

Impact of Variable Sex Ratios: Sea Lampreys

Summary

The sex ratio of sea lamprey larval depends on their growth rates, which is influenced by local conditions. Using sea lampreys as a case study and referencing the condition of the Great Lakes, we have constructed a generalizable Enhanced Lotka-Volterra model. This model aims to examine the impact of a species to alter its sex ratio depending on resource availability.

Firstly, we established a Growth model for sea lampreys based on **von Bertalanffy equation**, simulating the growth process under different conditions of food supply and water temperature. Subsequently, A **hierarchical Bayesian logistic regression model** was used to analyze the local sample statistics and predict the sex ratio of sea lampreys based on the growth time.

Secondly, considering factors involved and not involved in species interactions and mapping the sex ratio into factors influencing reproduction and reflecting sexual dimorphism, we established the **Enhanced Lotka-Volterra model**. In order to simulate a local ecosystem, taking into account the habits of sea lampreys, we constructed a three-level food chain. Subsequently, based on the characteristics of the food chain, we instantiated the Enhanced Lotka-Volterra equations to obtain a set of Enhanced L-V equation reflecting the evolution of each species (in the food chain).

Thirdly, employing the method of controlling variables, we simulated the evolution of sea lampreys and other species under scenarios of variable and constant sex ratio. Through **phase diagram** analysis and **Jacobian matrix** calculations, we conducted respectively qualitative and quantitative analyses of the stability of the local ecosystem. The results indicate that the variable sex of sea lampreys contributes more stability potential to the local ecosystem.

Furthermore, we examined the generalizability of the model. Building upon the consideration of the unique infection mechanism of parasites and a biased analysis of parasite characteristics concerning factors involved and not involved in species interactions, we expanded the infection rate of sea lampreys as an environmental input. This rate was then mapped onto the coefficients of the Enhanced Lotka-Volterra equations to simulate the evolution of the parasitic species' population. The results indicate that, in most cases, the **variable sex ratio** of sea lampreys leads to an increase in the population of the parasitic community.

Finally, the results of the convergence and sensitivity analysis of the model indicate that the Enhanced Lotka-Volterra Model exhibits good convergence and robustness.

In summary, this model avoids the complexity of modeling based on biological mechanisms and incorporates **the extraction of environmental characteristics** of the studied water bodies by utilizing a hierarchical Bayesian regression model. By abstracting the complex interactions among species in the ecosystem using the Lotka-Volterra equations, the model maintains relative simplicity without sacrificing accuracy, ensuring its generalizability.

Keywords: Enhanced Lotka-Volterra Model, the von Bertalanffy equation, Jacobean matrix stability analysis, Hierarchical Bayesian regression model, Phase diagram analysis

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1 Introduction

1.1 Problem Background

In the natural environment, the observation of skewed sex ratios is a pervasive phenomenon across diverse taxa. The ecological conditions might be influenced by sex ratios [1] in species with robust ecological interactions, particularly when sexual dimorphism aligns with ecological dimorphism.

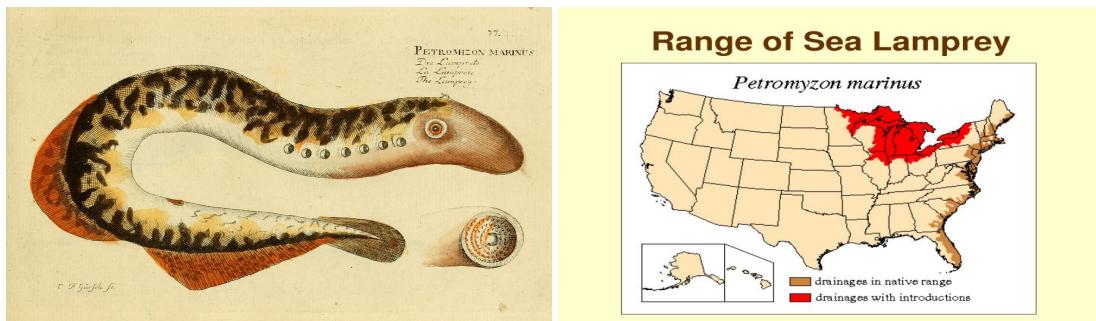


Figure 1: The sea lamprey(Left) and the distribution range of the sea lamprey(Right)

Take the sea lamprey as an example, several research studies indicate that the sex of sea lamprey is directly influenced by larval growth rate^[2]. In addition, since entering the upper Great Lakes beginning in 1921, sea lampreys have harmed the fishery and ecosystem, and changed the way of life in the region. We will use this as a background to explore the impacts of changing sex ratios among sea lampreys in the Great Lakes region on their individual populations and the entire ecosystem.

1.2 Restatement of the Problem

In order to better understand the advantages and disadvantages of a species being able to adjust gender ratios based on resource availability, it is essential to establish a mathematical model. This model should predict the evolution of the ecosystem under various interactive components. Our model should address the following questions:

- **Problem I:** We are required to develop a model to predict the effects of variable sex ratios of sea lampreys on ecosystems, such as changes in the abundance of other species in the ecosystem.
- **Problem II:** We are required to analyse the advantages and disadvantages that the sex ratio of the sea lampreys may bring to itself, particularly in terms of its impact on its own population size.
- **Problem III:** To analyze the effects of sex variation on ecosystem stability in sea lampreys.
- **Problem IV:** To analyze whether variable sex ratios for sea lampreys have a positive impact on other species, such as parasites.

1.3 Our Work

To avoid complicated description, intuitively reflect our work process, diagram is as shown in the figure below:

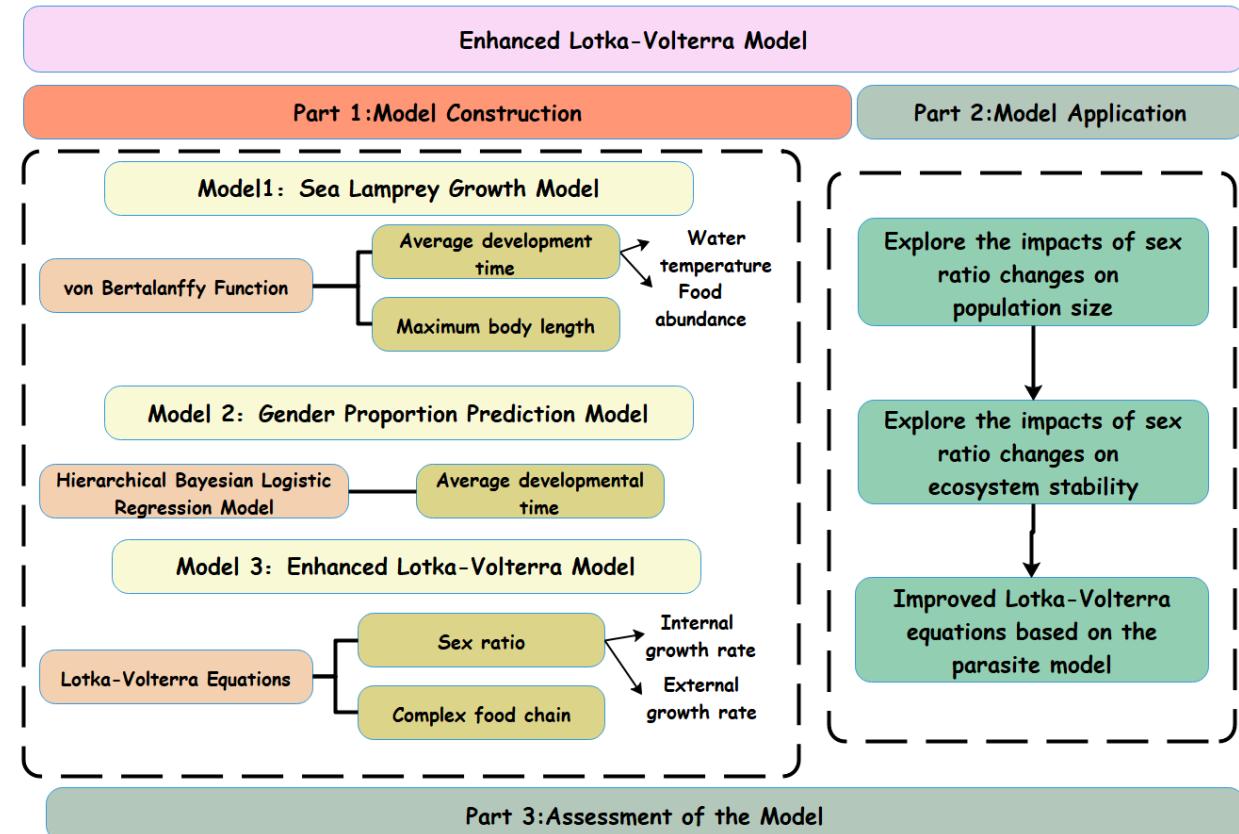


Figure 2: Our Work

2 Assumptions and Justification

To simplify the problem and make it convenient for us to simulate real-life conditions, we make the following basic assumptions:

- **Ignoring the population fluctuations caused by human factors.** To simplify the model, we neglect population changes caused by human factors such as overfishing, water pollution, habitat destruction, etc., and consider that the population is only influenced by natural factors.
- **Disregarding the potential sharp decline in population numbers due to extreme natural weather conditions.** Benefiting from the climate-regulating function of the Great Lakes effect, the temperature changes in the Great Lakes region are relatively small, and the likelihood of extreme weather events is low.

