Problem Chosen	2024	Team Control Number
A	MCM/ICM Summary Sheet	2426428

Lampreys are a vital species within their ecosystems. They make sure the population of other species stays in check as an apex predator while also naturally not overgrowing the ecosystem they are prevalent within, and they have the interesting capability to change the sex ratios of their population depending on surrounding environmental factors. This allows us to examine the impact that the lampreys have on their environment and prey based on various sex ratios.

Our model builds off of a previous model called the Lotka-Volterra model which builds a system of equations to demonstrate the interaction between a predator and a prey species. We extend this model to take into account environmental sex differentiation (ESD) in a predator species which in the context of this problem models our Lamprey population. Additionally, we posit that the rate of reproduction of the lamprey population is proportional only to the female population and the prey population, and we assume this value is not dependent on the male population. Furthermore, we justify this assumption based on ecological evidence and the method of reproduction of lamprey. This allows us to modify the equation representing the rate of change in predator population over time and generate two equations—one each for the rate of change in the female and male populations of the predator species. Solving this new system of equations allows us to gain insight into the benefit that ESD provides to the lampreys.

What results is a model that is robust in that it encapsulates the behaviors of the Lotka-Volterra models on which it is based and new behaviors that are further discussed. Some of these new behaviors manifest as a leveling out of all modeled populations when the death rate of male lampreys is higher than that of female lampreys producing a stable equilibrium in the involved populations. Additionally, we explain male bias using a new parameter that we introduce into the model that allows the rate of birth of males and females to be their respective proportions of the population based on an environmental factor.

From an ecological perspective, lampreys are necessary to maintain the levels of their prey within their ecosystem and without the presence of lamprey the ecosystem would deteriorate due to an unrestrained population of fish present in the ecosystem. The continued existence of the lamprey is beneficial to the filtration of the ecosystems where they are present. Lampreys are controversial within news outlets for their harm to trout and other big game fish within the United States leading to the controversial nature of removal and reduction methods to the lamprey population. These restraining efforts on the lamprey population lead to many side effects on both the lamprey and the ecosystem as a whole. Ultimately, our model helps explain how their relationship with their prey provides an advantage to their overall population and develops the role of lamprey in their ecosystem as a whole.

Contents

1 Problem

Sea lampreys take on the role of a parasite or prey depending on the ecosystem, and unlike humans and other mammals, the sex ratio of lampreys is determined by how fast they grow when they develop, which is influenced by environmental factors such as food availability. When there is less food, the proportion of males in the population can reach 78 percent, and when food is abundantly available, the proportion of males in the population is around 56 percent. We will create a model that simulates the interaction of prey and lampreys in an ecosystem, examining the sex ratio of lampreys and its effect on both populations and arriving at conclusions for the advantages and disadvantages of having an environmental sex determination.

2 Hypotheses

Hypothesis 1:

When the population of lampreys can alter their sex ratio due to their environmental impacts, then the overall population growth and total within the enclosed ecosystem will stabilize around a value because the adjusted amount of female lampreys for the population will eventually lead to an even state of births as the lamprey sex ratio adapts to their environment.

Hypothesis 2:

The female proportion of lampreys increases after the population decreases because the population is attempting to compensate for the lower numbers of lampreys.

3 Methods

The main purpose of our model is to represent the relationship between a prey population and a lamprey predator population that is split into male and female proportions, where the proportions are dependent on the prey population. The derivation of our model begins with the Lotka-Volterra model (2), which is used to model the competition between two species, a predator and a prey.

$$\frac{dx}{dt} = rx - axy$$

$$\frac{dy}{dt} = bxy - ky$$

Here, the x represents the prey and y represents the predator. r is the birth rate for prey, a is the death rate for prey, b is the birth rate for predators, and k is the death rate for predators.

To factor in the ratio of males to females in the lamprey population, we split the previous predator equation into two equations, denoted by y_f for the number of females in the population and y_m for the number of males in the population, where $y = y_f + y_m$. We also introduce the variable γ, which is the constant of proportionality found by a normal cdf based on environmental factors that determine the male-to-female ratio of the lamprey population. The environmental factors taken into consideration for the constant are based on the population density of the lampreys and the lamprey larva, availability of food for lamprey larva, time available for the lampreys to stay within their larva form, and temperature of the environment the lampreys are present within (3). γ is the proportion of males while $1-\gamma$ is the proportion of females. Ultimately, incorporating γ into our model allows us to scale the rate at which males and females are given birth to based on environmental conditions.

Further, we introduced the assumption that all eggs laid by females will be fertilized by male lampreys. This assumption is elaborated on further in the conclusion, and an ecological explanation for its validity is presented there. Nevertheless, this assumption allows us to base the rate-in of male lampreys on the number of female lampreys in the population since the number of male lampreys essentially would not increase the reproductive rate in representation. Again, this is scaled by the population proportions for male and female lamprey γ and $(1-\gamma)$ respectively. What results is a model that takes into account the environmental sex determination ability of lampreys, adjusts birth rates based on the interaction between prey and both male and female lampreys, and models the impact of the lampreys on the prey species accordingly.

$$\frac{dx}{dt} = rx - ax(y_f + y_m) \tag{1}$$

$$\frac{dy_f}{dt} = (1-\gamma)bxy_f - k_f y_f \tag{2}$$

$$\frac{dy_m}{dt} = \gamma bxy_m - k_m y_m \tag{3}$$

For this model, r represents the growth rate of the prey species, and a is the rate of interaction between prey and lamprey species resulting in the death of the prey. b represents the birth rate of lamprey based on the number of female lampreys and prey— using the prey species in this term is necessary since the Lotka-Volterra model assumes that prey species are needed as resources to produce offspring. k_f represents the death rate of the female lampreys, and k_m represents the death rate of the male lampreys. Again, γ is explained above.

