

Adaptive sex ratio changes in sea lampreys: ecological implications and population dynamics

Summary

Some species deviate from an even sex ratio, exhibiting **adaptive sex changes**. For lampreys, for example, the speed of development during the larval stage determines their sex. To understand the **advantages and disadvantages** of a species' ability to change its sex ratio based on **resource availability**, we developed a new model that measures the impact of sex changes on itself and its ecosystem.

First, in order to explore the advantages and disadvantages of sex ratio change, we establish Volterra model without considering sex ratio to compare with sex ratio model. Based on the original **Volterra model**, we modified its endowment **growth rate** term, **predation rate** term, and added the **effect of sex ratio** on them. We considered predation, environmental carrying capacity, and other factors. The impact on the ecosystem was measured by the change in the population size of the species. We find that changes in lampreys sex ratio **increase the frequency** and **decrease the magnitude of cyclical fluctuations** in species biomass.

Secondly, in order to investigate the advantages and disadvantages of the change of sex ratio on the lamprey, we built a Volterra model without considering the effect of sex ratio. The advantages and disadvantages were analyzed by comparing the trend of population development under **different situations** and the same initial conditions. Based on our knowledge of the actual situation, the different situations include: **fast population growth, low environmental carrying capacity, and insufficient initial resources**. Analyzing the results of the different situations, we believe that the change in sex ratio allows lampreys to **increase their adaptability** to the environment and **optimize their survival**. At the same time, however, they are not very competitive in species competition, and overly adaptive sex ratio changes may lead to **population instability**.

Third, in order to explore the impacts on the ecosystem, we developed a **multispecies** model. Based on the logistic model, we considered the effects of **mutualistic symbiosis, competition and predatory** relationships among species. For quantitative studies, we formulated total biomass, total biomass coefficient of variation and SW to evaluate the **stability of the ecosystem**. The experimental results showed that lamprey with adaptive sex ratio variation resulted in more frequent biomass fluctuations and smaller standard deviation of fluctuations in the ecosystem. Therefore, we believe that the stability of the **ecosystem benefited** from the sex ratio variation of lamprey.

Fourth, we followed the multispecies model, controlling for the presence and absence of lamprey in the multispecies model modeled separately in accordance with the principle of **controlling for variables**, and visualized the results for comparison. The final results show that ecosystems with varying sex ratios in lamprey populations can provide advantages for species such as **parasitoids**.

Finally, we analyze the sensitivity of the model through the relationship between the **stability of the model system** and the change of specific parameters. We find that our model is **interpretable** and **sensitive** to initial parameters. The advantages and disadvantages of the model are analyzed.

Keywords: Lotka-Volterra model, biodiversity, Parasites, Sex ratio, control variable

Contents

1	Introduction	3
1.1	Problem Background	3
1.2	Restatement of the Problem	3
1.3	Our Work	4
2	Assumptions and Explanations	4
3	Notations	5
4	Model Establishment and Solution	6
4.1	Volterra Modeling Based on Prey-Predator	6
4.1.1	The establishment of model	6
4.1.2	Model-based prediction	7
4.2	Further Model Analysis	9
4.2.1	Advantages and disadvantages associated with adjustments to the adaptive sex ratio	9
4.3	Expanding the model to include many species	12
4.4	Modified logistic modeling	12
4.4.1	Quantitative prediction using adjusted models	13
4.5	Explore the advantages offered to other species.	16
5	Sensitivity Analysis and Stability Analysis	18
5.1	Sensitivity analysis of the model for the producers' natural growth rate .	18
5.2	Model sensitivity analysis of the initial population size of the lamprey .	19
5.3	Model sensitivity analysis of the environmental carrying capacity of lam- prey populations	19
6	Strengths and Weaknesses	20
6.1	Strengths	20
6.2	Weaknesses	20
References		21

1 Introduction

1.1 Problem Background

In biology, adaptive sex ratio variation is a topic of significant interest. The pace of development of the larval stage, which is impacted by the availability of food, determines the sex ratio of lamprey. It also has distinct functions in various ecosystems; in the Great Lakes , it is acknowledged as a parasite with major effects on the ecology and as a food source in other places. Biotic and abiotic factors are thought to contribute to sex determination in lamprey species.^[1] The survival and procreation of the lamprey species as well as the ecosystem may be impacted by this fluctuation in the sex ratio based on resources. As a result, it is crucial to examine how changes in the lamprey sex ratio affect the ecology in relation to resource availability.



Figure 1: Worldwide distribution of lamprey.(The more red dots, the more dense the distribution.)

1.2 Restatement of the Problem

- Establish a mathematical model to forecast how changes in lamprey populations and sex ratios would affect the environment.
- Explore the features of the lamprey population and determine if changes in sex ratios have made it more adaptable or unstable.
- By expanding the model, one may create an ecological stability index and investigate the effects of changes in the lamprey sex ratio on it.
- Examine how changes in the sex ratio of lamprey interact with other biological populations to see whether there will be benefits for other species.

1.3 Our Work

We gradually build three mathematical models in accordance with the requirements. As demonstrated below.

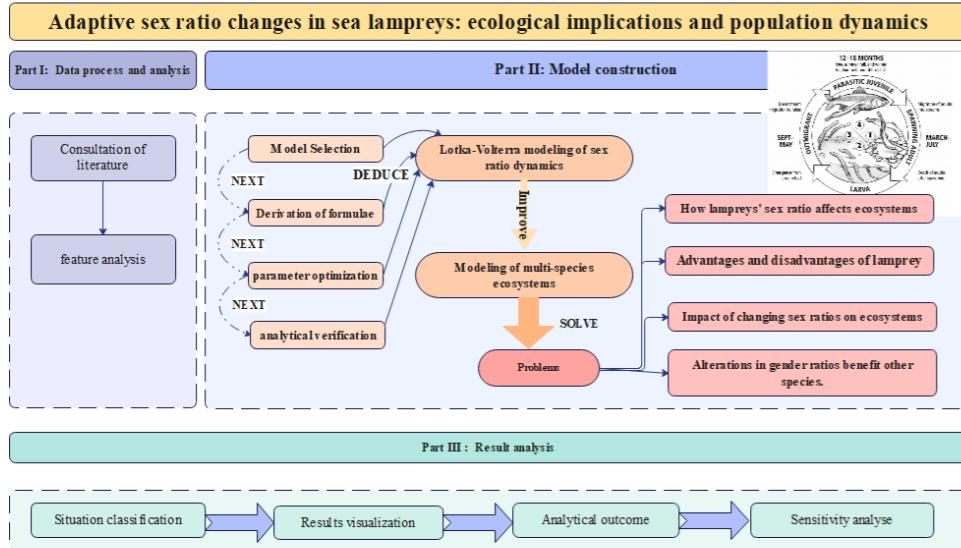


Figure 2: Our work

2 Assumptions and Explanations

Considering the complexity of the actual problem, the following assumptions are proposed for simplification, each of which is justifiable:

Assumption 1: The process of gender decision-making and gender reversal is combined without distinction between unstable gender decisions and genuine reversals.

Justification: Environmental factors impact sex determination up until the parasitism stage.^[2]

Assumption 2: Larval sex determination is determined by environmental factors alone, regardless of other factors.

Justification: Biotic and abiotic factors are thought to contribute to sex determination in lamprey species, such as larval density, temperature, pH, and when physiological resources are diverted into somatic growth, although mechanisms are not well established.^[1]

Assumption 3: Absence of anthropogenic interventions such as pesticides, substantial disruption of river systems by manmade constructions, loss of vertical connection, suppression of migration.

Justification: Because this model focuses on the relationships between natural ecosystems and lamprey populations, we should reduce the amount of human involvement.

Assumption 4: Competitive or mutually beneficial relationships between species in the community remain constant.

Justification: It is believed that in the short term, biological interactions remain unchanged.

Assumption 5: Species do not mutate, populations and the resources they control change over time.

Justification: In this model, resources and the resources they control are variables.

Assumption 6: The coefficient of growth rate on sex is fixed and does not vary over time or space.

Justification: According to ^[1], the mechanisms are not well established, Temporarily assumed to be fixed.

Assumption 7: Male and female mortality rates are affected by the same factors.