- **Neglecting the population changes brought about by the natural migration in and out of the ecosystem by organisms.** To simplify the model, we assume that all species coexist in a closed environment, and the change in the number of species is solely determined by survival competition among them.
- **Ignoring the potential sharp decline in population numbers due to microbial environmental changes.** Changes in the marine microbial environment are mainly related to seawater pH and temperature, which do not change significantly in a short period of time.

3 Notations

Table 1: **Notations**

Symbols	Description
F	Whether the region has sufficient food
N	Maximum environmental carrying capacity
t_{avg}	Average development time
x_i	The quantity of species i
p	The proportion of males to the total population
θ	Parasite infection rate
d_1^I	The mortality rate of fish infected by parasites
λ_i	Eigenvalues of the Jacobian matrix for the i -th dimension

where we define the main parameters while specific value of those parameters will be given later.

4 Analysis and Modeling

4.1 Sea Lamprey Growth Model Based on von Bertalanffy Equation

4.1.1 Preparation of the model

Considering the correlation between the sex ratio of the sea lamprey and its developmental time, we need to establish a model to investigate the developmental time of the sea lamprey.

First, we need to understand the lifecycle of the sea lamprey. The life cycle of the sea lamprey can be divided into four stages^[3]:

- **Larval Stage:** The juvenile stage typically lasts from three to ten years. During this stage, the larval sea lamprey exhibit lower activity and survival capabilities, making them susceptible to predation. The larval sea lamprey feed on organic detritus^[7].
- **Metamorphosis Stage:** In the metamorphosis stage, sea lamprey larvae begin dramatically, developing eyes, oral discs, and tongues covered with sharp teeth, and begin migrating downstream to the lake. After entering the metamorphic phase, the gender of the sea lamprey becomes fixed^[2]. At this stage, the sea lamprey does not feed.

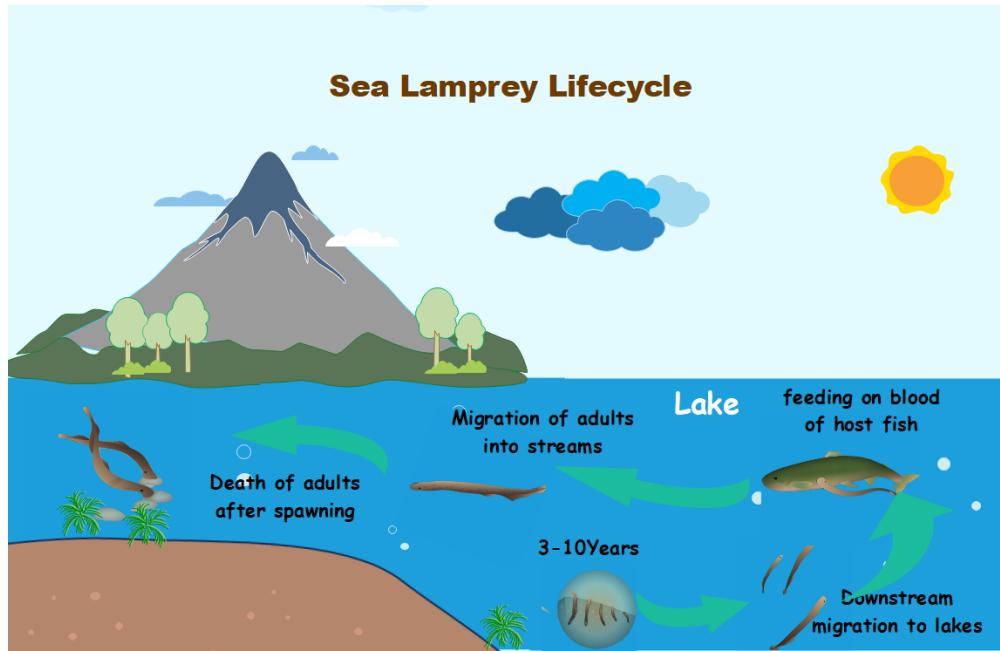


Figure 3: Sea Lamprey Lifecycle

- **Parasitic Stage:** When sea lamprey migrate to lakes, they become parasitic juveniles and feed on the blood of the host fish for twelve to eighteen months.
- **Spawning Stage:** In winter or early spring, the sea lamprey mature into spawning adults after finding and entering suitable spawning streams. They reproduce in spring and early summer, shortly after spawning, they die. At this stage, the sea lamprey does not feed.

4.1.2 Model establishment

von Bertalanffy equation is a type of growth curve for a time series and the equation is commonly applied in ecology to model fish growth.

For the sea lamprey, we denote its maximum length during growth as L_∞ . Simultaneously, let's denote t as the growth time during the larval stage of the organism. Thus, we have:

$$L(t) = L_\infty [1 - \exp(-kt)] \quad (1)$$

We consider that when $L(t_{avg}) = \alpha L_\infty$ the sea lamprey has reached the adult stage in its development.

Taking t_{avg} as the average individual developmental time for the sea lamprey, through a transformation of the original expression, we obtain:

$$t_{avg} = -\frac{1}{k} \ln(1 - \alpha) \quad (2)$$

4.1.3 Determination of parameters

We found that the growth rate coefficient of the sea lamprey is not only determined by its own species characteristics but is also influenced by environmental factors. Among these factors, water temperature^[3] and food abundance^[2] are the two major influencers. Therefore, the expression of k is acquired as follows:

$$k(T, F) = k_{\max} k(T) \cdot F \quad (3)$$

where k_{\max} is considered as the maximum growth coefficient that the sea lamprey can achieve under optimal temperature and abundant food supply.

Generally, a more suitable temperature range can promote the growth and reproduction of the sea lamprey, while extreme temperature conditions may have adverse effects. We have:

$$k(T) = \exp\left[-\left(\frac{T(t) - T_{\text{opt}}}{T_{\text{opt}}}\right)^2\right] \quad (4)$$

where T_{opt} represents the annual average water temperature of the habitat of the sea lamprey. We find that T_{opt} is 18°C.

We conducted a statistical analysis of the annual average water temperatures in the Great Lakes region from 1995 to 2023. To better capture the characteristics of the periodic fluctuations in annual average water temperatures, we employed trigonometric functions to fit the temperature trends and obtained the following results:

$$T = 0.6813 \cos(1.096t) - 0.3744 \sin(1.096t) + 6.55$$

$F \in [0, 1]$ is a food abundance index that we consider as a set parameter, indicating the food abundance situation for the sea lamprey, where 0 represents very scarce food, and 1 represents very abundant food.

By introducing the food abundance index, we can better characterize the impact of food on larval growth.

In summary, we can determine the average developmental time of the sea lamprey as a value jointly influenced by T and F that is:

$$t_{\text{avg}} = -\frac{\ln(1 - \alpha)}{k_{\max} \exp\left[-\left(\frac{T - T_{\text{opt}}}{T_{\text{opt}}}\right)^2\right] \cdot F} \quad (5)$$

4.2 Gender Proportion Prediction Model

4.2.1 Model establishment

We analyzed gender-growth time data of sea lamprey larvae obtained through the mark-recapture method in tributaries of Lake Michigan and Lake Huron (40-140mm) by Nicholas S. Johnson et al.^[1]. By establishing a Bayesian hierarchical logistic regression, we determined the distribution model of gender proportions in relation to growth time in this region.