Using experimental numbers from multiple sources, we were able to calculate the parameters of the proposed model to simulate the behavior in a real-world environment. The death rate of lampreys was calculated from the average mortality rate of lampreys before sexual differentiation with the average mortality rate after sexual differentiation. This is found by the following equation, which is separated by sex, i.e. use female or male subscripts depending on the desired result,

$$\frac{(\mu * \eta_f/_m) + (\rho * \tau_f/_m)}{\lambda}$$

where μ = lamprey mortality rate before sexual differentiation, $\eta_f/_m$ = number of years until lamprey finished sexual determination for each sex, ρ = mortality rate of lamprey after sexual determination, $\tau_f/_m$ = number of years until maturation after sexual differentiation for each gender, and λ = total number of years it takes to reach maturation.

First, the mortality rates of the lampreys were calculated by averaging a list of mortality rates provided to achieve the average mortality rate before sexual differentiation of .48 and a mortality rate after sexual differentiation of .24.(6) Then we needed to find the time that the lampreys spend in each phase of life which was given by a table and represented visually by Figure 8.(3) We can use this information to find the amount of time each sex of lamprey spends within each phase of life and in total. After averaging across multiple lamprey species, we concluded that the male lamprey spends 5.25 years before sexual differentiation and 3 years after sexual differentiation to reach maturation (3). Also after averaging across multiple lamprey species, we found that the female lampreys spend $2.\overline{6}$ years and the average female lamprey spends $6.91\overline{6}$ years after sexual differentiation until they have reached maturation.(3) This also tells us that the total time for both male and female lampreys until they reach maturation is on average 8.25 years.(3) We can then calculate that $k_f = \frac{0.48*2.\overline{6}+0.24*6.91\overline{6}}{8.25} = 0.31\overline{75}$ and $k_m = \frac{0.48*5.25+0.24*3}{8.25} = 0.39\overline{27}$

From the Lotka-Volterra system, we could create a stability analysis for the equilibrium solutions of the population of lampreys to prey. We chose the Lotka-Volterra model in order to represent the lamprey population as one whole rather than splitting it based on sex to avoid scenarios where the lamprey population becomes entirely male or female, which does not happen in the data observed. To find stability, we would find the equilibrium solutions from the two equations, which we expect will produce three equilibrium points: prey living while the lamprey population is extinct, the prey population going extinct while the lampreys live, and both populations living. Creating a linear matrix system with the eigenvalues and Jacobian matrices, we could analyze each equilibrium point to determine the stability of the model.

4 Results

After developing experimental values for the parameters of our model, we solved our system of differential equations using an out-of-the-box ODE solver in MatLab called $ode23$. This solver allowed us to plot numerical solutions for our model, and develop an understanding of how lamprey populations vary over time.

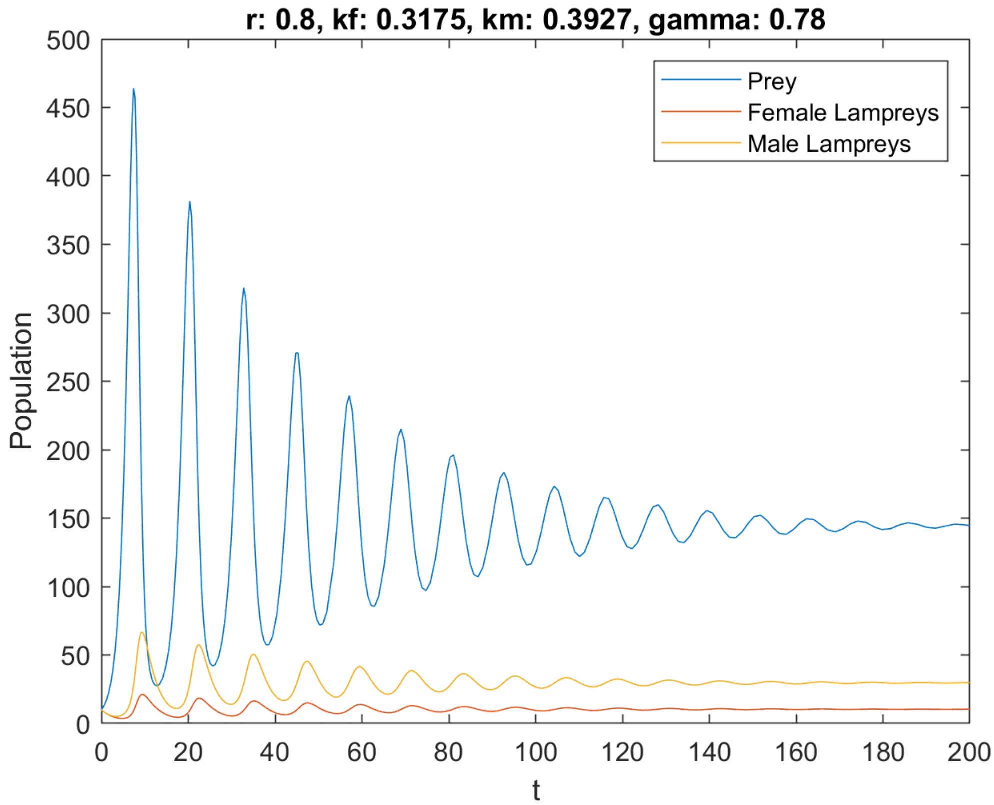

Figure 1: This solution presents our model's result for the lamprey population where the proportion of the population that is male is high— 78% of the total population of lampreys.

