}{\zeta + \frac{\psi\theta}{\beta}}$$
$$h^* = \frac{\nu}{\chi} - \frac{\kappa(\alpha\zeta + \theta(\phi+\lambda) - \lambda\zeta)}{\omega\left(\beta\zeta + \frac{\beta\zeta\kappa}{\tau} + \theta\psi\left(1+\frac{\kappa}{\tau}\right)\right)}$$

Substituting in our parameters, we get that $m^* = 2.9$, $f^* = 0.64$, $h = 25.77$, $A = 0.90$, $p = 0.98$ are our equilibrium values. To determine the local stability of this equilibrium, we analyzed the eigenvalues of the Jacobian. The Jacobian of our system is

$$\begin{pmatrix} \alpha - \beta m - \beta f - \theta p - \lambda & -\beta h & -\beta h & 0 & -\theta h \\ 0 & \gamma m\mu^2 - \omega A - \eta m & \gamma f \mu^2 - \eta f & -\omega f & 0 \\ 0 & \gamma m\mu(\rho-\mu) - \eta m & \gamma f\mu(\rho-\mu) - \omega A - \eta f & -\omega m & 0 \\ 0 & \psi A & \psi A & \psi(m+f) - \phi - \zeta p - \lambda & -\zeta A \\ \chi p & 0 & 0 & \chi p & \chi(h+A) - \nu \end{pmatrix}$$

We utilized Mathematica to evaluate the eigenvalues of this matrix numerically, based off our previously determined parameters. Eigenvalue analysis indicated that the equilibrium is unstable, as not all real parts of the eigenvalues are negative. We simulated the ecosystem with these parameters and initial conditions $h(0) = 5, m(0) = 2, f(0) = 1, A(0) = 3, p(0) = 6$. Unsurprisingly, we found that the system did not achieve stability, with lamprey and parasite populations decreasing drastically.

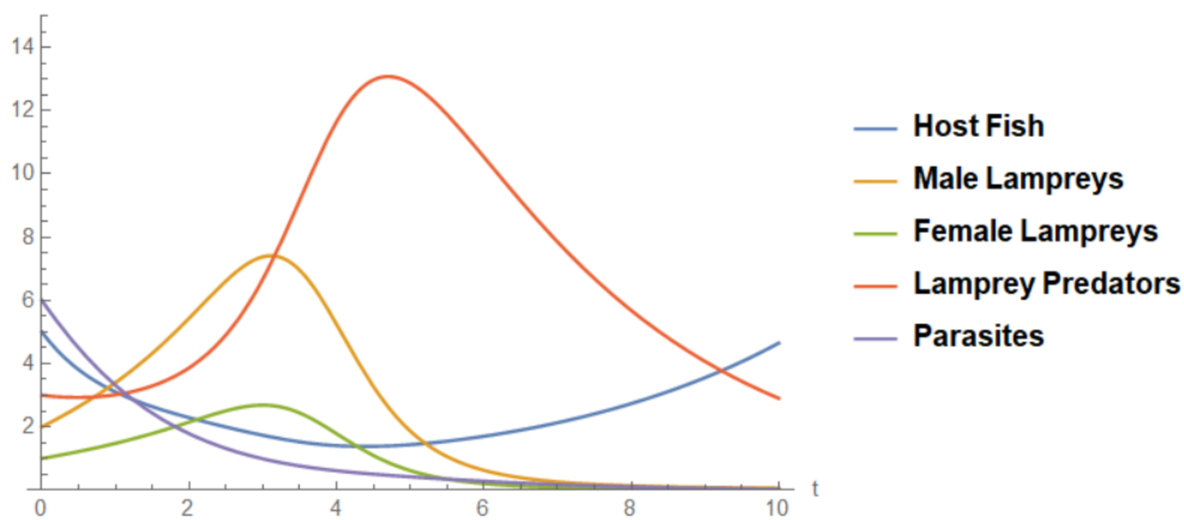


Figure 2: Adaptive sex ratio simulation results

To understand the impact of the adaptive gender ratio on the ecosystem as a whole, we perturbed the value of μ by 0.05 in both directions. The results of each simulation are shown below. In addition, we recalculated the equilibrium points and performed eigenvalue analysis for each case. In both cases, we found that the equilibrium point is still unstable.