We consider whether a labeled adult sea lampreys captured from the original waters in a given year is male as a Bernoulli random variable, the probability that it is a male is listed as follows:

$$\text{logit}(p_{i,t_{avg}}^j) = \log\left(\frac{p_{i,t_{avg}}^j}{1 - p_{i,t_{avg}}^j}\right) = a_i^j + b_i^j \cdot t_{avg} \quad (6)$$

where t represents the number of years it takes for juvenile lampreys to mature, and j represents the type of water body, including lakes and rivers. a_i^j, b_i^j refer to the intercept and slope for the water body. Its inverse is the sigmoid function:

$$p_{i,t_{avg}}^j = \frac{1}{1 + \exp(a_i^j + b_i^j \cdot t_{avg})} \quad (7)$$

Furthermore, in order to better understand and explain the differences between different locations while preserving the overall trends associated with location types, we will consider the average differences in parameter values for different types (such as rivers and lakes), while also taking into account the deviations of each location from the mean value of its type. Consequently, a_i^j, b_i^j can be represented as:

$$\begin{aligned} a_i^j &= a_0^j + \delta_i \\ b_i^j &= b_0^j + \gamma_i \end{aligned} \quad (8)$$

where a_0^j, b_0^j is the overall average of intercepts and slopes for a given water type, and δ_i, γ_i is the deviation of the intercept and slope of a particular body of water from the population. For this model, we assume the following vague priors:

Table 2: **Probability Distribution of Parameters**

Parameters	Vague Priors
a_0^j, b_0^j	MVN(0, Σ^j)
δ_i	N(0, σ_δ)
γ_i	N(0, σ_γ)
$\sigma_\delta, \sigma_\gamma$	U(0, 100)
Σ^j	W($\mathbf{I}_{2 \times 2}$, 3)

where MVN represents the multivariate Normal distribution, N represents the Normal distribution, W represents the Wishart distribution, and U represents the average distribution.

Based on the analysis of the relevant data^[2], we can determine the values of the parameters a and b in the equation 7 for the Great Lakes region, that is:

$$a = 0.9444, b = -0.2454$$

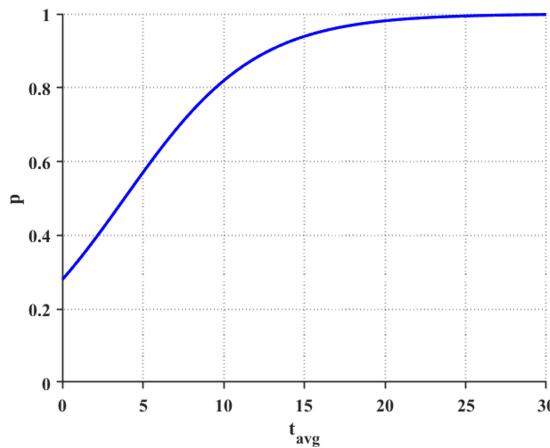


Figure 4: The relationship between male probability and mean developmental time

From the above figure we can easily see that the male probability increases with the average development time.

- **Note:** It is reasonable to use the calculated male probability of sea lampreys as the proportion of males in the actual population. Because the Law of Large Numbers states that with an increase in sample size, the sample mean tends to approach its expected value, which is the true male ratio of the population. Therefore, if we perform calculations based on a sufficiently large sample size, the calculated probability of males will more accurately reflect the actual male ratio in the population of sea lamprey. This provides a crucial reference for ecological research and management.

4.2.2 Determination of parameters

Solving equation 7 in conjunction with equation 10, we can obtain an equation for the relationship between resource availability and the sex ratio of sea lampreys:

$$\begin{cases} t_{\text{avg}} = t_{\text{avg}}(T, F) = t_{\text{avg}}(t, F) \\ p = p(t_{\text{avg}}) = p(t, F) \end{cases} \quad (9)$$

With this equation we are able to correlate the sex ratio of the sea lamprey with the mean annual water temperature T and food availability F .

Given that the development time range of the lamprey is between 3 and 10 years or more, we assume that when $F = 1$, the food supply imposes no restrictions on the growth rate of lampreys, and the development time is 3 years. At the same time, \bar{T} takes the average T of the 1995-2023 data.

$$\bar{T} = 6.5528, \alpha = 0.95, k_{\max} = 0.15$$

From the above figure we can easily see that the male probability increases with the average development time.

Table 3: Value of parameters

F	t_{avg}	p
1	3.0478	0.4510
0.3	10.1593	0.8247
0.2	15.2389	0.9424

When $F = 0.2$, an unrealistic proportion of males is observed due to insufficient food abundance for sea lamprey larval development. Consequently, we adjust the range of $F : F \in [0.2, 1]$

By varying different values of F , we can determine different male probability P and their corresponding development times t_{avg} .

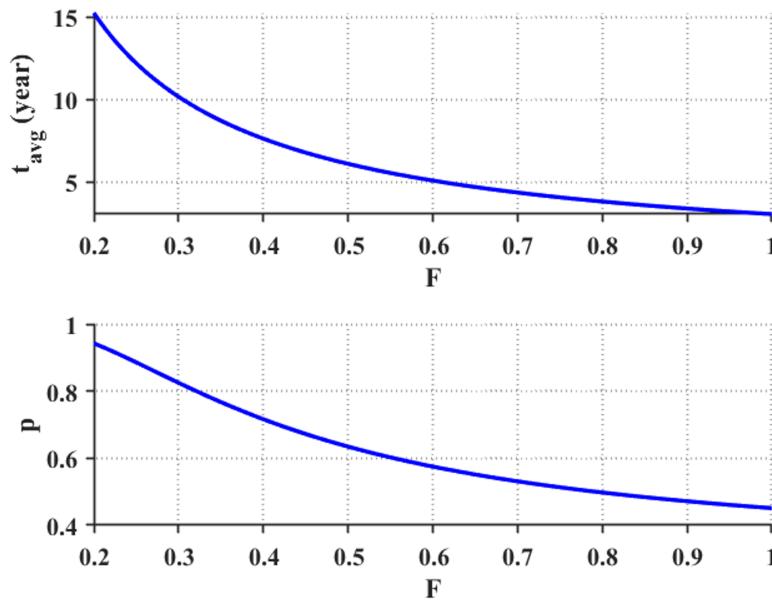


Figure 5: The relationship between t_{avg} and F as well as the relationship between p and F

4.3 Enhanced Lotka-Volterra Model

4.3.1 Enhanced Lotka-Volterra model establishment

Lotka-volterra model is often used to describe competition between species.

Based on the Lotka-Volterra equations, we comprehensively considered the factors involved in species interaction and factors not involved in species interaction, establishing an Enhanced Lotka-Volterra model.

$$\frac{dx}{dt} = (r_{\text{nint}} + r_{\text{int}})x \quad (10)$$

where r_{nint} is the net growth rate determined by the factors not involved in species interaction, r_{int} represents net growth rate determined by the species interacting with other species.

We define the net growth rate as r_{nint} consisting of a birth rate b and a death rate d , that is:

$$r_{\text{nint}} = b - d \quad (11)$$

The birth rate b is not only affected by the population size x , the maximum environmental carrying capacity N , but also related to its variable sex ratio, so we have:

$$b = b_{\max} \cdot f(p) \left(1 - \frac{x}{N}\right) \quad (12)$$

where b_{\max} is similar to k_{\max} in equation 3, b_{\max} represents as the birth rate under the most ideal conditions of gender ratio and population size. $f(p)$ is used to describe the effect of sex ratio on birth rate.

Next, considering $f(p)$, we assume that there exists an optimal gender ratio that maximizes the birth rate b , and extreme gender ratios would cause a decrease in b .

Assuming that in a certain environment, the probability of an adult sea lamprey being male is p_0 when the entire population has the maximum $f(p_0) = 1$, we use the logistic function to approximate this relationship:

$$f(p) = \begin{cases} \frac{2}{1+\exp\{-\gamma[1-(p-p_0)]\}}, & p \geq p_0 \\ \frac{1}{1+\exp[-\gamma(p-p_0)]}, & p < p_0 \end{cases} \quad (13)$$

where $\gamma = 10$, $p_0 = 0.5$

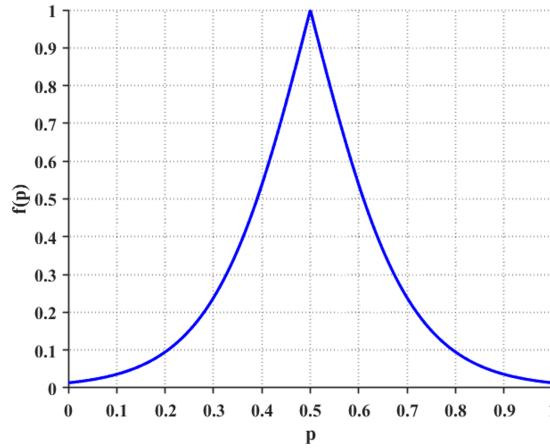


Figure 6: The relationship between $f(p)$ and p

N is the maximum environmental carrying capacity determined by environmental factors, and its value is closely related to the environmental conditions of the area. For simplicity, we only consider the impact of food resource abundance F on N . We believe that $N = N_0 \cdot F$, where N_0 is the maximum environmental carrying capacity under ideal food supply conditions.