In Figure 1 it is important to notice that all species start with the same population. This is intentional and it gives the prey population the ability to grow with very little hindrance. Then, the lamprey population spikes and the pattern of spike and trough continues with the amplitude of the pattern decreasing over time. Once again this is resultant from the consumption of the prey species by the male lampreys not contributing to the production of offspring and the death rate of males being higher than that of females. Also important to note is that $r = 0.8$ for the prey species allows the lamprey populations to be visible in the full graph, so it is not dwarfed by a prey population orders higher than that of the predator as would be expected in a typical food chain.

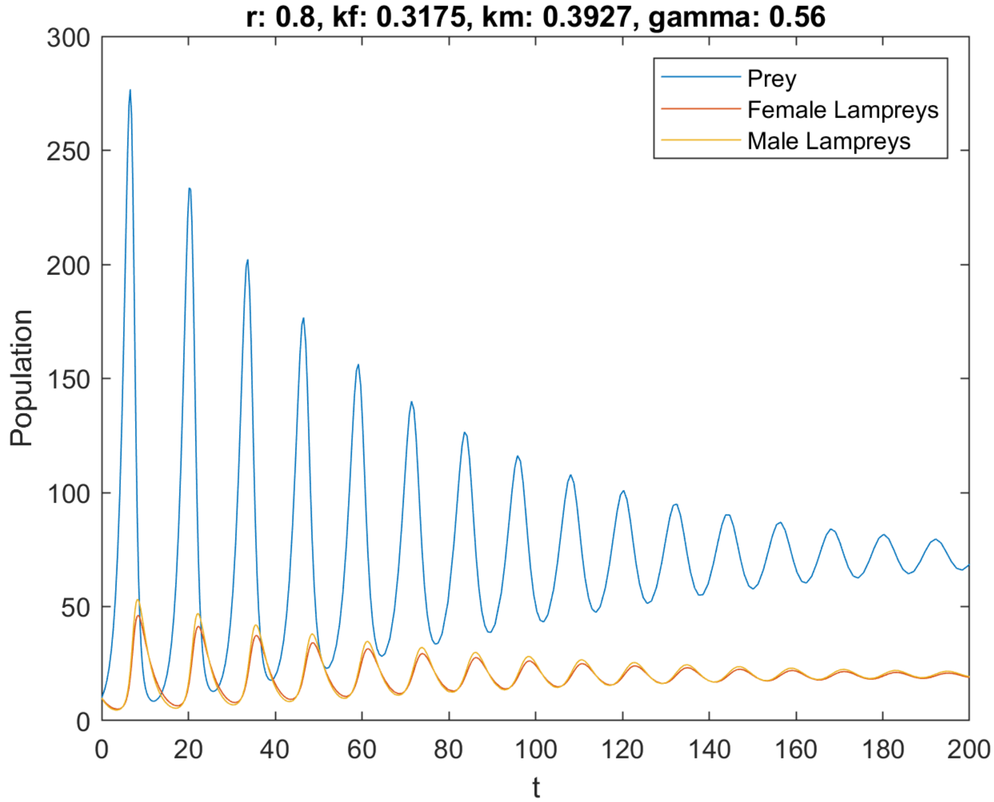

Figure 2: Repeating the solution using a low proportion (56%) of the population which is male reveals a similar result to that shown in Figure 1.

4.1 Further Exploration of the Model

In order to get a better understanding of the parameters of the model, and how those parameters affect the resulting numerical solutions for a given time frame t, we can explore cases where the parameters produce different behaviours.