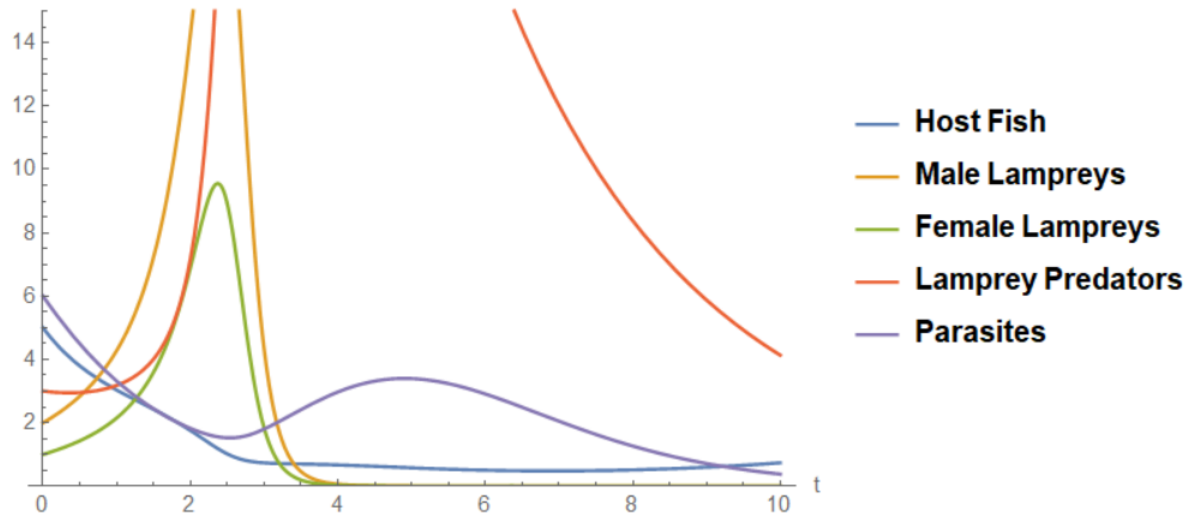


Figure 3: Adaptive sex ratio simulation results for $\mu = 0.35$

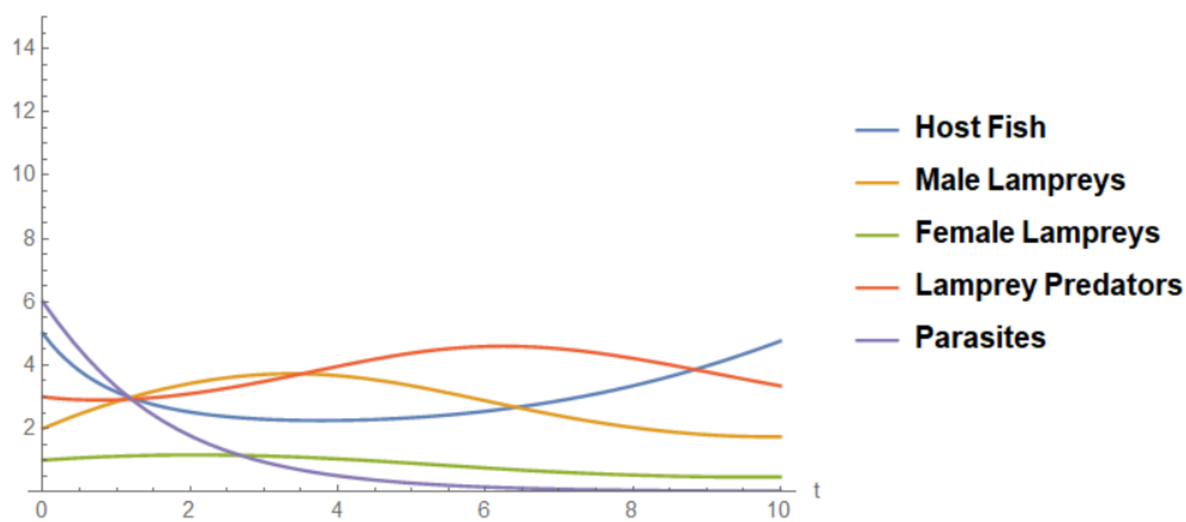


Figure 4: Adaptive sex ratio simulation results for $\mu = 0.25$

6.2 50:50 Sex Ratio Model

Using the same value for κ as the adaptive sex ratio analysis, we calculated the equilibrium values of the system to be