In an ecosystem, the net growth rate of a species is not only influenced by factors not involved in species interaction but also by factors involved in species interaction within the food chain. We can express it as:

$$r_{\text{int}} = v - u \quad (14)$$

where v is the growth rate increase brought by the species preying on species downstream in the food chain, and u is the decrease in species growth rate due to being preyed upon by species upstream in the food chain.

Clearly, these two parameters should depend on the population size, that is:

$$\begin{cases} v = \lambda_{ij} \cdot x_j \\ u = \psi_{ij} \cdot x_i \end{cases} \quad (15)$$

where λ_{ij} is the ability of species i to prey on species j , and ψ_{ij} is the ability of species i to supply prey for predator j .

4.3.2 Instantiating the enhanced Lotka-Volterra model - based on a local ecological system

Taking into account the lifestyle of the sea lamprey and the most direct predator-prey relationships, we designed a local ecological system model consisting of a three-level food chain. This model primarily considers the sea lamprey itself and the two trophic levels above and below it, i.e., the sea lamprey's food source and its predator.

In this model, the first level represents the food source of adult sea lamprey, namely its host. The second level consists of the sea lamprey itself, and the third level includes large fish and birds that prey on the sea lamprey. By establishing such a three-level food chain model, we can gain a more comprehensive understanding of the complex relationships between the sea lamprey and its ecological environment, as well as its role and impact in the food web.

The food chain is shown below:

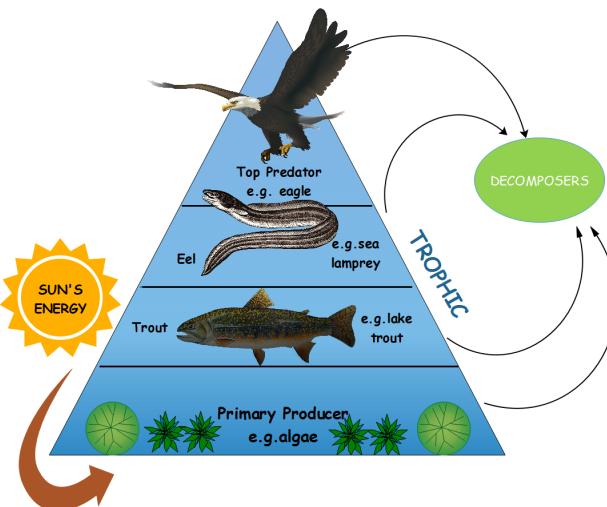


Figure 7: Food chain

We obtained a somewhat complex set of Lotka-Volterra (L-V) equations, which describes the dynamic evolution of this three-tier food chain, that is:

$$\begin{cases} \frac{dx_1}{dt} = (r_{\text{nint1}} + r_{\text{int1}})x_1 \\ \frac{dx_2}{dt} = (r_{\text{nint2}} + r_{\text{int2}})x_2 \\ \frac{dx_3}{dt} = (r_{\text{nint3}} + r_{\text{int3}})x_3 \end{cases} \quad (16)$$

Substituting the respective parameters, the formula can be organized as follows:

$$\begin{cases} \frac{dx_1}{dt} = \alpha_1 x_1 + \beta_1 x_1^2 - \psi_{12} x_1 x_2 \\ \frac{dx_2}{dt} = \alpha_2 x_2 + \beta_2 x_2^2 + \lambda_{21} x_1 x_2 - \psi_{23} x_2 x_3 \\ \frac{dx_3}{dt} = \alpha_3 x_3 + \beta_3 x_3^2 + \lambda_{32} x_2 x_3 \end{cases} \quad (17)$$

For species other than sea lamprey, the sex is determined solely by the type of gametes at the time of fertilization, and it is not influenced by the acquired environment, so the sex ratio to 1:1.

We found that the sea lamprey exhibits sexual dimorphism, with the metabolic rate of adult male sea lamprey being 17% higher than that of females.

$$\lambda_{21} \propto 1 - 0.17p$$

Furthermore, considering that only adult sea lamprey exhibit parasitic behavior, the proportion of adult sea lamprey p_{adult} is reflected in the parameters ψ_{12} and λ_{21} :

$$p_{\text{adult}} \propto \frac{t_{\text{adult}}}{t_{\text{life}}}, \psi_{12}, \lambda_{21} \propto p_{\text{adult}}$$

From this, we get:

$$\begin{cases} \alpha_1 = b_{\max_1} - d_1 \\ \alpha_2 = b_{\max_2} f(p) - d_2 \\ \alpha_3 = b_{\max_3} - d_3 \end{cases}, \begin{cases} \beta_1 = -\frac{b_{\max_1}}{N_1} \\ \beta_2 = -\frac{b_{\max_1} f(p)}{N_2} \\ \beta_3 = -\frac{b_{\max_3}}{N_3} \end{cases} \quad (18)$$

4.4 Jacobian-Based Evaluation Model for Ecological System Stability

Describing the stability of dynamic systems typically involves two methods: phase diagrams and Jacobian matrices. These two approaches have different advantages and disadvantages in various application contexts:

- **Phase Diagram:**
 1. It provides an intuitive graphical representation, facilitating a better understanding of the system's evolution in the state space.
 2. For nonlinear systems, phase diagrams can become complex and difficult to interpret.

- **Jacobian Matrix:**

1. It provides accurate mathematical tools by linearizing system equations, allowing for local stability analysis.
2. For complex nonlinear systems, the computation and analysis of matrices may become difficult.

4.4.1 System stability analysis based on phase diagram

Typically, a typical phase diagram of a Lotka-Volterra equation involving only two species is illustrated in the following figure:

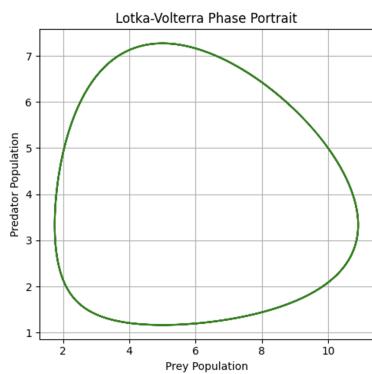


Figure 8: Typical phase diagram

Closed curves represent periodic oscillations in the quantity of prey and predators within a certain range.

4.4.2 System stability analysis based on Jacobian matrix

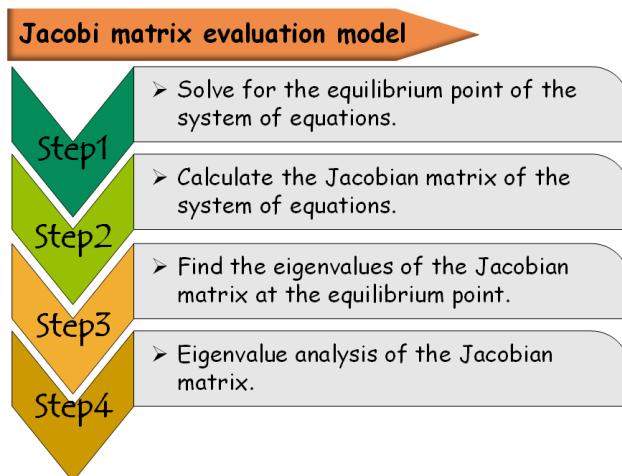


Figure 9: Steps for solving the eigenvalues of the Jacobi matrix

We take the example of a basic Lotka-Volterra model for a three-level food chain to study the methods of quantitative analysis of system stability using the Jacobian matrix.

$$\begin{cases} \frac{dU}{dt} = a_1 U - b_1 U V_1 \\ \frac{dV_1}{dt} = a_2 V_1 + b_2 U V_1 - c_1 V_1 V_2 \\ \frac{dV_2}{dt} = a_3 V_2 + b_3 V_1 V_2 - c_2 V_2^2 \end{cases} \quad (19)$$