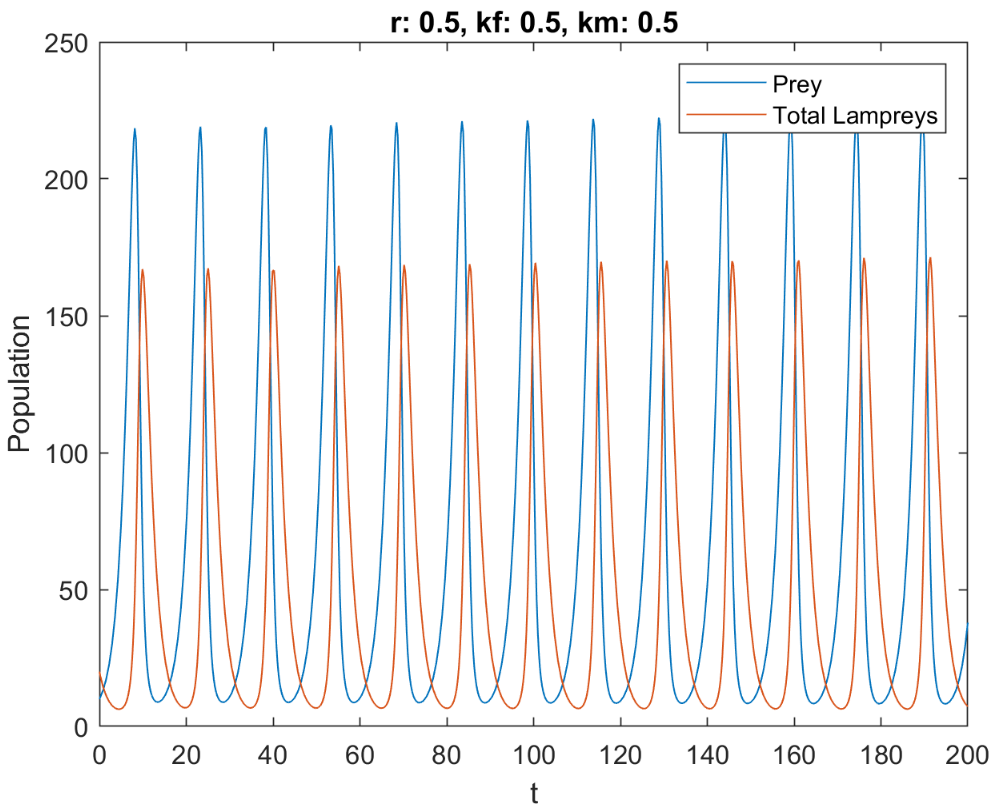

Figure 3: A graph depicting our model that shows a relation often seen in Lotka-Volterra models whereby a spike in predator population follows a spike in prey population due to the nature of predation. This was calculated using a γ of 0.618.

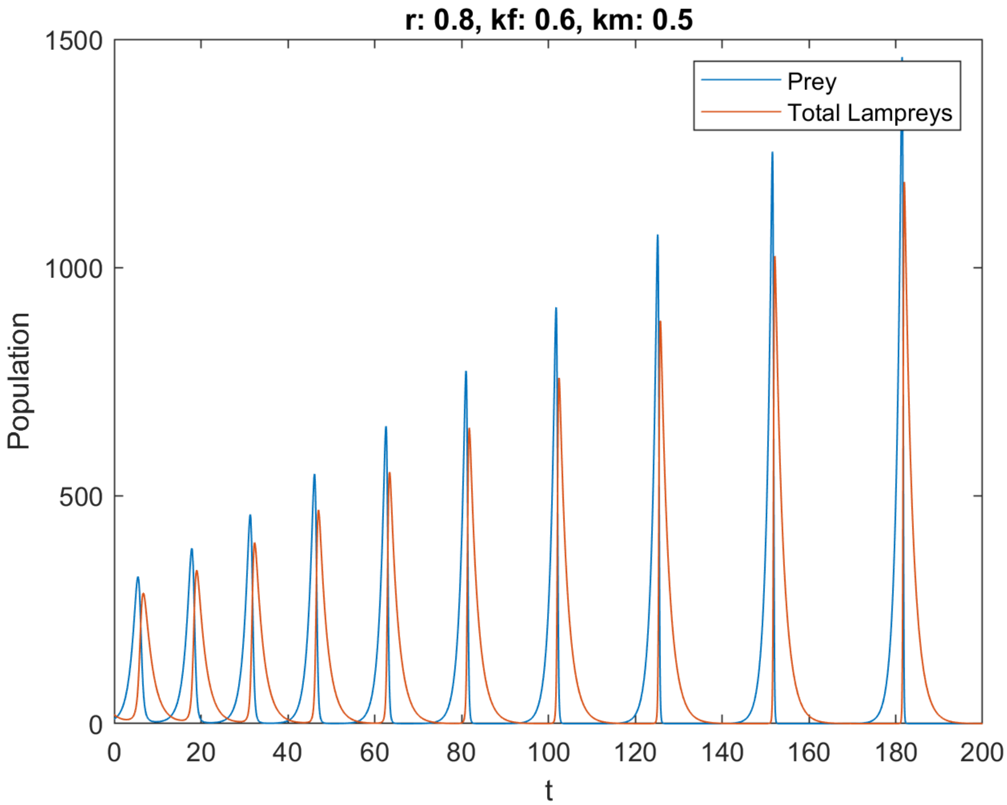

Figure 4: This graph depicts an instance where the total population of prey and lampreys is unbounded and increasing. This can be explained due the the death rate of females being higher than that of males meaning that the lamprey population takes longer to recover since their recovery is based entirely on the number of females, so prey is enabled to grow over time. Again this is using a γ of 0.618.