Justification: These characteristics are not taken into account since higher energy requirements during gonadal development have a lower influence on female mortality.

Assumption 8: Considering that a parasite's activity is considered to be a form of longer-lasting and less lethal predation.

Justification: It is believed that most parasites absorb resources from their hosts and spread infections, which raises the likelihood of host mortality over time.

Assumption 9: When faced with the parasitic activity of the parasite, lamprey of various sexes exhibit the identical behaviors, i.e., the same markers of lethality and predation rate.

Justification: Parasite sex selection on lamprey is not currently studied, and to simplify the model, the same is assumed here.

Assumption 10: Considering that no creature in the environment preys on lamprey, other from parasitism by parasites, and that human hunting results from.

Justification: Only a very tiny percentage of lamprey overall mortality is caused by predator-related causes.

Additional assumptions are made to simplify analysis for individual sections. These assumptions will be discussed at the appropriate locations.

3 Notations

Some important mathematical notations used in this paper are listed in Table 1.

4 Model Establishment and Solution

4.1 Volterra Modeling Based on Prey-Predator

4.1.1 The establishment of model

In the natural world, predation is a means of survival that involves both constraints and dependence. For example, population A depends on an abundance of natural resources to grow, while population B depends on predation on population A to survive.

Table 1: Notations used in this paper

Symbol	Description
k_1	Self-growth rate of preys
k_2	Negative self-growth rate of predators
b	The capacity of the predator to consume prey
c	The bait's capacity to nourish the predator
x	Population size of the prey
y	Population size of the predator
Y_1	Population size of the predator
Y_2	Population size of the prey
r_1	Endogenous growth rate of predator
r_2	Endogenous growth rate of and prey
K_1	Predators' environmental carrying capacities
K_2	Prey's environmental carrying capacities

*There are some variables that are not listed here and will be discussed in detail in each section.

In terms of ecology, this is known as the bait-predator system, or P-P system, wherein population A is the predator and population B is the prey.

When only the availability of food resources is taken into account, there are no predators, preys net relative growth rate is a normal number. While there are no preys, predators net relative growth rate is a negative constant, and the likelihood of two species coming into contact is determined by the product of their populations, as represented by Equation 1:

$$\begin{cases} \frac{dx}{dt} = k_1x - bxy = x(k_1 - by) \\ \frac{dy}{dt} = -k_2y + cxy = y(-k_2 + cx) \end{cases} \quad (1)$$

Without considering sex differences, species are influenced by practical factors such as environmental carrying capacity, and the Volterra prey-predator system is modeled as Equation 2:

$$\begin{cases} \frac{dY_1}{dt} = r_1Y_1 \left(1 - \frac{Y_1 + \alpha_{12}Y_2}{K_1}\right) - \beta_{12}Y_1Y_2 \\ \frac{dY_2}{dt} = r_2Y_2 \left(1 - \frac{Y_2 + \alpha_{21}Y_1}{K_2}\right) - \beta_{21}Y_1Y_2 \end{cases} \quad (2)$$

Because lamprey has a unique pattern of sex change. Sex determination in sea lamprey is directly influenced by larval growth rate.^[2] Thus, it is necessary to take the gender ratio's effects into account.

Define the sex ratio R_σ as the ratio of the number of males to the total population:

$$R_\sigma = \frac{\text{male_number}}{\text{female_number} + \text{male_number}} \quad (3)$$

Define $R(A)$ as the change in sex determination ratio with respect to the availability of food resources, A, as shown in the following equation 4. When food resources

are scarce, the proportion of males increases; when food resources are plentiful, the proportion of males and females approaches equilibrium.

$$R(A) = \alpha \ln(A + \beta) + \gamma \quad (4)$$

The amount of food resource A is related to the ratio of the number of prey groups to the number of predator groups:

$$A = \frac{P}{\sum Y_j} \quad (5)$$

The following Equation 6 represents the separate modeling of the male and female lampreys after the aforementioned elements were combined:

$$\begin{cases} \frac{dY_1}{dT} = \left(1 - \frac{Y_1 + Y_2}{k_1}\right) \left[\sigma \frac{Y_1 Y_2}{Y_1 + Y_2} \cdot R_a - \text{death_rate} \cdot Y_1 \right] + m \cdot R_a \\ \frac{dY_2}{dT} = \left(1 - \frac{Y_1 + Y_2}{k_1}\right) \left[\sigma \frac{Y_1 Y_2}{(Y_1 + Y_2)^2} (Y_1 + Y_2) (1 - R_a) - \text{death_rate} \cdot Y_2 \right] + m \cdot (1 - R_a) \\ \frac{dY_3}{dT} = \text{prey_add} \cdot Y_3 \left(1 - \frac{Y_3}{k_2}\right) - \text{preyed_rate} \cdot Y_3 (Y_1 + Y_2) \\ R_a = -0.1514 \ln \left(\frac{Y_3}{Y_1 + Y_2} + 0.4585 \right) + 0.7569 \\ m = \text{preyed_rate} (\text{male_prate} \cdot Y_1 + \text{female_prate} \cdot Y_2) \cdot Y_3 \end{cases} \quad (6)$$

The three numbers are Y_1 , Y_2 , and Y_3 , which represent the number of male, female, and prey items, respectively. Modeling the male and female sexes separately, which make it possible to make a lag in the effect of sex changes due to species availability on the true sex ratio of a population.

4.1.2 Model-based prediction

This article uses a time step of 0.5 and a total duration of 1000 to model ecological development. Furthermore, there are no natural adversaries for lampreys, which are an invasive foreign species in the Great Lakes region, according to ^[2]. Here, to make things easier, think of two species in the community: sea lampreys and the bait that they eat. Larvae remain burrowed for 3–5 years on average, and filter-feed on seston, diatoms, and biofilm.^[3] Sex ratios are determined in a process influenced by predation.

The table presents a reasonable approximation of the quantitative values of the other coefficients in the differential equation model. Field surveys and published works can provide specific values.

Variations in the number of sea lampreys, availability of food resources and gender ratio can be inferred from Figure 3, Figure 4.

The populations of prey and lampreys in Figure. 3 fluctuate periodically before steadily stabilizing. Under initial conditions, there is a dramatic reduction in the amount of prey, which corresponds to an increase in lamprey numbers due to the absence of natural adversaries. Because there are less food supplies available to them, lamprey populations drop with a lag rather than an instantaneous response when the prey population declines. This is due to the fact that an increase in prey does not immediately result in the predator starving to death, which would imply an abrupt and substantial

Table 2: Values of the Model Assumptions Parameters

Parameters	Initial Value
Birth rate(birth_rate)	0.15
Mortality rate(death_rate)	0.20
Male predation efficiency(male_prate)	0.4
Female predation efficiency(female_rate)	0.38
Probability of prey being attacked by predators (preyed_rate)	0.0006
Prey natural increase rate(prey_add)	0.1
Lampreys' environmental carrying capacities(k1)	5000
Prey's environmental carrying capacities(k2)	5000
Initial male count(x_0_male)	50
Initial female count(x_0_female)	50
Initial prey count(x_0_prey)	500
Debugging parameters(σ)	$0.56 \leq \sigma \leq 0.64$

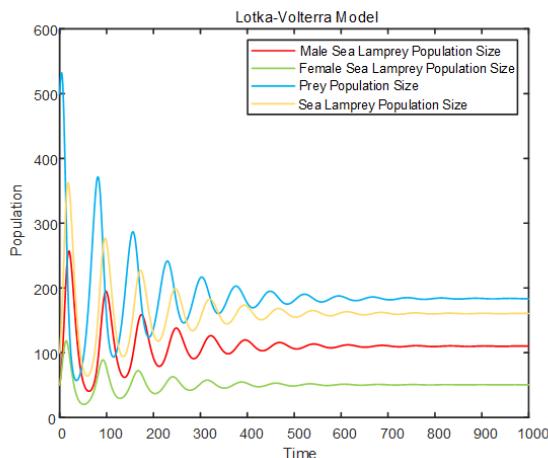


Figure 3: Lotka-Volterra Model

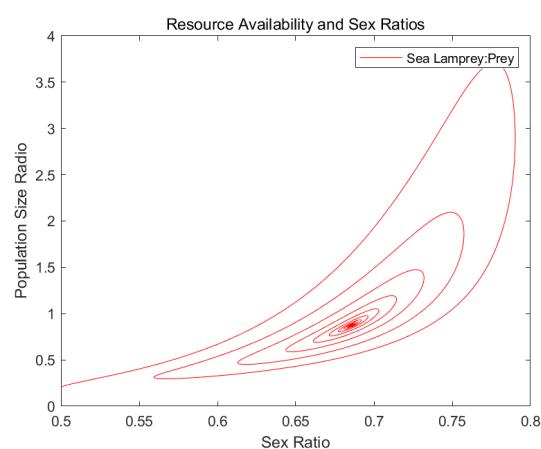


Figure 4: Resource Availability and Sex Ratios

rise in mortality. Rather, an increase in prey takes time for the number of lampreys to grow. Ultimately, cyclical fluctuations and population stabilization result from these limitations and interdependence.