Step 1: Solve for the equilibrium point

We define $\frac{dU}{dt}, \frac{dV_1}{dt}, \frac{dV_2}{dt} = 0$

We obtained a set of equilibrium points. For the first equilibrium point, which corresponds to zero, it signifies an extinction equilibrium in the context of this model and is therefore not meaningful. Hence, we only consider the second equilibrium :

$$\begin{cases} U^* = \frac{1}{b_2} [a_2 + \frac{c_1}{c_2} (\frac{a_1 b_3}{b_1} - a_3)] \\ V_1^* = \frac{a_1}{b_1} \\ V_2^* = \frac{1}{c_2} (\frac{a_1 b_3}{b_1} - a_3) \end{cases} \quad (20)$$

Step2: Find the Jacobian matrix of the system of equations

We define:

$$\begin{cases} \frac{dU}{dt} = f_1(U, V_1, V_2) \\ \frac{dV_1}{dt} = f_2(U, V_1, V_2) \\ \frac{dV_2}{dt} = f_3(U, V_1, V_2) \end{cases} \quad (21)$$

Therefore, the third-order Jacobian matrix has the following form:

$$J = \begin{bmatrix} \frac{\partial f_1}{\partial U} & \frac{\partial f_1}{\partial V_1} & \frac{\partial f_1}{\partial V_2} \\ \frac{\partial f_2}{\partial U} & \frac{\partial f_2}{\partial V_1} & \frac{\partial f_2}{\partial V_2} \\ \frac{\partial f_3}{\partial U} & \frac{\partial f_3}{\partial V_1} & \frac{\partial f_3}{\partial V_2} \end{bmatrix} \quad (22)$$

The following can be obtained by organizing:

$$J = \begin{bmatrix} a_1 & -b_1 U^* & 0 \\ b_2 V_1^* & b_2 U^* - c_1 V_2^* & -c_1 V_1^* \\ 0 & b_3 V_2^* & -a_3 + b_3 V_1^* - 2c_2 V_2^* \end{bmatrix} \quad (23)$$

Step 3: Solve the eigenvalues of the Jacobian matrix at the equilibrium point:

$$\det(J - \lambda I) = 0$$

where \mathbf{I} is the unit matrix and λ is the matrix eigenvalues.

Step 4: Eigenvalue analysis

We note that the eigenvalues obtained by solving the third-order Jacobian matrix J are $\lambda_1, \lambda_2, \lambda_3$. When all eigenvalues at the equilibrium point of the system have negative real parts, the point is a stable equilibrium point, that is:

$$\operatorname{Re}[\lambda_1], \operatorname{Re}[\lambda_2], \operatorname{Re}[\lambda_3] < 0$$

When at least one eigenvalue has a positive real part, the point is unstable, and the degree of instability is related to the magnitude of the positive eigenvalue. Therefore, for two systems of the same type, we can judge the difference in their stability by comparing the magnitudes of the real parts of their eigenvalues. The smaller the real part, the better the stability is considered to be.

4.5 Improved Lotka-Volterra equations based on the parasite model

4.5.1 Problem analysis

In ecological system modeling, when considering additional influencing factors, it is necessary to carefully assess whether these factors tend to be involved in species interaction or not to be involved in species interaction. This assessment determines the way in which the model should be adjusted to more accurately reflect the complexity of real ecological systems.

nint-environmental input, e.g. F .

int-species input, e.g.

$$\frac{dx_4}{dt} = (r_{\text{self}4} + r_{\text{ext}4})x_4 \quad (24)$$

We need to analyze the categorization of parasitic factors:

- **From the perspective of environmental factors:** Parasite species, distribution density, activity, etc. are closely related to environmental factors such as flow rate, water quality, etc. There are significant differences between different environments, indicating that parasites tend to be influenced by environmental conditions, which is not involved in species interaction.
- **From the perspective of infection mechanisms:** Parasitic infections can be transmitted through intermediate hosts along the food chain, resulting in different symptoms in various hosts. Therefore, utilizing environmental variables better reflects the unique transmission mechanisms of parasites and their distinct impacts on different hosts.

In conclusion, when incorporating parasites into the model, we treat them as environmental variables. We define several parameters:

Table 4: Parameters of Infection Rate

Parameters	Definition
θ	The infection rate of sea lampreys
θ_1	The infection rate in host fish

Based on the data^[5] for the parasitic θ in the Great Lakes, we set the range of values for θ to be 0.05-0.25.

The symptoms of the infected individuals

- **The infected sea lampreys:** Damaged skin and muscles leading to reduced mobility.

1. A decline in the feeding capability of sea lampreys.

$$\begin{aligned}\lambda'_{21} &= 0.8\lambda_{21} \\ \lambda'_{21} &= (1 - 0.2\theta)\lambda_{21}^I\end{aligned}\quad (25)$$

2. An increase in the predatory fish's ability to prey on sea lampreys.

$$\lambda'_{32} = 1.2\lambda_{32} \quad (26)$$

- **The infected host fish:** Gastrointestinal damage leading to reduced survivability in infected host fish.

$$\begin{aligned}d_1^I &= 1.05d_1 \\ d'_1 &= d_1 + 0.05\eta \cdot \theta \cdot d_1 \cdot \lambda'_{21} \cdot \frac{x_2}{x_1}\end{aligned}\quad (27)$$

The number of infected individuals The primary target of parasitic infection is the adult sea lamprey^[5], and it infects its host fish through the food chain.

To simplify the problem, it is assumed that the infected sea lampreys will invariably lead to parasitic infection in their host fish. Thus, we obtain:

$$\begin{cases} x_2^I = x_2\theta \\ x_1^I = x_1\theta_1 \end{cases} \quad (28)$$

where

$$\theta_1 = \eta \cdot \theta \cdot \lambda'_{21} \cdot \frac{x_2}{x_1}$$

4.5.2 The Lotka-Volterra equation based on the parasitic model

$$\begin{cases} \lambda'_{21} = (1 - 0.2\theta)\lambda_{21} \\ \lambda'_{32} = 1.2\lambda_{32} \\ d'_1 = d_1 + 0.05\eta\theta d_1 \lambda'_{21} \frac{x_2}{x_1} \end{cases} \quad (29)$$

By substituting the above-mentioned parameters, we obtain:

$$\begin{cases} \frac{dx_1}{dt} = \alpha_1 x_1 + \beta_1 x_1^2 - \psi_{12} x_1 x_2 - \varphi x_2 \\ \frac{dx_2}{dt} = \alpha_2 x_2 + \beta_2 x_2^2 + \lambda'_{21} x_1 x_2 - \psi_{23} x_2 x_3 \\ \frac{dx_3}{dt} = \alpha_3 x_3 + \beta_3 x_3^2 + \lambda'_{32} x_2 x_3 \end{cases} \quad (30)$$

where

$$\varphi = 0.05\eta \cdot \theta \cdot d_1 \cdot \lambda'_{21}$$

5 Application of the Model

5.1 Effects of sex ratio changes on population size

We used resource abundance as the independent variable to create a plot of the number of organisms in each group of the three-tier food chain at steady state against resource abundance:

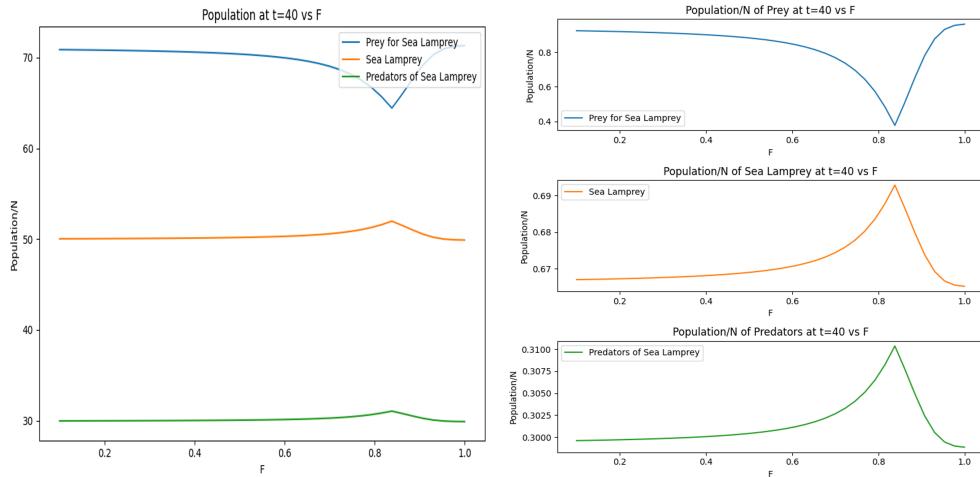


Figure 10: Population dynamics chart at different food abundances

The graph illustrates the trend of sea lamprey population size in response to changes in food resource abundance. It is evident that there exists an optimal value for food resource abundance (approximately 0.8), resulting in the maximum population size of sea lamprey.