$$f^*, m^* = \frac{\alpha - \lambda + \theta\left(\frac{\phi+\lambda}{\zeta}\right)}{2\beta + \frac{2\theta\psi}{\zeta}}$$

$$A^* = \frac{\kappa\left(\kappa\alpha - \lambda + \theta\left(\frac{\phi+\lambda}{\zeta}\right)\right)}{\omega(2\beta + \frac{2\theta\psi}{\zeta})}$$

$$p^* = \frac{\psi\left(\frac{\alpha-\lambda}{\beta}\right) - \phi - \lambda}{\zeta + \frac{\psi\theta}{\beta}}$$

$$h^* = \frac{\nu}{\chi} - \frac{\kappa\left(\kappa\alpha - \lambda + \theta\left(\frac{\phi+\lambda}{\zeta}\right)\right)}{2\omega\left(\beta + \frac{\theta\psi}{\zeta}\right)}$$

Substituting in the values of our parameters, we find that some of the equilibrium points have negative populations, so the system lacks a nontrivial equilibrium (that is, $h, m, f, A, p > 0$. As such, we did not conduct eigenvalue analysis of the system since it would be meaningless. Numerical simulation with the same starting conditions as the adaptive sex ratio simulation except with $m(0) = 1.5$, $f(0) = 1.5$

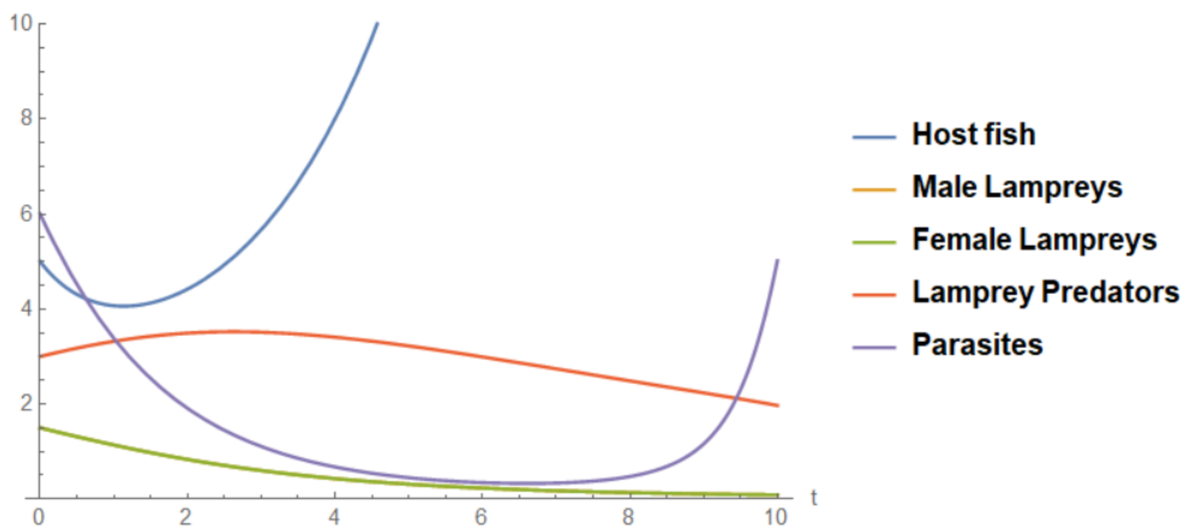


Figure 5: 50:50 sex ratio simulation results

7 Effects of Adaptive Sex Ratio on Sea Lampreys and Their Ecosystem

Our simulations show that having an adaptive sex ratio tends to make lampreys more likely to survive in low plankton and detritus environments where there are a large proportion of males. In addition, the adaptive sex ratio of lampreys also causes changes in plankton and detritus concentration to affect higher trophic levels, often drastically. However, we found that it is generally difficult to predict whether changes in plankton and detritus concentrations would hurt or harm a certain group, and we believe that this is at least in part due to the unstable dynamics of the system.