Figure 4 depicts how the sex ratio of lampreys and food supplies change throughout time. When food resources are abundant, the sex ratio is close to the even sex ratio of 0.5, whereas when food resources are scarce, the proportion of males increases significantly. Such a variation is consistent with the actual situation.

These alterations can be explained, for instance, by the possibility that in cases of growth limitation, female mortality may be greater because of the increased energy requirements during gonadal development. It's possible that men have decreased their total need for food supplies. Males may use resources more efficiently than females when it comes to predation, meaning that less food resources are needed for development in the male than in the female.

4.2 Further Model Analysis

4.2.1 Advantages and disadvantages associated with adjustments to the adaptive sex ratio

Consider enhancing the Volterra predator-prey system model by excluding the impact of sex ratio on predation efficiency and reproductive success, i.e., there is no adaptive sex ratio change, in order to investigate the benefits and drawbacks of sex ratio changes for lampreys.

Taking the gender difference into account, see the previously stated Equation(4) .

The following Equation(5), which disregards gender differences, is as followed:

$$\begin{cases} \frac{dx_1}{dt} = \left(1 - \frac{x_1}{k_1}\right) \cdot x_1 (0.25\sigma - \text{death_rate}) + 0.5n \cdot \text{preyed_rate} \cdot x_1 \cdot x_2 \\ \frac{dx_2}{dt} = \left(1 - \frac{x_2}{k_2}\right) \text{prey_add}x_2 - \text{preyed_rate} \cdot x_1 \cdot x_2 \\ n = \text{male_prate} + \text{female_prate} \end{cases} \quad (7)$$

Under the same initial conditions, assuming that there exists a species with identical habits to lampreys except for variations in adaptive sex ratios, let the two species compare population trends. Regardless of interspecific competition, we grow them individually. In order to derive findings for the study of strengths and weaknesses, the trajectories of the two species were compared in three scenarios: excessive population growth rate due to high predation rate, poor environmental carrying capacity of the population, and insufficient beginning food supplies.

In the case of low environmental carrying capacity of populations:

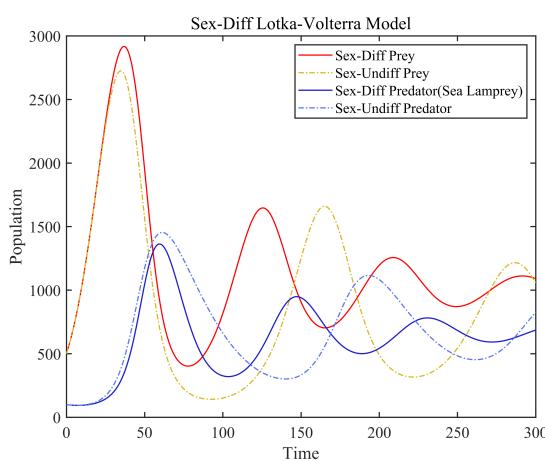


Figure 5: sex diff(low environmental capacity)

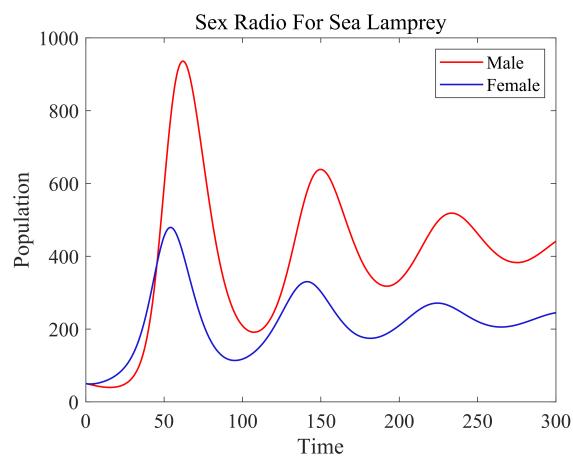


Figure 6: sex diff ratio

According to the experimental visualization results,figure 5,figure 6, the species biomass showed periodic fluctuations, the fluctuation amplitude gradually decreased during the fluctuation process, and the species size gradually converged to a stable value. lamprey fluctuation period was shorter, and the convergence speed was faster.

At high predation rates:

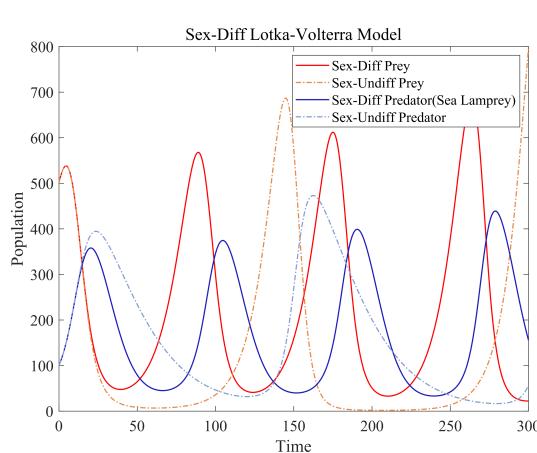


Figure 7: sex diff(high predation rate)

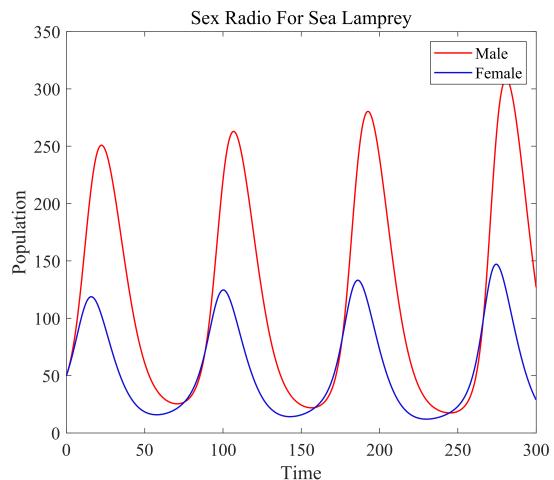


Figure 8: sex diff ratio

The figure 7, figure 8 makes it clear that the population of the lamprey control species has been growing for a longer time period and on a greater scale, which has caused the prey numbers to drop to a level from which it is impossible to recover. The curve along the model's axis represents a species that is in danger of going extinct, which in turn causes the extinction of the species that feeds on it in a genuine ecosystem with complicated environmental conditions.

When food is scarce, lamprey with adaptive sex ratio modifications have unbalanced sex ratios and decreased reproductive capacity, which limits the rate and frequency of population growth. The ecosystem was able to establish a shorter iteration cycle because of the lag in sex ratio adjustment, which led lamprey populations to decline due to the poor reproductive capacity from the imbalance and the lack of food. This, in turn, expedited the recovery and growth of prey populations.

This is particularly true in settings with high rates of predation, excessively plentiful beginning resources, or excessively rapid natural food increase. Since the species in question is vulnerable to both overpopulation and ecological collapse, the lamprey's sex change characteristic effectively prevents overpopulation. Although extinction is an extreme scenario, this feature is typically accompanied by instability and significant cyclical variations in population size.