This phenomenon is attributed to the influence of population sex ratio on the reproduction of sea lamprey, where the sex ratio is indirectly controlled by growth rates, which, in turn, are influenced by food resource abundance.

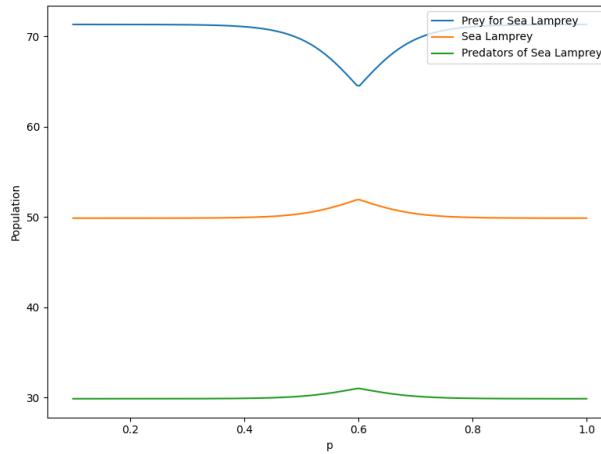


Figure 11: The relationship between male probability p and population

As seen from the graph, when the parameter p , influenced by food resource abundance, continuously changes, there is a maximum population size at positions slightly deviating from p_0 , corresponding to F in the figure 10 at the position where $F = 0.86$.

When the food relative abundance is at a higher level, the population size determined by sex ratio reaches a maximum. However, excessively high F levels may lead to extreme sex ratios due to the shorter development time of larval. Therefore, when F is too high, the population size decreases instead.

Furthermore, combining the $p - F$ plot, we can observe that the maximum population density occurs at a point where p is slightly below 50%. If we assume that the sex of the sea lamprey is determined from its larval stage and ignore differences in the survival conditions between male and female fish, the sex ratio of the fish population under this condition can be considered as 50%. However, this condition has not yet reached the maximum population size of the sea lamprey

Therefore, it is not difficult to conclude that the variability in sex provides a potential advantage for the increase in population size.

5.2 Effects of sex ratio changes on ecosystem stability

When conducting trajectory analysis of the system stability changes caused by gender variations resulting from resource fluctuations, we selected nine points at evenly spaced intervals within the range of $F \in [0.2, 1.0]$, plotted their phase diagram, and observed whether there were noticeable changes in stability.

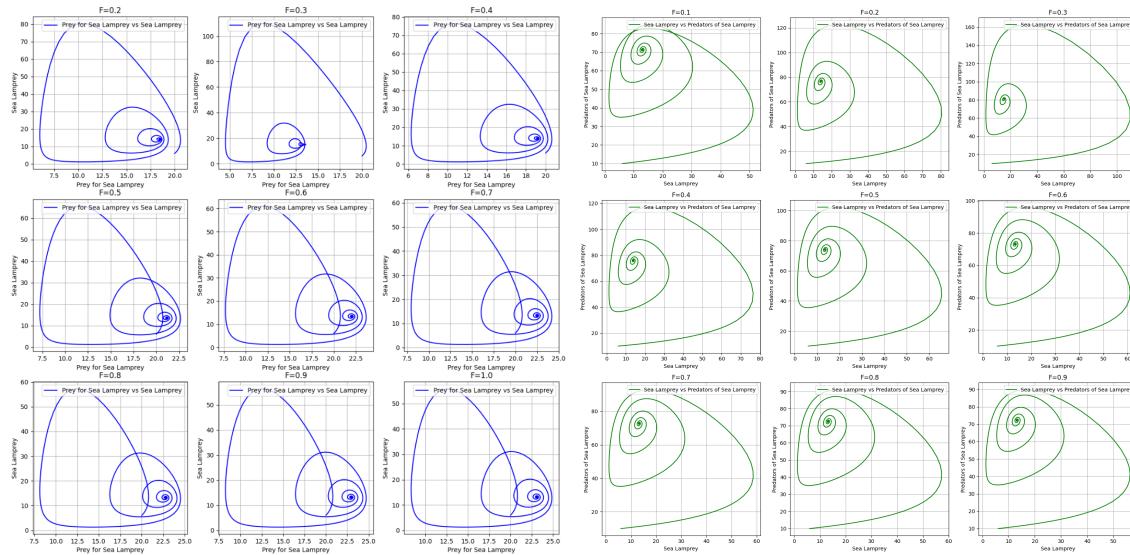


Figure 12: The phase diagram of sea lamprey and prey at different food abundances(Left) and phase diagram of sea lamprey and predators at different food abundances(Right)

We observe that as the parameter F increases, the spiral pattern in the phase diagram gradually becomes more sparse, which suggests that the system tends towards a certain equilibrium point.

Additionally, the progressively sparse spiral indicates that the oscillations in the population sizes are relatively small, implying that the system is a relatively stable dynamic system.

When the proportion of males in the population, represented by p continuously changes, the eigenvalues vary as shown in the graph:

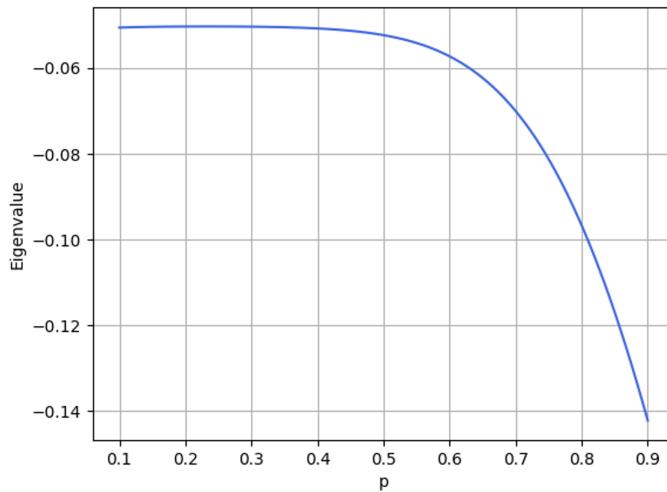


Figure 13: The relationship between male probability p and eigenvalues

This variation in eigenvalues indicates that as the proportion of males increases in the population, the stability of the ecosystem is gradually improving.

Assuming that the gender of the sea lamprey is fixed and considering equal survival rates for both genders, we assume an equal number of males and females in the sea lamprey population. Consequently, corresponding eigenvalues when $p = 0.5$ represents the stability under this condition.

Clearly, when the proportion of males is high, the local stability of the ecosystem also increases. but when the male ratio, or p , is low, the curve indicates that the stability of the system is nearly the same as that at $p = 0.5$.

Therefore, we can conclude that the variable sex ratio of hagfish provides a potential stabilizing factor for its ecological environment.

5.3 Effects of sex ratio changes on parasitism

According to the enhanced Lotka-Volterra equations, we plotted the relationship between the gender ratio of the sea lamprey and the quantity of parasites in two scenarios: considering the impact of parasitic factors and not considering the impact of parasitic factors.

We observe that introducing the influence of parasites into the equations has little effect on the population dynamics of the sea lamprey. The population size of the host shows a noticeable decrease at the peak of the sea lamprey population, indicating the lethal impact of parasites.