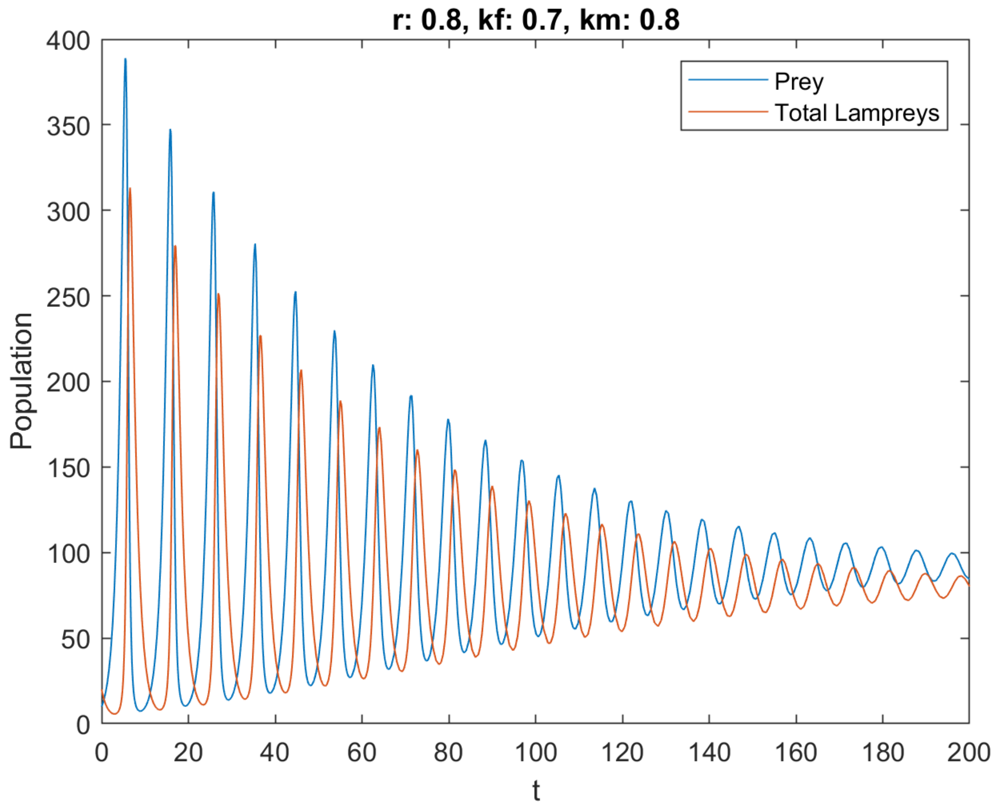

Figure 5: This graph depicts a special case that our model initially sought to capture. This is the case where the death rate of males is higher than that of females. Using a γ of 0.618 means the environmental conditions create a bias towards male offspring. It is due to this that the prey population shrinks over multiple cycles since over-consumption by male lampreys does not produce offspring. Ultimately, the population of lampreys and prey levels off creating much less dramatic fluctuations in both species populations.

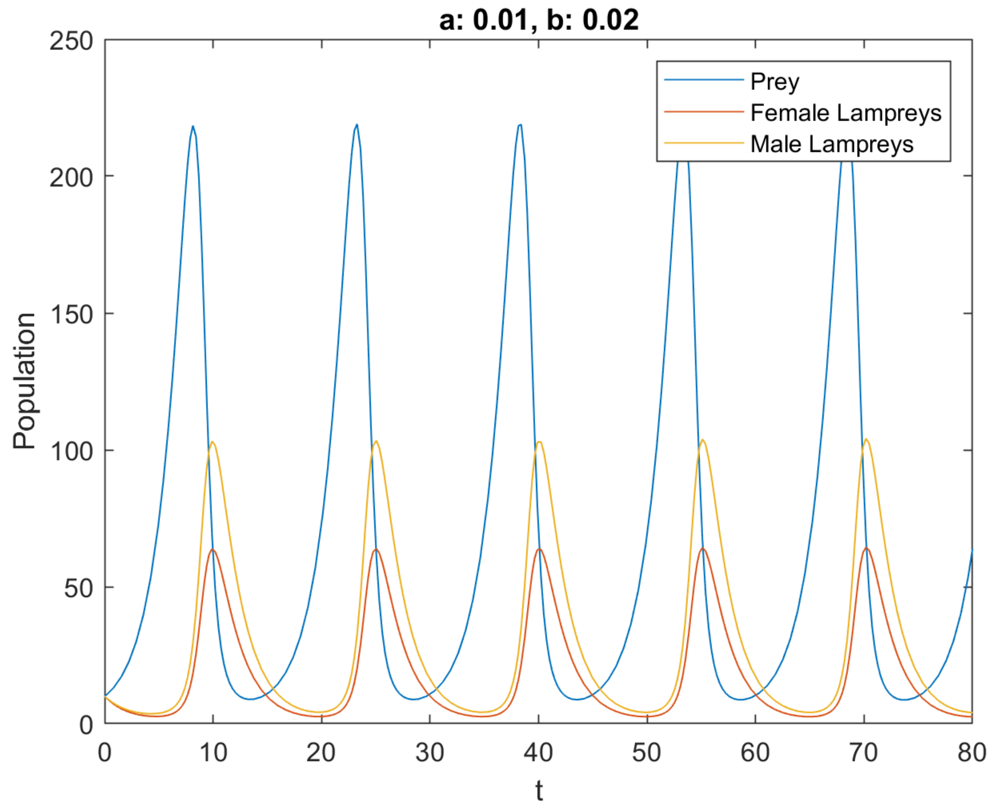

Figure 6: Using a γ of 0.618 and values for a and b which are 0.01 and 0.02 respectively, the resulting graph displays the relationship between lamprey and prey while showing the respective male and female lamprey populations.