In case of insufficient initial food resources, the result are as followed Figures:

The figure 9, figure 10 make it clear that the lamprey's chances of survival are reduced when there are limited early feeding sources. We think that the reason might be that the high percentage of males in an environment with limited resources causes the lamprey to have a reduced reproductive capability and a higher predation efficiency, which prevents the population from growing and speeds up its own decline.

From these three comparison findings, several inferences concerning the influence on ecosystems may be made:

Effect of species diversity: In an ecosystem, diversity refers to the quantity and variety of species present. Increasing variety lessens the effect of outside disruptions and boosts system stability. According to ^[4], in general, a greater diversity should:

- (1). increase community temporal stability;

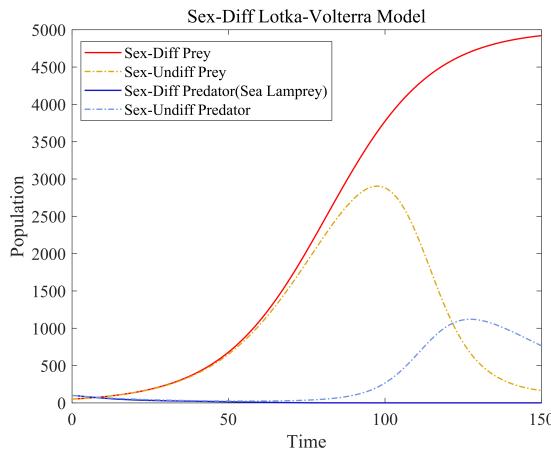


Figure 9: sex diff(low initial food)

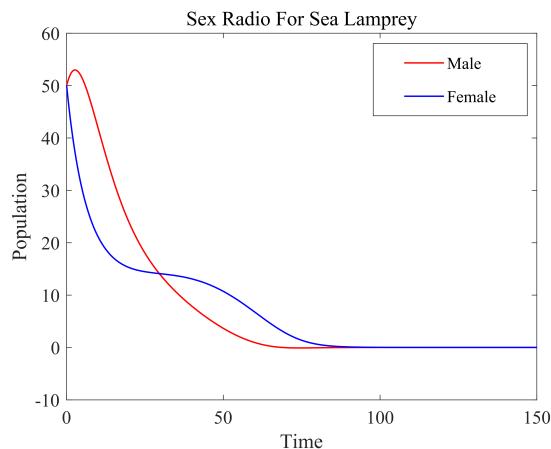


Figure 10: sex diff ratio

- (2). decrease population temporal stability;
- (3). increase community standing crop and/or productivity;
- (4). decrease amounts of unconsumed limiting resources;
- (5). increase ecosystem stores of limiting nutrients by decreasing loss;
- (6). decrease invasions by exotic species.

Possible **advantages** of adaptive sex ratio changes:

- (1). Adaptation to environmental changes: Lampreys are able to enhance their ability to adapt and maximize their survival in response to changes in their surroundings, such as notable variations in food sources. This may also be the key to their ability to live and procreate for hundreds of millions of years.
- (2). Minimizing intraspecific battles means lowering the quantity of resources required for survival and facilitating access to these resources for each individual. Improved effectiveness in the use of available resources.
- (3). Preserving genetic variety and population stability: assisting in the long-term development of populations as well as the optimization of population dynamics.

Possible **disadvantages** of adaptive sex ratio changes:

- (1). Population stability: Population imbalance or even extinction can result from excessive adaptive sex ratio shifts.
- (2). Instability of the population's natural balance: notable shifts in the sex ratio have an impact on the population's natural balance. For example, a low number of females causes a sharp drop in reproduction rates, which undermines stability.
- (3). Population biomass expansion is limited, and species competition is not very fierce.

4.3 Expanding the model to include many species

In this part, we built a model that considers resource utilization and interactions between many species, which we used to simulate changes in species populations over time.

4.4 Modified logistic modeling

First, we examine the best-case scenario, in which species sizes are infinitely expandable given an infinite amount of room and other resources.

$$\frac{dN}{dt} = r \cdot N \quad (8)$$

The following equation is the logistic model for the optimum population increase of a single species under real-world circumstances, when the ecosystem has a maximum carrying capacity:

$$\begin{cases} \frac{dx_i}{dt} = r_i x_i \left(1 - \frac{x_i}{N_i}\right) \\ r_i = \text{birth_rate} - \text{death_rate} \end{cases} \quad (9)$$

N_i indicates the maximum number of a single species at a particular environmental capacity, x_i indicates the number of a single species i , and r_i indicates the average growth rate of each individual under optimal conditions in the equation above.

Food availability affects larval growth rate, and in turn sea lampreys affect sex ratio. When considering the predation relationship, it is necessary to introduce a correction value, as in Equation.

$$\frac{dx_i}{dt} = r_i x_i \left(1 - \frac{x_i}{K_i}\right) - \sum_{j \neq i} \alpha_{ij} c_{ij} x_i x_j \quad (10)$$

The intensity of predation between x_i and x_j is denoted by α_{ij} . $\alpha_{ij} = -\alpha_{ji}$. c_{ij} denotes the conversion rate of the predator to the food resource, and c_{ji} denotes the predation (parasitism) lethality of the prey. Together, the two coefficients indicate the predation intensity of the population. And when $\alpha_{ij} > 0$, predation causes a rise in the rate of species growth.

Sea lamprey larvae are more prone to carry and spread parasites due to their eating patterns and adult parasitic behavior^[2]. Species diversity is a crucial indicator of ecosystem health, and when taking interspecific connections into account, a correction value must be included.

$$\frac{dx_i}{dt} = r_i x_i \left(1 - \frac{x_i}{K_i} - \sum_j \sigma_{ij} \frac{x_j}{K_j}\right) - \sum_{j \neq i} \alpha_{ij} c_{ij} x_i x_j \quad (11)$$

where the index of the interspecies link between X_i and X_j is indicated by σ_{ij} . A mutualistic connection is described when $\sigma_{ij} > 0$, and the population of a single species will expand more quickly. Additionally, the interspecies interaction is competitive when $\sigma_{ij} < 0$, and species growth rates will drop or even turn negative.

We propose that the degree of predation is correlated with the sex ratio and that behavioral differences between male and females may influence the predators' effectiveness. Furthermore, resource usage in predation may differ between males and females, and variations in sex ratios allow individuals to adapt resource utilization to suit their own developmental requirements in response to varying environmental conditions.

The following equation shows the link between the sex ratio S and the index of predation intensity among species:

$$\alpha_{ij}(s_i, s_j) = \alpha_0 + \frac{\beta}{1 + e^{-\gamma(s_i - s_j)}} \quad (12)$$

Growth rate and reproduction are impacted by the sex ratio. After depositing eggs, mature sea lampreys perish. The following equation shows the link between the sex ratio and growth rate:

$$S(R, A) = \alpha R(1 - R) \quad (13)$$

S denotes the reproductive success rate and α is the coefficient. The amount of food resource A is related to the ratio of prey to predator numbers. It is assumed that all non-producer populations are driven by predation and therefore have a constant natural growth rate < 0 .

$$A = \frac{P}{\sum Y_j} \quad (14)$$

For a given species X_i , P denotes the amount of all food, and Y_j denotes the number of species competing with X_i for food (including the number of X_i)

The aforementioned analysis may be used to create differential equations that describe the number of species and their interactions, as well as to effectively design mathematical models.

4.4.1 Quantitative prediction using adjusted models

We simulated the evolution of ecosystems including producer, competitor, and parasite populations in order to investigate the impacts on ecosystems qualitatively. Changes in the quantity of male and female lamprey were taken into consideration independently. After then, we looked at how the species' biomass changed in this environment. We extended the simulation period to make the model more reflective of long-term changes, and the outcomes are displayed below.

Competitor 1 is a different species than lamprey and they compete with each other for food resources.

The only difference between competitor 2 and lamprey is the adaptive sex ratio.