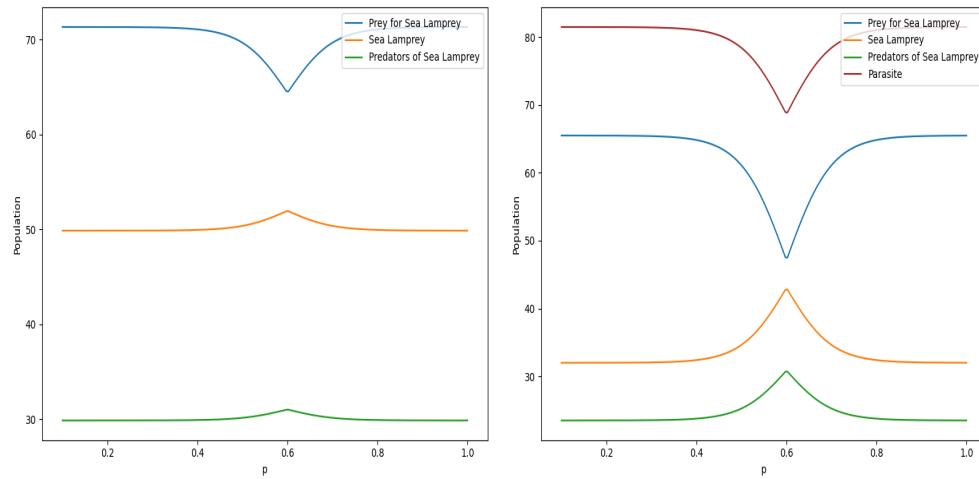


Figure 14: The relationship between sex ratio and population quantity without the inclusion of parasitic factors(Left) and relationship between sex ratio and population quantity with the inclusion of parasitic factors(Right)

We still assume that the gender of the sea lamprey is fixed (determined in the larval stage). We can find that only around $F = 0.55$, when the food resource conditions are moderate, the variability in sea lamprey sex significantly reduces the population size of parasites compared to when gender is fixed. Conversely, at other levels of food resource conditions, the impact of gender variability is to slightly increase the population size of the parasite population.

6 Sensitivity Analysis and Convergence Assessment

In this paper, we explored a vast ecological interaction system, where mechanisms of interaction among individuals, temporal variations in individual internal properties, and the influence of the external environment all needed to be considered. Consequently, we inevitably utilized a considerable number of parameters to describe these intricate relationships.

For certain key parameters, although the relevant literature did not provide explicit values, their significance to the model was crucial.

Therefore, we conducted sensitivity analyses to explore the impact of these parameter values. This aids in assessing the robustness and scalability of the model, providing valuable insights for further research.

6.1 Hierarchical Bayesian logistic regression model convergence assessment

We conducted Markov Chain Monte Carlo (MCMC) sampling to obtain the posterior distributions of the intercept and slope, and created trace plots and probability density plots:

- **Trace plot:** The trace plot shows random and stable characteristics, with no apparent trend or periodicity.
- **Probability density plot:** The probability distribution exhibits distinct peaks.

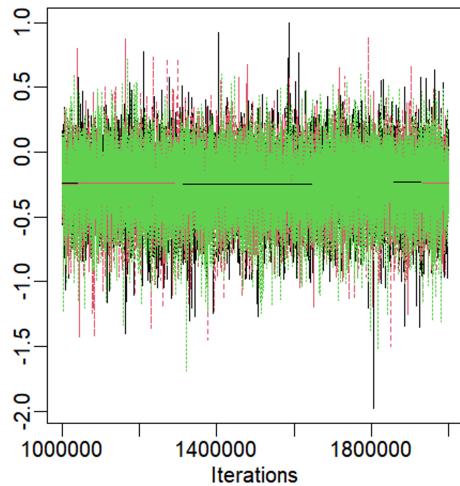


Figure 16: Trace plot for the intercept

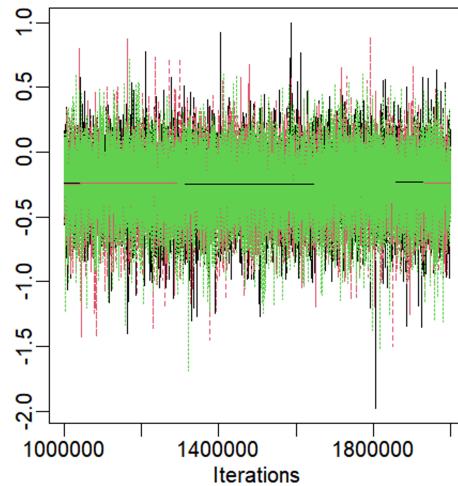


Figure 17: Trace plot for the slope

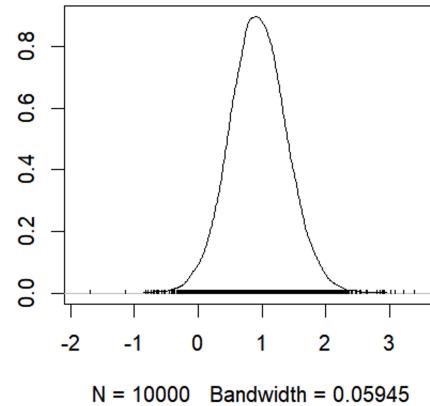


Figure 18: Probability density for the intercept

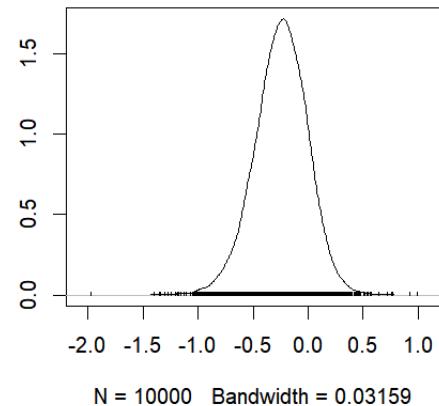


Figure 19: Probability density for the slope

As a result, the model demonstrates good stability and robust convergence.

6.2 Sensitivity analysis of the Lotka-Volterra equations based on the parasite model

6.2.1 Sensitivity analysis on initial conditions

In general, the quantity of higher-level organisms is usually less than that of lower-level organisms, primarily due to energy transfer and losses in the food chain.

The ratio between the quantities of these two is influenced by various factors such as the types and diets of organisms, environmental conditions, and the length of the food chain. It is generally considered to be between 40% and 60%. We simulate this ratio under different conditions by setting various initial conditions to evaluate the robustness of the model.

Situation when the quantity ratio is 40% (initial population density [30, 12, 5]):

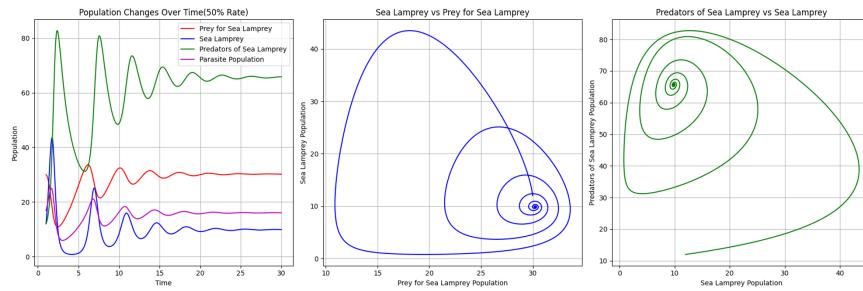


Figure 19: Population dynamics chart for Scenario One

Situation when the quantity ratio is 50% (initial population density [20,10,5]):

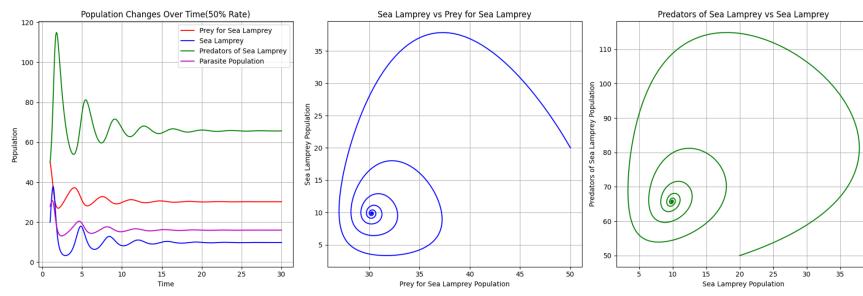


Figure 20: Population dynamics chart for Scenario Two

Situation when the quantity ratio is 60% (initial population density [50,30,18]):

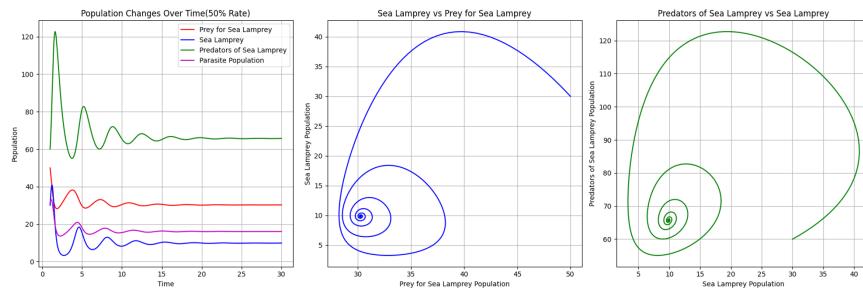


Figure 21: Population dynamics chart for Scenario Three

Based on the sensitivity analysis of the initial values for the enhanced Lotka-Volterra model, the results indicate good convergence within a reasonable range. Different initial conditions tend to stabilize over the iterative process with time , converging to nearly identical values. This stability and consistency suggest low dependence of the model on initial conditions, demonstrating strong robustness and reliability.