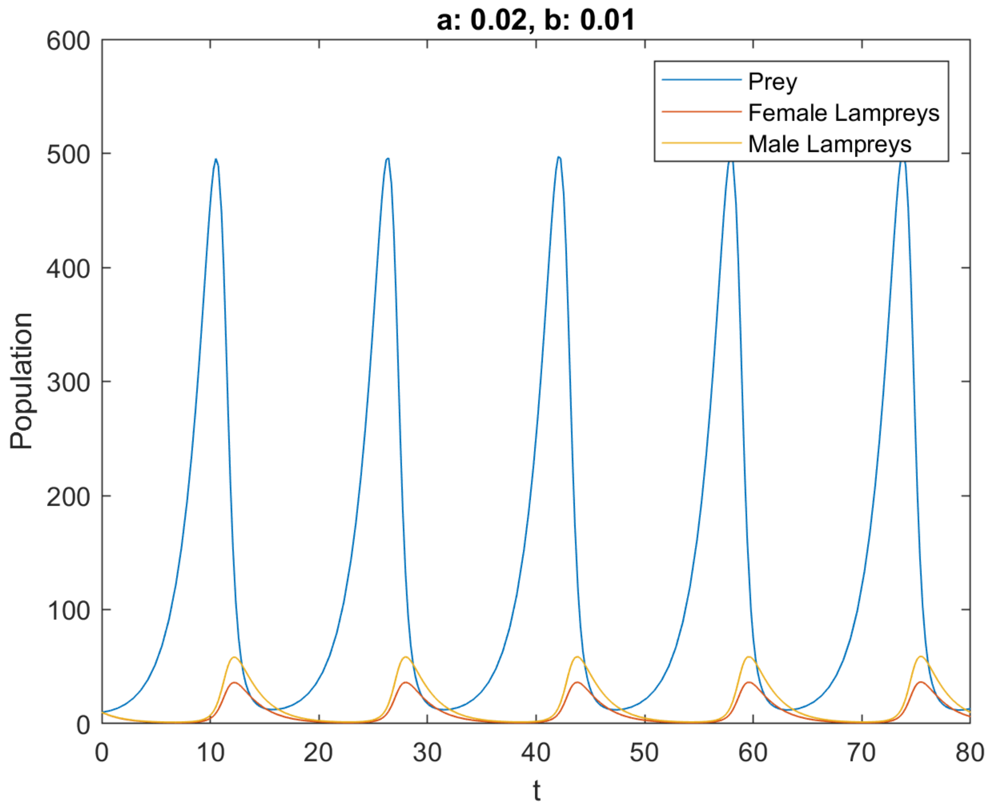

Figure 7: Again using a γ of 0.618, but now $a = 0.2$ and $b = 0.1$, the resulting graph shows that a higher birth rate for prey and a lower death rate for lampreys counter-intuitively results in a lower spike for lampreys. However, this is to be expected as the interaction between prey and lamprey is less likely to result in offspring due to the lower value of b. Ultimately, while it may seem like a special case, this case is actually evidence of the flexibility of our model since it models expected ecological behaviour— i.e. it is less likely for lamprey to produce offspring from consuming prey than it is for prey to reproduce.

Ultimately, the results provided show comparisons of many different possible behaviors that emerge from the same model. The model is able to capture behaviors that are often seen in traditional Lotka-Volterra models, while giving parameters to new behavior in the form of environmental sex differentiation in a species where few males are required to fertilize many eggs. Ultimately, stable behavior is observed in the long term for models with $k_m > k_f$. This model provides insight into the benefits to ESD since in some instances— including that modeled using experimental parameters; see Figures 1 or 2— the population is able to reach a stable equilibrium without suffering major losses due to food scarcity. Additionally, this has the same effect on the prey population affected by the predator species with ESD.

5 Conclusions

A lamprey is an ancient fish with a serpentine-like body lacking any jaw, scales, bones, or paired fins.(5) They vary in size greatly from region to region and species to species with some being as small as 200 mm and others as long as 600 mm. They have cartilaginous skeletons, one nostril between their two eyes, and several pairs of gills along their body.(5) They have a circular mouth along the front of their body that forms an oral disc filled with horny teeth. Lampreys live throughout a wide number of regions within the world including lakes, rivers, and streams in North America and Europe. Lamprey depending on species can have a life span between 4-9 years with the average lifespan amongst species we were concerned with being 8.25 years. (3)

The population of lamprey stabilizing has an important ecological impact on the ecosystems in which they are present. As shown above, through adjusting their sex ratios lamprey are able to stabilize their population with respect to the amount of prey within the ecosystem.(7) This allows a balance to naturally be created between the predator (sea lamprey) and the prey (ex. lake trout, Atlantic salmon, etc.).(1) This allows the populations of both the lampreys and their prey to coexist within an ecosystem instead of a normal relationship that would be expected if the lamprey did not adjust their sex ratios based on environmental factors (7).

For hypothesis 1 if the lamprey did not adjust their sex ratios then the overall model shown by Figure 1 would not stabilize into the smaller peaks of populations of the present species and instead would either continue with the same magnitude of peaks throughout the model or the lamprey would increase their population too far, causing the extinction of the prey population within the ecosystem. This shows that the presence of the lamprey's ability to alter their sex ratio allows them to maintain the biodiversity of the regions they are present within by naturally ensuring that they do not overfeed on the prey species present.(7) This natural limiting factor on the lamprey population within the example also has some applications outside of a world in which only the lamprey and their prey exist within the ecosystem. For example within an ecosystem in which humans are not harvesting the fish that lamprey uses as prey for both sport and food production, then one of the only predators to a majority of those fish would be the lamprey.(8) In this way, the lamprey would be a natural mechanism to curb their prey's populations to make sure that they do not cause an ecological collapse by growing past the natural carrying capacity of their environment. This is an even more necessary factor in that the lamprey themselves have a natural system of adjusting sex ratios that allow them to make sure their own population stabilizes in turn making it so that without outside interference the lamprey are able to make sure that the whole population of the ecosystem stays within a healthy limit. For example, utilizing Lake Ontario as an example of an ecosystem with lamprey as the apex predator we would realize that the lack of lamprey within the ecosystem would cause an increase in a minimum of nine fish species for which the lamprey are the sole predator.(1) This would also cause an increase in the population of nine other fish species for which the lamprey is one of the multiple predators of. (1) The increase in the secondary consumers within the ecosystem would also provide a greater amount of prey for the tertiary consumers that the lamprey would have been the sole predator of, causing probable drastic increases within the populations of the tertiary consumers. This increase within the population of the large fish could cause negative cascading effects through the ecosystem through a possible increase in excrement released by the fish as their populations continue to increase and the possible results of unhampered competition between different fish species leading to some of the species becoming extinct within the specific ecosystem. In this way, the lack of the presence of lamprey within an ecosystem could lead to a possible decrease in overall biodiversity as well as a cascading effect of an increase in the pH value of the ecosystem along with an exaggerated need for filter feeders to be able to maintain the normal water quality that would be previously present within the ecosystem.