The problem was studied and analyzed by controlling the variables to create a model that included lamprey or competitor 2 and compared as follows:

Changes to ecosystems with parasites, rivals, lamprey, and producers:

Changes to ecosystems with parasites, rivals, and producers (without lamprey):

Some conclusions can be drawn from the comparison of the above figures:

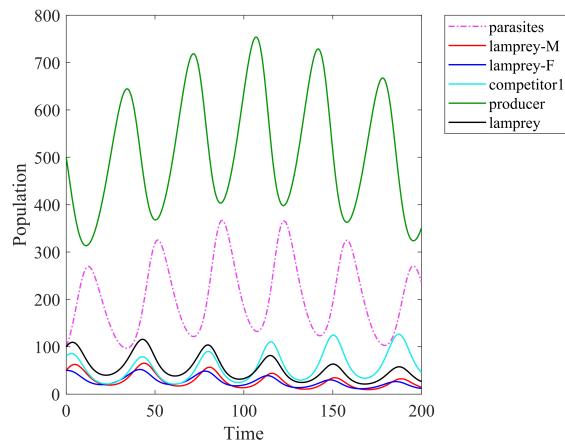


Figure 11: Short-term

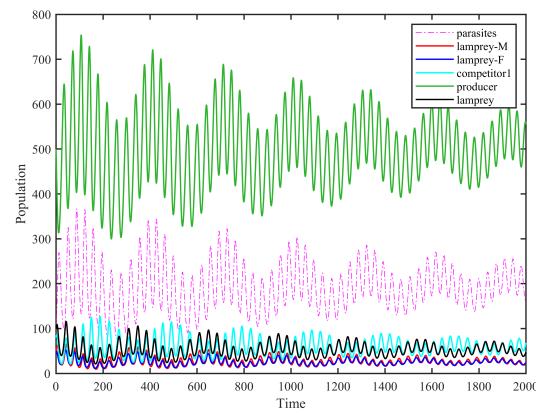


Figure 12: Long-term

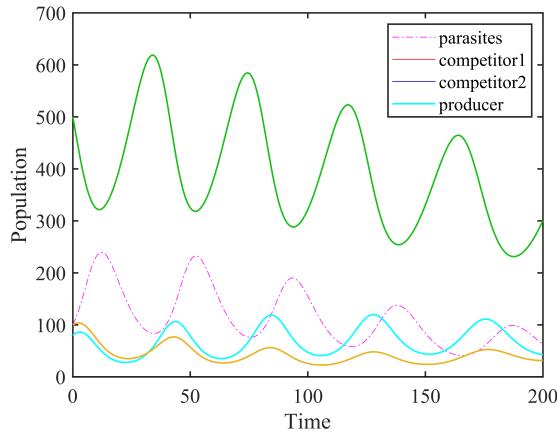


Figure 13: Short-term

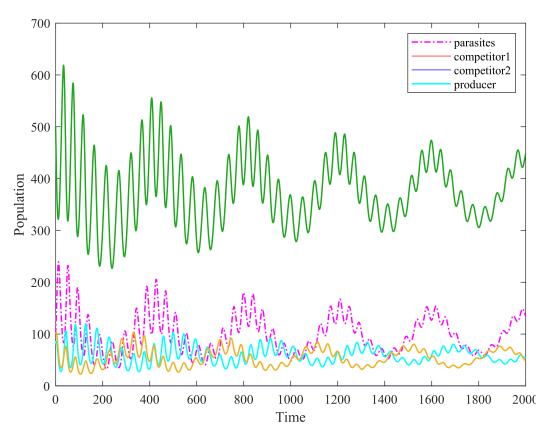


Figure 14: Long-term

- (1). Changes in the sex ratio of lampreys in response to their environment result in more frequent biomass fluctuations.
- (2). The variations in biomass in lampreys and competitor 1 exhibit an inverse relationship. This is due to the fact that competition between species for food and other resources has a dampening effect on the growth of each other's populations.
- (3). Because of the increasing interrelationships between species, the overall biomass of species in an ecosystem is smaller than the total biomass of individual species in culture. Consider more than just predatory relationships.

Variations in biomass might result from interactions between species that are interspecific. According to the species diversity effect, total biomass swings less when species coexist, suggesting higher stability in ecosystems with diverse species.

We should quantitatively quantify the presence of lamprey and other species with varying sex ratios to confirm that it truly contributes to the stability of the ecosystem. We want to evaluate the ecosystems using a number of representative and readily computed measures.

The overall biomass of an ecosystem, which reflects the growth condition of the populations of each species inside it, is its most significant indicator. The biomass of

all species added together is the total biomass of the community, TB , if the biomass of the i th species is represented by x_i .

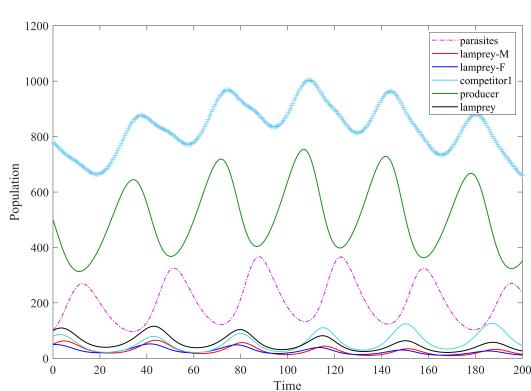


Figure 15: Sum 1

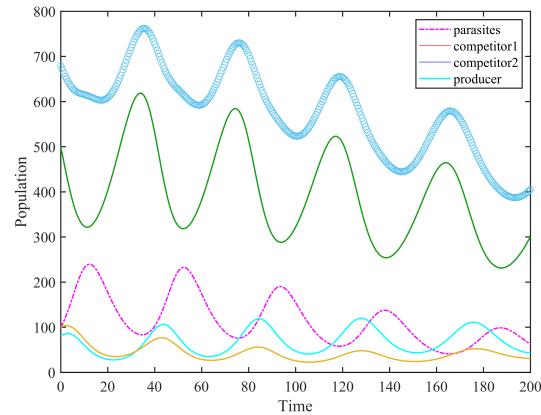


Figure 16: Sum 2 (without lamprey)

It is evident from the above comparison of the two graphs that the ecosystem's total biomass with lamprey is more stable than the ecosystem's total biomass with competitor 2, which is trending downward. The shift in the quantity of parasitic organisms is mostly responsible for this.

The total biomass of the ecosystem showed cyclical fluctuations over time, where T_{max} is the total time required to run the program.

$$\overline{TB} = \frac{1}{T_{max}} \int_0^{T_{max}} \sum_{i=1}^n x_i(t) dt \quad (15)$$

Stability can refer to resistance to disturbance, resilience (the rate of recovery after disturbance), and constancy (degree of temporal stability)^[4]

We know that the stability of an ecosystem is correlated with its total biomass change over time; the smaller the change, the more stable the ecosystem. Generally speaking, the standard deviation of total biomass may be used to gauge change; however, the measurement's size and the data mean have an impact on the standard deviation. We define a dimensionless measure, the coefficient of variation (CoV) of total biomass, to remove this effect:

$$CoV = \frac{std(TB)}{TB} = \frac{\sqrt{\int_0^{T_{max}} (TB(t) - \overline{TB})^2 dt}}{\overline{TB}} \quad (16)$$

In physics, we use 'entropy' to measure the degree of disorder in a system, and the Shannon-Wiener index^[5] is a measure of species evenness inspired by the concept of entropy: in a community, the average number of each species is $\overline{X}_i = \int_0^{T_{max}} \frac{x_i(t)}{T_{max}} dt$. The total biomass is \overline{TB} as previously mentioned. Define the Shannon-Wiener index as:

$$H = \sum_{i=1}^n -\frac{\overline{x}_i}{\overline{TB}} \log \frac{\overline{x}_i}{\overline{TB}} \quad (17)$$

According to its formulation, when the percentage of each species is the same, the index reaches its maximum value. The Shannon-Wiener index decreases with increasing

ing distributional unevenness. Consequently, establish the Pielou index to gauge relative homogeneity:

$$J = \frac{H}{\log_n} \quad (18)$$

This number, which ranges from 0 to 1, represents the connection between the current uniformity and the highest possible uniformity.