6.2.2 Analysis of the stability on parasite infection rate θ

We varied θ from 0.2 to 1 at regular intervals and plotted the phase diagrams under different θ values:

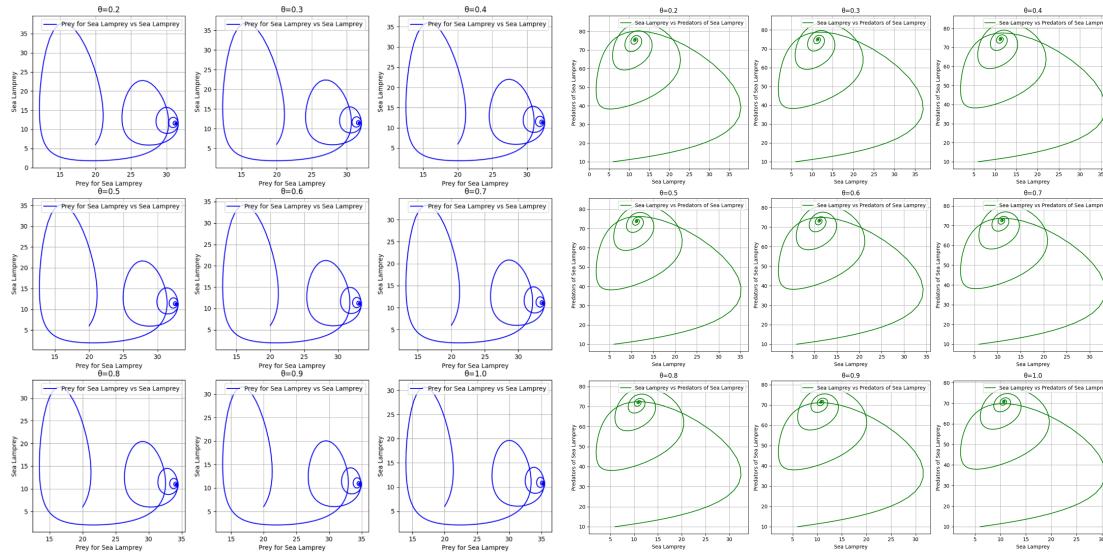


Figure 22: The phase diagrams under different θ values

It can be observed that, regardless of the values of θ within the range of 0 to 1, the quantity trajectory plots of the sea lamorey, prey, and predator all exhibit asymptotic characteristics towards equilibrium points, forming a spiral pattern.

This indicates that the variation in the parameter θ does not lead to an overly significant impact on the stability of the system and the interactions among species. It also confirms the reliability and effectiveness of the model.

7 Model Evaluation and Further Discussion

7.1 Strength

- The Enhanced Lotka-Volterra Model has more adjustable parameters, which are adjusted on a case-by-case basis to better adapt to different ecosystems and species with variable sex ratios.
- When a new influence factor is added, it can be used as a species input or an environmental input according to whether it prefers factors involved in species interaction or non-interaction, and the modification mode of the model can be adjusted.
- The model avoids the complexity of modeling based on biological mechanisms by utilizing a hierarchical Bayesian regression model. Through the analysis of locally collected small-sample data, we can extract environmental characteristics of the studied water area at a relatively low cost. The model abstracts the complex interactions among species in the ecosystem using the Lotka-Volterra equations, ensuring the generalizability of the model.

- The Enhanced Lotka-Volterra Model introduces more non-linear effects by incorporating quadratic and interaction terms. These non-linear effects aim to better capture the complexity of species interactions in the ecosystem.

7.2 Weakness

- In the real world, data is continuous. We argue that iterating T in years makes the continuous data lose some information. Similarly, F and infection rates are not constant with respect to an ecosystem.
- The Enhanced Lotka-Volterra Model introduces more non-linear effects by incorporating quadratic and interaction terms. These non-linear effects aim to better capture the complexity of species interactions in the ecosystem.

8 Conclusion

Through model simulations, we found:

- The variable gender of the sea lamprey provides more potential for stability in the local ecosystem.
- In most cases, the variable gender of the sea lamprey tends to increase the population of the parasite community compared to a fixed gender ratio.
- When food resources are abundant, the variable gender of the sea lamprey leads to a larger population size. However, when food resources are inappropriate (too scarce or too abundant), the extreme gender ratio of the sea lamprey results in a reduced population size.
- Changes in the population size of the sea lamprey caused by gender variations propagate through the food chain, manifesting in similar population trends for its predators upstream, while the prey of the sea lamprey exhibit opposite trends.

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Report on Use of AI

1. OpenAI ChatGPT(Feb 3,2024 version 3.5)

Query1: What models can we use to study the effect of sex ratio on birth mortality?

Output: To study the effect of sex ratio on birth mortality, various models can be employed, each capturing different aspects of the relationship between sex ratio and mortality. Here are several models that can be used for this purpose:

1. Mortality Rate Models: -Logistic Regression Models.
- 2.Survival Analysis Models: Kaplan-Meier Survival Analysis.
- 3.Population Dynamics Models: Lotka-Volterra Model.
- 4.Demographic Models. 5.Epidemiological Models.
- 6.Bayesian Models.

When choosing a model, it's essential to consider the specific characteristics of the population under study, the available data, and the research question at hand. Integrating multiple models or approaches can provide a more comprehensive understanding of the complex relationship between sex ratio and birth mortality.

2. OpenAI ChatGPT (Feb 4,2024 version 3.5)

Query1: Are there any requirements for the Lotka-Volterra equation in terms of conditions of applicability?

Output: The Lotka-Volterra equations, commonly used to model predator-prey interactions, come with certain assumptions and conditions:

1. **Two-Species Interaction:** - Designed for a single predator and prey species.
2. **Constant Parameters:** - Assumes stability in predation and reproduction rates.
3. **No Immigration/Emigration:** - Assumes a closed population system.
4. **Homogeneous Environment:** - Assumes uniform resource distribution.
5. **Linear Functional Responses:** - Assumes direct and proportional relationships.
6. **No Time Delays:** - Assumes instantaneous responses to changes.
7. **Sustainable Resources:** - Assumes a consistent resource base.
8. **Deterministic Nature:** - Does not consider stochastic events.
9. **Single Prey, Single Predator:** - Most suitable for one prey and one predator.
10. **No Evolutionary Changes:** - Does not account for evolutionary adaptations.
11. **Continuous Populations:** - Assumes continuous populations.

Despite these simplifications, the model provides valuable insights into population dynamics. Researchers should be aware of its limitations and context when applying it.

3. OpenAI ChatGPT (Feb 3,2024 version 3.5)

Query1: What is the significance of probability density plot and trace plot in MCMC

Output: The probability density plot and trace plot in MCMC have specific significance in the context of Bayesian statistics:

1. **Probability Density Plot:** - **Significance:** The probability density plot visualizes the distribution of samples obtained from MCMC in the parameter space. By observing the probability density plot, one can intuitively understand the possible range of parameter values and their relative likelihoods. This is crucial for determining the posterior distribution of parameters and constructing confidence intervals. - **Operation:** On the probability density plot, the x-axis represents the parameter values, and the y-axis represents the corresponding probability density. Kernel Density Estimation (KDE) is often used to smoothly estimate the probability density.
2. **Trace Plot:** - **Significance:** The trace plot displays the evolution of MCMC chains. Each chain's trajectory illustrates the variations in parameter values during the MCMC process, and multiple chains' trace plots provide an assessment of convergence and stability under different initial conditions. - **Operation:** On the trace plot, the x-axis typically represents the iteration number, and the y-axis represents the parameter values. Each chain is represented by a different color or line. Ideally, you want to see chains stabilizing over time, forming a stationary trajectory.

These graphical representations aid in the analysis of MCMC performance, such as checking for convergence to the target distribution and assessing issues like autocorrelation. If the probability density plot shows a reasonable posterior distribution and the trace plot exhibits stable chains, one can have more confidence in using the sampled data for parameter estimation and inference. Conversely, abnormal patterns in these plots may indicate the need for adjustments or improvements to the MCMC algorithm.