Similarly, since the lamprey feed off of the tertiary consumers within their food webs as apex predators, then lamprey would be providing an advantageous service to other organisms within the ecosystem by curbing the population of their predictors, which would allow them to have a greater population due to the reduction of their predators. This provides a benefit to those species that are not the favored prey of the lamprey and are the favored prey of the tertiary consumers. In other words, the lamprey population within an ecosystem helps to create a beneficial balance of species that would not have been present without its existence. The brook lamprey species provide many different benefits to the ecosystems in which they are present. These species of lamprey primarily function as filter feeders and are able to maintain the cleanliness of the ecosystems in which they are present. this allows the bodies of water that they are within to maintain the correct pH levels, turbidity, controlling nutrient values, and many other factors that help encourage other aquatic life to thrice within the ecosystem. (9) Also the brook lamprey species function as prey throughout the various ecosystems that they are a part of. (9) For example, within the ecosystems where brook lampreys are present within Portugal they are seen as prey by river otters. (6) The river otter viewing the brook lamprey as prey allows for the lamprey's presence within the ecosystem to provide a service as nutrition to another organism and is just one example of an ecosystem in which the brook lamprey and other lampreys, in general, are viewed as prey by other organisms.

One of the assumptions that we made within model 1 is that all of the eggs that are being released by the female lamprey will be able to be fertilized by the male lamprey. We believed that this assumption was reasonable due to the mating practices of the lamprey, the amount of male lamprey that would be within the population, and the overall nature of spermatogenesis.(3) The mating process of the lamprey starts once they have reached maturation and traveled up the stream or lake in which they live to a prime location to form their nests and lay their eggs.(3) One of the male lampreys begins the process of building the nest by attaching itself by its sucker to a loose gravel ground of the stream or aquatic ecosystem.(3) This then causes the male lamprey to release a mass amount of pheromones to attract other male and female lampreys to its location and have them all join together to make a nest.(3) The lampreys then build a nest deep enough for them to be able to swim inside and lay their eggs.(3) Once a female swims inside the nest, she releases all of the eggs that were inside of her body hoping that they will catch in the gravel and sand within the floor of the aquatic body.(3) Then the female will swim out of the nest and proceed to die within the next one to two weeks.(3) Afterward, once multiple females have released their eggs within the nest the males start to travel within the nest and once inside the males release the spermatozoon to hopefully fertilize the oocytes that the females have left within the nest previously.(3) After the males have released all of the spermatozoons they then swim away and die within one to two months.(3) If all went right, the eggs would be fertilized by the males and would be able to become new larvae within one to four months.(3) This process, which utilizes one nest of multiple females' eggs, allows for the assumption that all of the eggs are going to be fertilized due to the presence of males and females within one of the nests for the lamprey.(3) The second reason why we believed that this assumption would hold up well within the model is because the amount of male lampreys are the majority of the population.(3) When the lampreys decide their sex there is a bias towards the lamprey ending up as male and this fact allows there to be a greater male population of lamprey than female within the overarching ecosystem. With a greater presence of male lamprey to female lamprey, the amount of male lamprey will be able to fertilize all of the eggs produced by the female lamprey causing us to make the logical assumption that all of the eggs that are being produced are being fertilized. (3)

Currently, lampreys are receiving a lot of negative attention from conservation agencies, to limit or curb their spread and population some of which is taking place in regions where the lamprey is a natural part of the ecosystem. This can be seen through a variety of methods such as building small obstacles within streams and rivers that the lamprey typically navigates to stop them from traveling down certain paths, while others put a lampricide within the ecosystems in which they are present causing the deaths of many lamprey to occur.(5) The use of prevention methods against the lamprey can have many far-reaching negative side effects both on the lamprey and on the ecosystems that it is present within. Some of these side effects are an extra addition of chemicals within the ecosystem that not only harm the lamprey but can cause severe harm to other species that are present within the ecosystem. This can also cause a change within the lamprey population regulation of their sex ratios as well.(4) The lampricide can cause genetic mutation within the lamprey that inadvertently can change the lamprey's sex from lamprey that were originally male to female lamprey and those that were originally female into male lamprey.(5) This change in the sex of the lamprey can lead to a breakdown of their defined sex ratios that allow the lamprey to maintain the populations of the ecosystem they are present within. This could then have an undesired consequence of causing a possible increase in the lamprey population beyond where it would typically move to. This in turn would have cascading consequences throughout the ecosystem as the lamprey would cause drastic decreases in the amount of prey available while also decreasing the amount of fish the farmers could harvest. Since there would be fewer fish for the farmers to harvest the overall reasoning behind the lampricide would become useless since the population of fish that the fishermen are trying to harvest would continue to be decreased by the treatment plan being used to control the lamprey.(5)

Our hypothesis 2 has been proven to be inaccurate because we have now learned that the proportion of the lamprey that differentiates into being female lamprey is based on the growth time of the larva and environmental factors. (7) This is shown by the proportion of female lamprey being correlated to the environmental surroundings and not a reaction of the lamprey themselves to have more eggs within their environment. (7) So we no longer believe that our hypothesis 2 is correct and instead believe that the past literature about the sex ratios of lamprey helps to explain that the need for having a higher proportion of male lamprey in society is to stem the overall growth of the lamprey instead of from the lamprey's perceptions of what their species needs to continue growing.