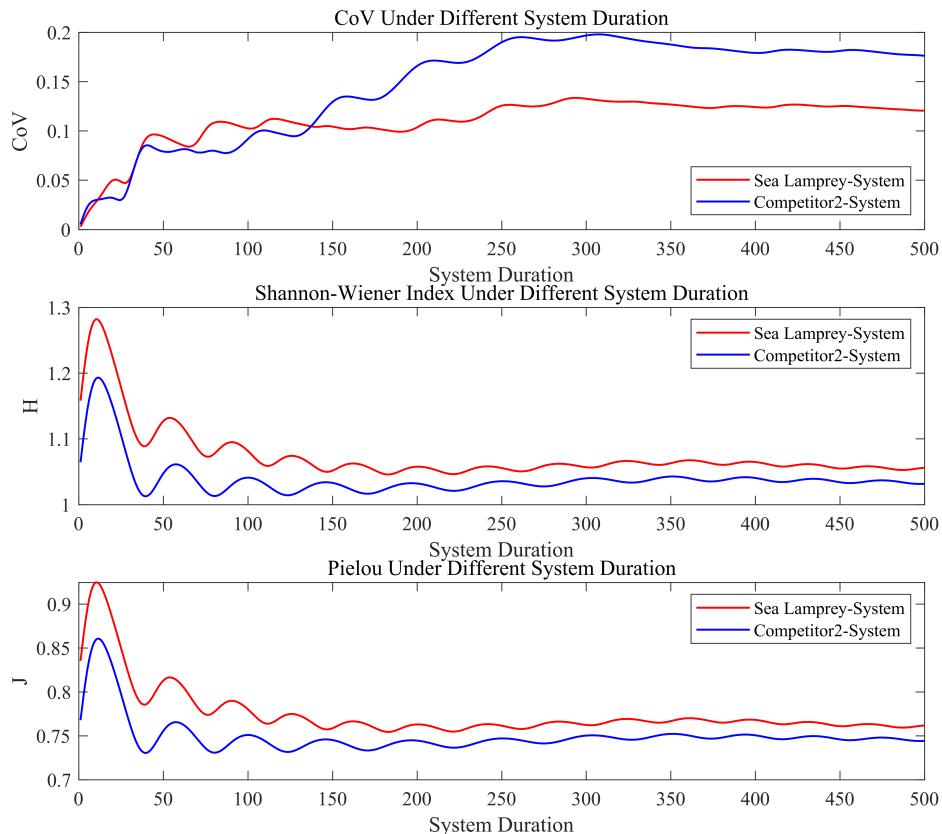


Figure 17: Stability indicators

The results(figure 17) demonstrate that adaptation sex ratio changes contribute to the stability of the ecosystem and that, despite species heterogeneity in the ecosystem, the magnitude of changes in total biomass decreases. These findings are in line with the findings of the qualitative analyses and support the viability of the model.

4.5 Explore the advantages offered to other species.

Based on the prior model, we concluded that the adaptive sex ratio shift in lampreys enhances their ability to adjust to their environment and increases their chances of surviving. Different species interact differently; some are more competitive than others, while some are dominated by symbiotic relationships that are mutually beneficial. Exploring the interaction between lamprey and parasites is necessary to investigate the benefits lamprey offers to other species, such as parasites.

According to Megan A. Shavalier et al^[6], at least 46 species of parasites have been documented to be found on lamprey. We consider the parasitic behavior of parasites on

lamprey as another special type of predatory behavior and apply the model developed in the previous question.

To investigate their impacts on parasite biomass, we similarly constructed comparison models in which competitor 1 and lamprey were removed individually from a multispecies model.

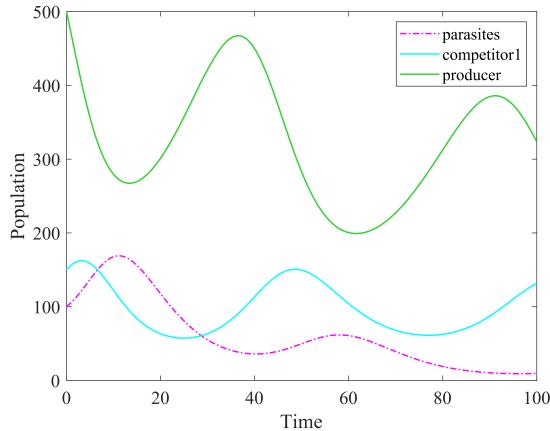


Figure 18: parasites,com1,product

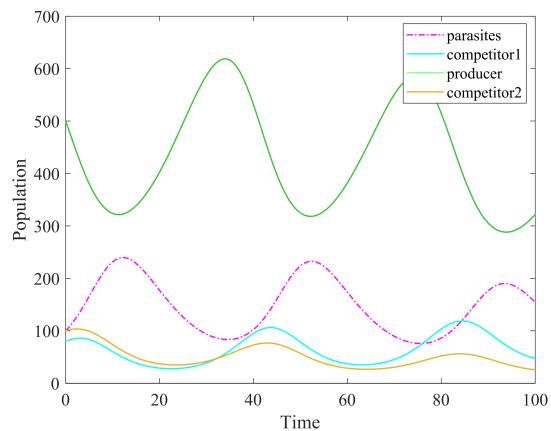


Figure 19: parasites,com1,product,com2

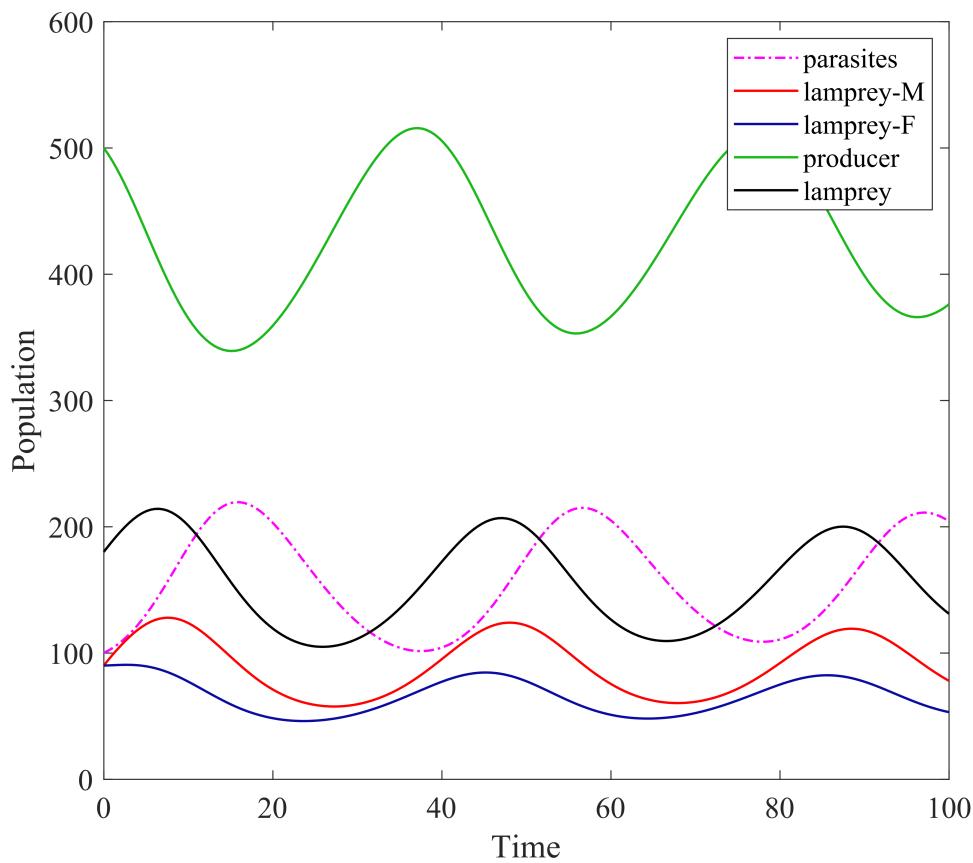


Figure 20: parasites,lamprey, male, female, product

From the figure 18, figure 19, figure 20, we can draw the following conclusions:

- (1). Under identical conditions, competitor 1 finds it more difficult to sustain the parasite's existence, whereas lamprey can offer a somewhat more conducive envi-

ronment. One possible explanation for this might be the increasing imbalance in the sex ratio of lampreys that occurs as the population grows, which lowers their capacity for reproduction and limits the rate and maximum value of population growth, similarly, as the population shrinks, reproductive capacity rises with the sex ratio, limiting the similar rate and absolute value of population decline. As a result lamprey has shorter iteration cycles and more stable population sizes, which provide a stable food source for the parasite.