In terms of advantages and disadvantages of adaptive sex ratio for sea lampreys, we found that having an adaptive sex ratio is generally disadvantageous for sea lampreys, and that there are no significant advantages for species with an adaptive sex ratio. In our model, the reproductive rate of sea lampreys is proportional to both male and female population. As such, assuming a fixed population, sea lampreys will always want a 50:50 male to female ratio, as that is what maximizes $\gamma m f \mu$, the total reproduction of sea lampreys. As such, the imbalanced sex ratio of sea lampreys reduces the total amount of offspring they are able to reproduce. The only advantage that we could find for the adaptive sex ratio of sea lampreys involved human involvement. One technique that is used to control sea lamprey populations in regions in which they are invasive is the sterilization and then release of male sea lampreys [22]. Since the adaptive sex ratio of sea lampreys gives them a greater number of males than females in all but the most plankton and detritus-rich environments, the greater proportion of males to females decreases the effectiveness of male sea lamprey sterilization when compared to a 50:50 sex ratio. Since reproduction is based off our $\gamma m f \mu$ term, note that reduction of the fertile male population by a certain percent would have the same effect as reduction of the fertile female population by that same percent. However, since the population of male sea lampreys is greater than that of female sea lampreys, it would take a greater number of sterilizations to get the same impact when sterilizing males as compared to sterilizing females. As such, sea lampreys get some resilience against human control through their imbalanced sex ratio.

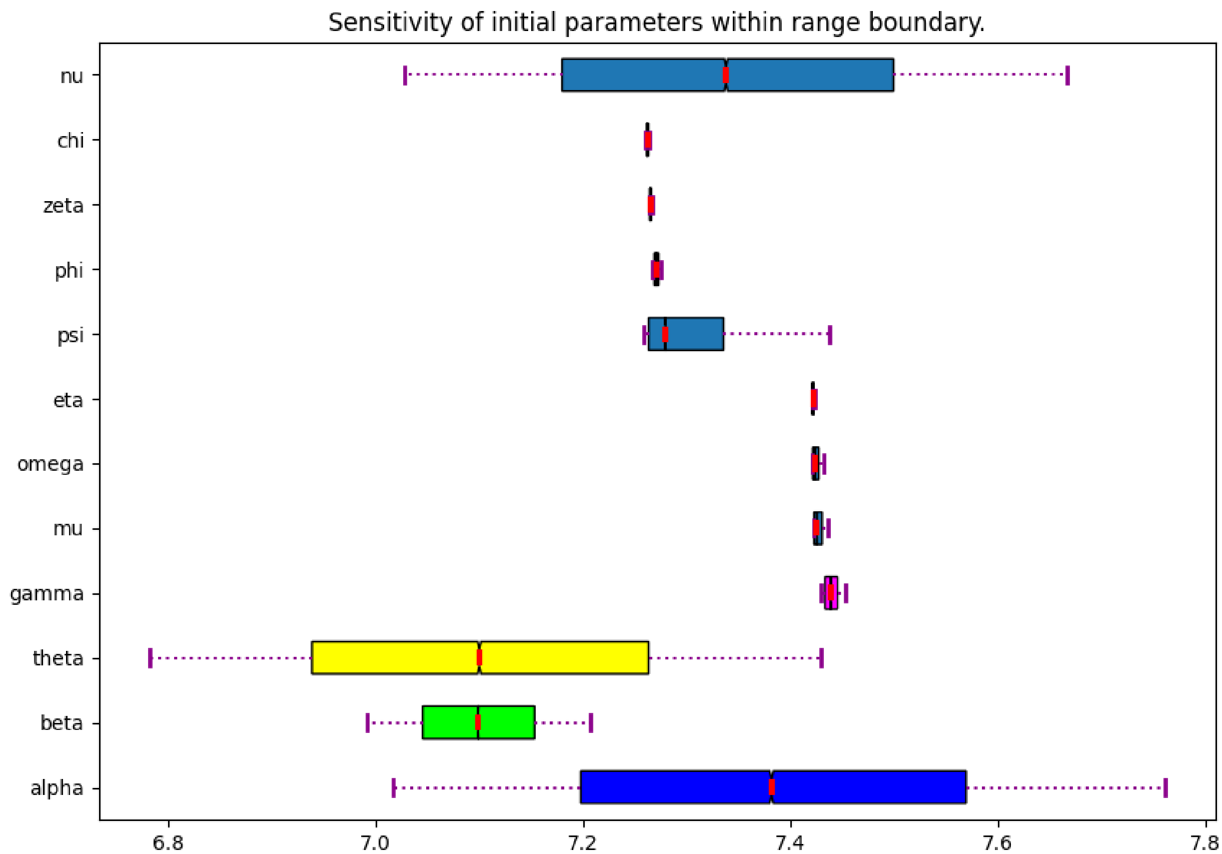
Our stability analysis indicated that the ecosystem our model simulated is highly unstable, regardless of the sex ratio of the sea lampreys. In our analysis of both the adaptive sex ratio model and the 50:50 sex ratio model, we found that the system lacks any stable equilibria points and will generally exhibit unstable behavior. Varying the μ parameter that influences the proportion of males against females does not create any new stable equilibrium points either. As such, we say that the adaptive sex ratio is mostly irrelevant to the stability of the ecosystem, as our model indicates that it is unstable either way.