6 Appendix

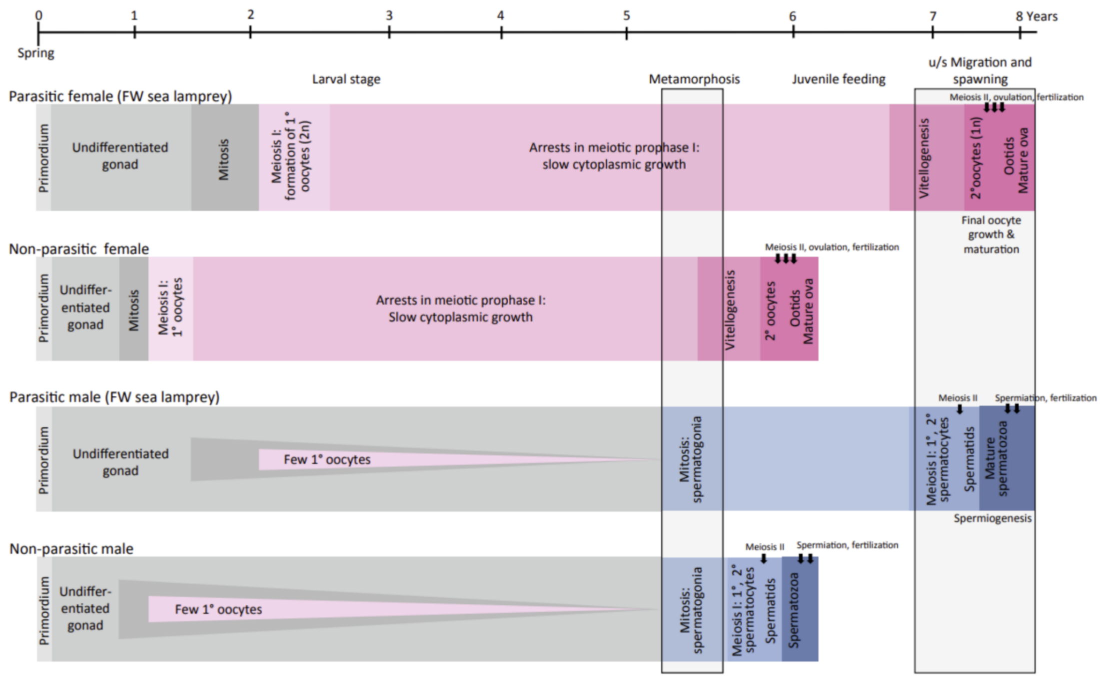

Figure 8: Lamprey development From: (3)

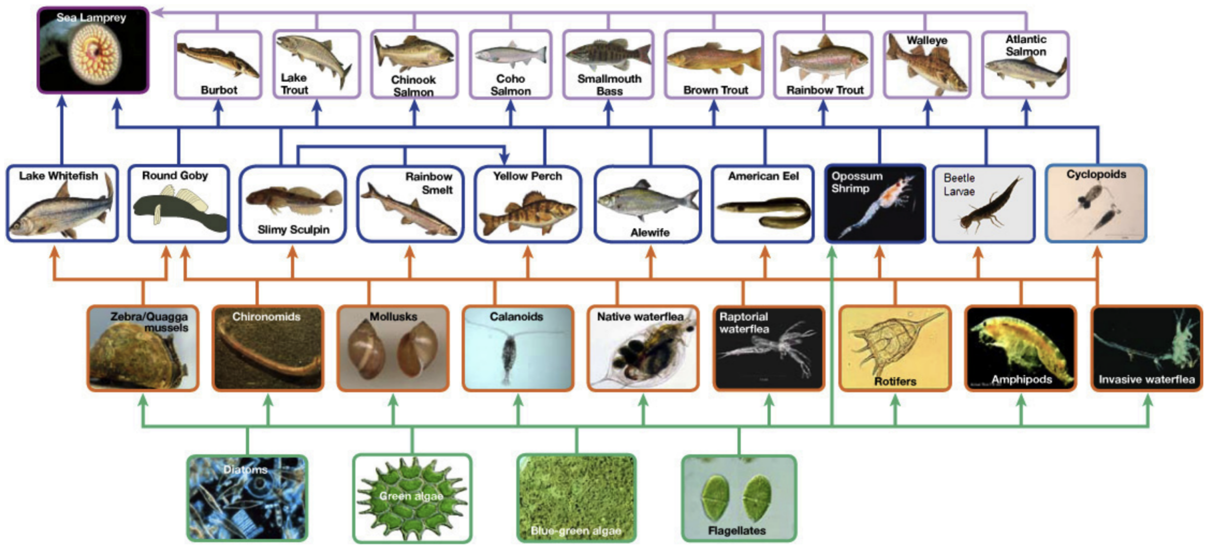

Figure 9: Food web of Lake Ontario From: (1)

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