- (2). The increased biomass of lamprey has a lower demand for food resources, and ecosystems with adapted sex ratios of lamprey have a greater number of producers.

The sea lamprey and competitor 1's population sizes are suppressed as parasite numbers stabilize, giving producers more room to live. Larger producer populations mean richer resources and more stability for the ecosystem as a whole.

5 Sensitivity Analysis and Stability Analysis

5.1 Sensitivity analysis of the model for the producers' natural growth rate

Producers, as the original energy suppliers in an ecosystem, play an important role in ecosystem biomass, iteration and stability. The amount of energy a producer can provide depends on its natural growth rate, and the sensitivity of the model is assessed by calculating the stability of the model at different natural growth rates.

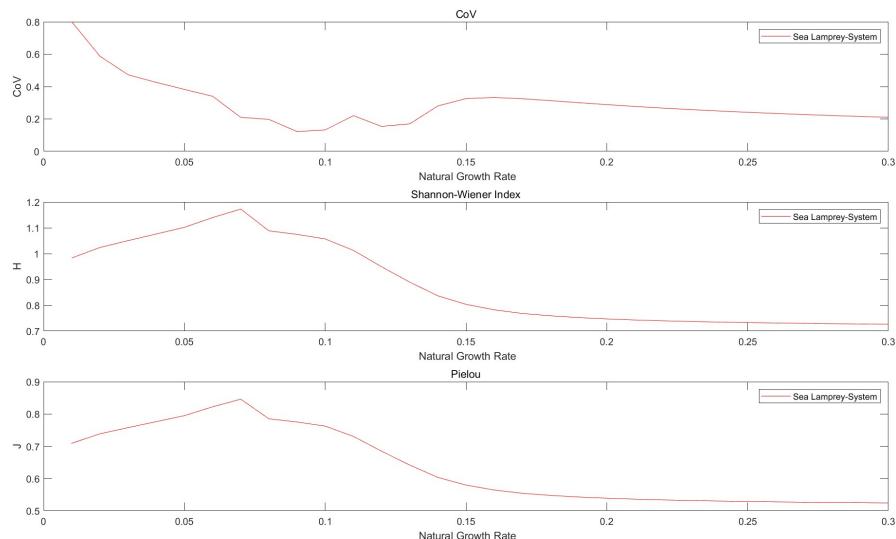


Figure 21: Sensitivity analysis for the producers' natural growth rate

From the figure 21, it is obviously that the model is more stable in the interval [0.01, 0.15] where the natural rate of growth is higher than 0.15, causing the system to break down.

5.2 Model sensitivity analysis of the initial population size of the lamprey

The initial size of lamprey's population also plays an important role in the iterative status of the whole ecosystem, and the sensitivity of the model was assessed by calculating the stability of the model at different natural growth rates over a short period of time.

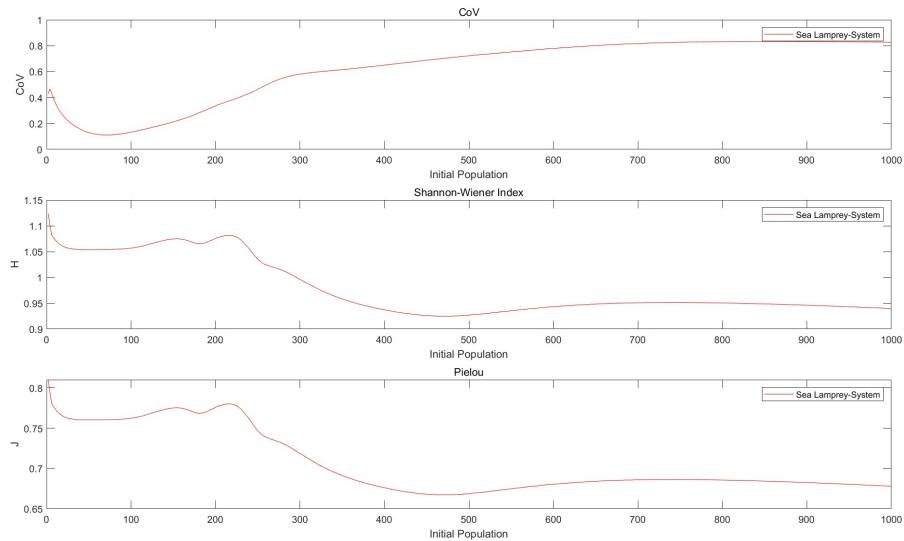


Figure 22: Model sensitivity analysis of the initial population size of the lamprey

From the figure 22, In a short period of time, the initial population size is in the range of [20, 300] the model is more stable, too high initial number will lead to lamprey competing species and producers due to the survival pressure is too lamprey large and rapid extinction, so the stability of the system decreases and convergence. Due to efficiency issues, only the sensitivity of ecosystem stability over a shorter period of time is examined here, and since changes in initial population size may also change the iteration period and trend of the system, the iteration length of growing the system may lead to different results.

5.3 Model sensitivity analysis of the environmental carrying capacity of lamprey populations

Environmental carrying capacity determines the upper limit of how much the lamprey population can expand, and the sensitivity of the model was assessed by calculating the stability of the model under different environmental carrying capacities.

From the figure 23, When the environmental carrying capacity is higher than 3000, the model performance is more stable, too low environmental carrying capacity will severely limit the survival of lamprey, leading to its rapid extinction and elimination from the ecosystem lamprey

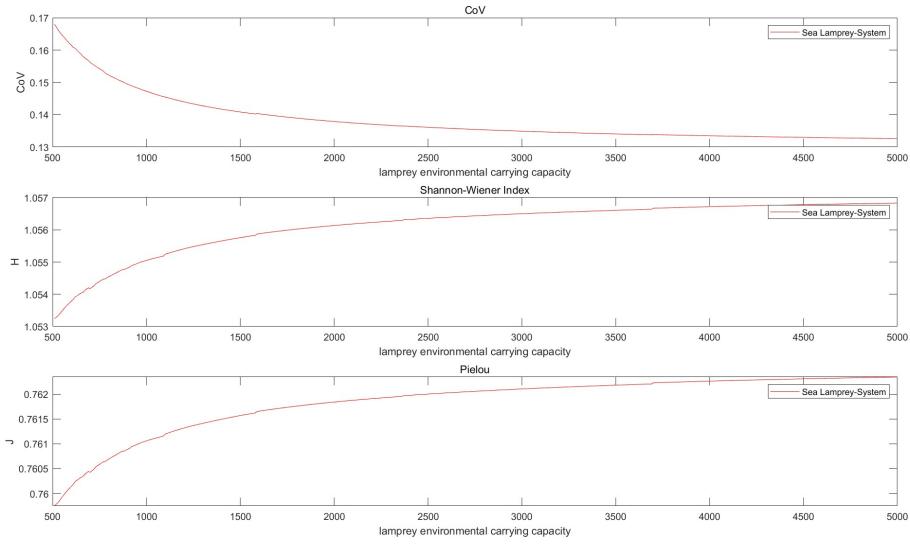


Figure 23: Model sensitivity analysis of the environmental carrying capacity of lamprey populations

6 Strengths and Weaknesses

6.1 Strengths

- Our team utilized the lotka-Volterra model as a basis, taking into account the characteristics of male and female lamprey individually. We included variables such as predation conversion rate and environmental carrying capacity and we creatively create a revised model that considers a variety of elements, including interactions between species, the impact of sex ratio on development and reproduction, etc.
- Modeling the male and female sexes separately, which make it possible to account for a lag in the effect of sex changes due to species availability on the true sex ratio of a population. It is more appropriate to represent the impact of sex differences in the lamprey using separate models.
- Using biomass to rationalize a model for evaluating the effects of sex ratio changes on ecosystems
- To construct our overall comprehensive model, we combined many scientific ecological models and expanded upon them with certain tweaks, simplifications, and adjustments.

6.2 Weaknesses

- This work's model was constructed based on the Lotka-Volterra model, which overlooked some of the complexities of the ecosystem, such as fish migration, geographic distribution, and human influences.
- The numerical solution of the model may be highly sensitive to the initial conditions and parameter choices, necessitating further sensitivity analysis is required.