Variability in the sex ratio of lampreys also creates effects for other organisms in the ecosystem, although most of these effects are caused by the disadvantageous nature of adaptive sex ratio. Due to adaptive sex ratio hurting lamprey reproduction, they are not as prevalent within the ecosystem as they would be with a 50:50 sex ratio. As such, the predators of adult sea lampreys are affected negatively, since increased populations of sea lampreys would increase the reproduction of adult sea lamprey predators (due to adult sea lamprey predator reproduction being proportional to total sea lamprey population). The effects of these then carry over to the parasite population, as a lower population of adult lamprey predators means a lower amount of potential hosts for marine parasites, decreasing their reproduction. As such, the inefficiency of sea lampreys' adaptive sex ratio causes decreased population numbers in both sea lamprey predators and marine parasites.

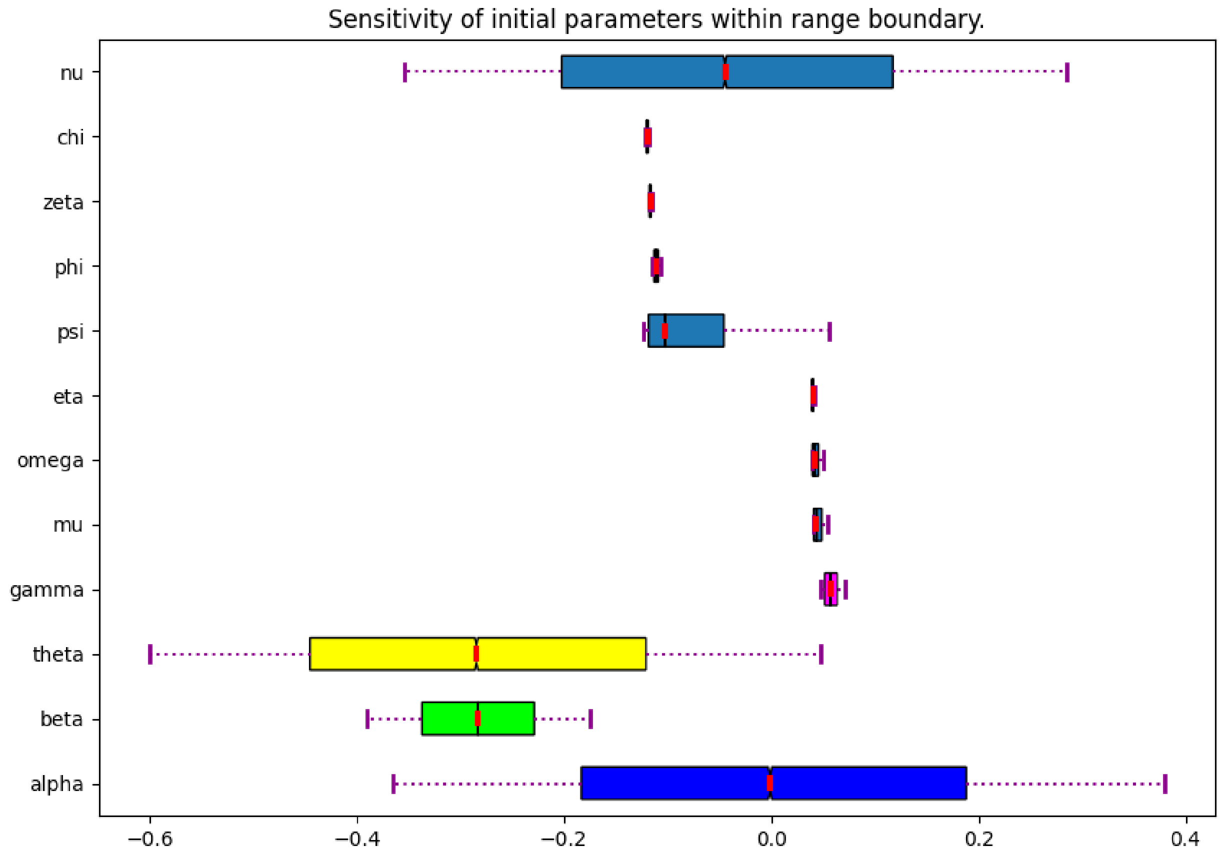
8 Sensitivity Analysis

8.1 Naive Monte Carlo Simulations

We use the Monte-Carlo simulations by determining expected values ranges for the bounded parameters. Our parameter bounds in the model can be used to determine the sensitive of the variables by random sampling and measuring the delta of the resulting normalized parameter space vector. We look at the distribution of one parameter given that it has normal distribution and sample 100 thousand time within the distribution.



After correction by our mean delta vector norm:



8.2 Parameter Sensitivity

From our results (both graphically and numerically) we see that the parameters for alpha, beta, theta, psi, and nu are the most sensitive parameters. We can also see the data when it is corrected by our mean delta vector norm.

$$\text{Where out delta vector is, } \vec{V} = \begin{pmatrix} \frac{dh}{dt} \\ \frac{dm}{dt} \\ \frac{df}{dt} \\ \frac{dA}{dt} \\ \frac{dp}{dt} \end{pmatrix}$$

The most sensitive parameters were generally reproduction rate multipliers and rates of predating. This also empirically shown form real world data where these are the most sensitive ecosystem parameters. [11] [17]

9 Strengths and Weaknesses of Our Model

9.1 Strengths

1. **Our model can be adjusted to account for macroscopic differences in ecosystems that lampreys live in.** Lampreys primarily live in two environments: one that consists of the Atlantic, Eastern United States, and Western Europe, and another that comprises of the Great Lakes. Within the Great Lakes, lampreys are a invasive threat to local host fish populations, whereas within the Atlantic, they are closer to being threatened/endangered [20]. Because our model accounts for various different species that would affect lampreys within their ecosystem, we think that it is possible to adjust our model for differing environmental conditions that lampreys face within different ecosystems.