References

- [1] Hansen, Michael J. , et al. "Population ecology of the sea lamprey (*Petromyzon marinus*) as an invasive species in the Laurentian Great Lakes and an imperiled species in Europe." *Reviews in Fish Biology and Fisheries* (2016).
- [2] Johnson Nicholas S., Swink William D. and Brenden Travis O. 2017 Field study suggests that sex determination in sea lamprey is directly influenced by larval growth rate *Proc. R. Soc. B.* 284:20170262.20170262
- [3] Michael J. Hansen, et al. "Population ecology of the sea lamprey (*Petromyzon marinus*) as an invasive species in the Laurentian Great Lakes and an imperiled species in Europe." *Reviews in Fish Biology & Fisheries* (2016).
- [4] Ma, Zilong , and H. Y. H. Chen . "Effects of species diversity on fine root productivity in diverse ecosystems: a global meta-analysis." *Global Ecology & Biogeography* (2016).
- [5] Strong, W. L . "Biased richness and evenness relationships within Shannon–Wiener index values." *Ecological Indicators* (2016).
- [6] Shavalier, Megan A. , et al. "Parasites and microbial infections of lamprey (order Petromyzontiformes Berg 1940): A review of existing knowledge and recent studies." *Journal of great lakes research* S1(2021):47.
- [7] Stéphanie Boulêtreau, et al. "High predation of native sea lamprey during spawning migration." *Scientific Reports* 10.1(2020).

Appendices

Listing : Multi-species ecosystem modeling

```

1
2
3 % Consider a more complex ecosystem, with four species:
4 % Parasites-Competitors 1+ Lamprey, three levels of the food chain
5 clear;
6 clc;
7 close all;
8
9 % In the initial population, lamprey and competitor 2 can only choose one
10 init_value = [100, 50, 50, 80, 500, 0, 0];
11 % Parasite;Male-Lamprey;Female-Lamprey;Competitor 1;Producer;Competitor 2
12
13 % time range
14 Time = linspace(0, 500, 1000);
15
16 % solving equations
17 [T1, Y1] = ode45(@question_4_2_B, Time, init_value);
18
19 function eq = question_4_2_B(T, Y)
20 %
21     init_value = [100, 50, 50, 80, 500, 0, 0];
22     Under this parameter set, although the number of each species does not
23     converge stably, it presents periodic stability, and there are alternate
24     changes in the proportion of population with large and small periodic competitors.
25     1. Keeping other parameters constant, [a14a41] = [-2e-3 -2e-3] can make
26     the model converge slowly, and decreasing [a14a41] can accelerate convergence
27     and shorten the period.
28     2. Based on this model, either the heptagill or competitor species are
29     deleted, and the same amount removed is added to the initial number
30     of the other. Looking at the model, it is found that the competitor
31     has difficulty maintaining the survival of the parasite, while the
32     heptagill can provide a relatively superior living environment for the parasite.
33 %
34
35 eq = zeros(7,1);
36 % Subfunctions and Parameter Definitions
37 A = (Y(5)+Y(6))./(1e-50+Y(2)+Y(3)+Y(4)); % 1e-50 Prevent denominator from zero
38 % R = alpha * ln(A + beta) + gamma; (5:3, 78%) (1:5, 50%) (1:20, 40%)
39 p_alpha = -0.1514;
40 p_beta = 0.4585;
41 p_gamma = 0.7569;
42 R = p_alpha .* log(A + p_beta) + p_gamma; % Sex determines the proportion of males
43 R_r = Y(2)./(1e-50+Y(2)+Y(3)); % The true male ratio of lamprey populations at a given t
44
45 % Lamprey birth rate
46 p_sigma = 0.72;
47 birth_rate = p_sigma.*R_r.* (1-R_r);
48 % Lamprey mortality
49 death_rate = 0.20;
50
51 f_m = [ % Transmission efficiency
52 % Since the parasite natural growth rate is negative, f<0 should be set to help it survive
53 0, -0.8, -0.8, 0, 0, 0, 0;
54 0, 0, 0, 0, 0, 0, 0;
55 0, 0, 0, 0, 0, 0, 0;
56 0, 0, 0, 0, 0, 0, 0;

```

```
57 0, 0, 0, 0, 0, 0, 0;
58 0, 0, 0, 0, 0, 0;
59 0, 0, 0, 0, 0, 0, 0;
60 ];
61
62 a_m = [
63 0, 2.5e-3, 2.5e-3, 2.5e-3, 0, 0, 0;
64 -2.5e-3, 0, 0, 0, (6e-4).*((1+Y(3))./(Y(2)+1e-50)), 0, 0; % M
65 -2.5e-3, 0, 0, 0, (6e-4).*((1+Y(2))./(Y(3)+1e-50)), 0, 0;
66 -2.5e-3, 0, 0, 0, 1e-3, 0, 0;
67 0, -6e-4, -6e-4, -1e-3, 0, 0, 0;
68 0, 0, 0, 0, 0, 0, 0;
69 0, 0, 0, 0, 0, 0, 0;
70 ];
71
72 c_m = [
73 0, 0.55, 0.55, 0.55, 0, 0, 0;
74 0.2, 0, 0, 0, R.*((0.4.*Y(2) + 0.38.*Y(3))./(Y(2)+Y(3)+1e-50)), 0, 0; % M
75 0.2, 0, 0, 0, (1-R).*((0.4.*Y(2) + 0.38.*Y(3))./(Y(2)+Y(3)+1e-50)), 0, 0;
76 0.2, 0, 0, 0, 0.39, 0, 0;
77 0, 1, 1, 1, 0, 0, 0;
78 0, 0, 0, 0, 0, 0, 0;
79 0, 0, 0, 0, 0, 0, 0;
80 ];
81
82 p_v = [
83 Y(1);
84 Y(2)+Y(3);
85 Y(2)+Y(3);
86 Y(4);
87 Y(5);
88 Y(6);
89 Y(7);
90 ];
91
92 r_v = [
93 -0.16;
94 ((1+Y(3))./(Y(2)+1e-50)).*R.*((birth_rate) - death_rate);
95 ((1+Y(2))./(Y(3)+1e-50)).*(1-R).*((birth_rate) - death_rate);
96 -0.1;
97 0.1;
98 0;
99 0;
100 ]; % Natural Growth Rate
101 % k_m = [1e6, 5e3, 5e3, 1e4, 1e5, 1e5, 1e8]';
102 k_v = [ % k2 == k3
103 5e3;
104 5e3; % M
105 5e3; % F
106 4e3;
107 5e3; % Producer
108 1e-9;
109 1e-9;
110 ]; % Environmental carrying capacity
111
112 eq(1) = r_v(1).*Y(1).*(1-(p_v(1)-f_m(1,:)*Y)./k_v(1)) + Y(1).*((a_m(1,:).*c_m(1,:))*Y);
113 eq(2) = r_v(2).*Y(2).*(1-(p_v(2)-f_m(2,:)*Y)./k_v(2)) + Y(2).*((a_m(2,:).*c_m(2,:))*Y);
114 eq(3) = r_v(3).*Y(3).*(1-(p_v(3)-f_m(3,:)*Y)./k_v(3)) + Y(3).*((a_m(3,:).*c_m(3,:))*Y);
115 eq(4) = r_v(4).*Y(4).*(1-(p_v(4)-f_m(4,:)*Y)./k_v(4)) + Y(4).*((a_m(4,:).*c_m(4,:))*Y);
116 eq(5) = r_v(5).*Y(5).*(1-(p_v(5)-f_m(5,:)*Y)./k_v(5)) + Y(5).*((a_m(5,:).*c_m(5,:))*Y);
```

```
117 eq(6) = r_v(6).*Y(6).*(1-(p_v(6)-f_m(6,:)*Y)./k_v(6)) + Y(6).* (a_m(6,:).*c_m(6,:))*Y;
118 eq(7) = r_v(7).*Y(7).*(1-(p_v(7)-f_m(7,:)*Y)./k_v(7)) + Y(7).* (a_m(7,:).*c_m(7,:))*Y;
119 end
```