2. **Our model's foundation has been influenced by well-established mathematical frameworks obtainable throughout literature.** Particularly, we use parts of the Lotka-Volterra equations to simulate predator-prey relationships. Utilizing the reliability and applicability of this widely verified model strengthens the robustness of our method. Using this paradigm provides various ideas and techniques, resulting in a stronger theoretical foundation for our differential equations.

3. **Our model takes these treatments' effects into account, making it possible to investigate different population control tactics, such as lamprey food availability and reproduction rate controls.** This element increases the model's applicability for conservationists and decision-makers who want to successfully manage lamprey populations.

9.2 Weaknesses

1. **Our model does not take into account mating/spawning seasons of lampreys or seasonal plankton blooms.** Sea lampreys breed primarily in the spring and early summer [5], and plankton typically have a large bloom in the spring and sometimes one in the fall as well [14]. Our model assumes that lamprey spawning occurs continuously over the course of a year and that plankton levels stay constant throughout the year. A model that accounts for these seasonal changes could potentially see different behavior.

2. **Our model greatly simplifies the wide range of interactions possible between different organisms in our ecosystem.** Due to the wide variety of different species within the environments that sea lampreys live in and their myriad different interactions, modeling this problem required some degree of simplification. In reality, there are many more interactions between the predators, host fish, parasites, and sea lampreys that were not included in our model that may cause differing dynamics in the real ecosystems sea lampreys live in.

3. **Our model groups many different species of fish and parasites into broad predator, host, and parasite groups.** Different species of organisms within each of these groups each have their own interactions with other species, such as how certain parasites can only have certain types of fish as their host. Our model ignores these differences by categorizing many different species into hosts, predators, and parasites.

4. **Our model does not take into account likely differences between areas where the lampreys live for most of their life and where they spawn.** There are many likely differences between the ocean or lake environments that sea lampreys live much of their adult life in and the streams that they reproduce in. There may be differences in survival rates or prevalence of food between these different environments, however our model ignores this.

5. **Our model loses accuracy in situations where lamprey populations significantly impact host fish populations and disturb their own ability to find hosts.** Since we assumed that there is an abundance of host fish within the ecosystem, our model becomes inaccurate in situations where sea lampreys are able to significantly decrease the population of host fish. In these situations, the lack of hosts would make it more difficult for lampreys to find sustenance to survive and reproduce, likely decreasing their reproduction rate.

10 Appendix

Code is available here.

11 References

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