

Mystery of Sea Lampreys: Ecological Insights into Gender Ratios

Sea lampreys, among the oldest vertebrates globally, possess distinctive sex-determining characteristics that significantly influence both population dynamics and the ecosystem. To delve deeper into the intricacies of the sex-determining features of sea lampreys, we have devised the following mathematical models.

In Model I, we formulate equations based on the framework of **evolutionary game theory** in biology. By applying the principle of maximizing population size, we unveil the underlying mechanism behind the sea lamprey's strategy of "more males, fewer females" during periods of limited energy resources, such as food scarcity. Subsequently, we introduce the **$V - L$ Competition Equation**, representing the interplay between males and females. The stable solution reveals the overall sex ratio (R_M). To differentiate between R_M and individual sex differentiation ratio (P_M), we establish a specific relationship between P_M and external energy (CPE_n) through the **Logistic Model**.

In Model II, we initially categorized sea lampreys into six groups based on their biological behaviors: $L_1, L_2, M_1, M_2, F_1, F_2$. Employing the individual sex differentiation equations from Model I, we constructed a **Time-series-related Difference Equation Model** among these clusters to simulate variations in cluster numbers under diverse conditions. The outcomes revealed a correlation between the overall sex presentation ratio and external energy, represented by $R_M = 0.24e^{-123CPE_n} + 0.52$. Fitting the relationship between the overall sex presentation ratio and individual sex differentiation ratio, we get $R_M = -6.13e^{-4.63P_M} + 0.98$. Our findings suggested that **sex differentiation enhances sea lamprey population size under low energy conditions and fortifies their resilience against abrupt environmental degradation. However, it diminishes population resilience in times of environmental improvement.** Lastly, in examining species parasitizing sea lampreys, we incorporated a parasitism factor analysis, revealing that sex differentiation in sea lampreys contributes to heightened population fluctuations.

In Model III, we expanded upon the parasitic factors introduced in Model II, exploring diverse interspecific relationships. We innovatively introduced the concept of **population eigenvalues** and applied it to analyze interactions among sea lamprey populations, competitors, and predators. Our findings indicated that **sexual differentiation (1) enhances the competitive and predatory capabilities of sea lampreys, and (2) results in an increase in the population size of both sea lampreys and their predators, with a simultaneous extension in the period of change.** Based on this, we examined the sea lamprey's invasive impact on a lake ecosystem with multiple food chains, and assessed the stability using the **Shannon-Wiener index**. The results revealed a 10.2% reduction in ecosystem stability due to sea lamprey invasion, and the variable sex differentiation further increased destabilization by 17.3%.

Finally, we performed a sensitivity analysis on the parameters within the individual sex differentiation equation. The results indicated that, at a steady state, the model exhibited variations of no more than 10%, showcasing its robustness and generalizability. In addition, the strengths and weaknesses of the model were also analyzed.

Keywords: Sea lampreys, Sex Ratios, Evolutionary Game Theory, Difference Equation, Population eigenvalues, Ecological System Stability, Logistic Model

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1 Introduction

1.1 Problem Background

Lamprey is an ancient and mysterious aquatic creature that has attracted widespread attention in the fields of ecology, biology and environmental science due to its unique adaptive sex ratio changes and important role in aquatic ecosystems.



Figure 1: Picture of sea lampreys

Lampreys have no scales, fins, or operculum, and their skeletons are made of cartilage. It has a disc-shaped sucker-like mouth surrounded by sharp horny teeth that suck the blood and body fluids of host fish, making them efficient killers of lake trout and other bony fish. Studies show that one lamprey can kill approximately 40 fish each year, which is why they cause serious ecological damage to the Great Lakes in the United States.

By specifically exploring the sexual differentiation of lampreys and their interactions with ecosystems, we can reveal their unique biological characteristics, which in turn provides important clues for a more comprehensive understanding and protection of the operation of aquatic ecosystems. We use this as the background of our model.

1.2 Restatement of the Problem

Through in-depth analysis and research on the background of the problem, combined with the specific constraints given, the restatement of the problem can be expressed as follows:

- Establish a mathematical model to describe the evolution of lamprey population size and sex ratio over time under different external conditions (mainly food supply). And compare the advantages and disadvantages of sexual adaptive differentiation of lamprey populations on population development.
- Extend the population model to a higher-level ecosystem model to analyze the impact of sexual differentiation of lamprey populations on ecosystem stability.
- Based on the analysis of the impact on ecosystem stability, the influence of sexual differentiation of lamprey populations on the overall ecosystem is further studied.
- Determine specifically whether sex changes in lamprey populations will bring benefits to other organisms in the ecosystem (such as parasites).

1.3 Literature Review

This question is mainly about mobilizing the sex ratio and its impact. we mainly focus on the **Mechanism** and the **Description of the phenomenon**.

- In terms of the mechanisms of sex differential: Bryan[5] et al. established a molecular-level model related to sex hormones. From a macro perspective Wang[1] drew on the concept of elasticity in economics to build a game model describing gender differentiation at the macro level.
- In describing the phenomenon of sexual differentiation, Johnson[3] et al. found that the larval growth rate directly influences the sex determination in sea lamprey. Since growth rate is closely related to population density, Docker[2] et al. and HARDISTY, M.[4] studied the relationship between the sex ratio and population density.
- To study the impact of sexual differentiation on ecosystems, Drossel and McKane[6] modeled the food webs using difference equations. Also, McCann[8] stated that diversity can be expected, on average, to give rise to ecosystem stability. Based on this, Nolan and Callahan[7] used the Shannon-Weiner index to measure ecosystem diversity and further evaluate ecosystem stability.

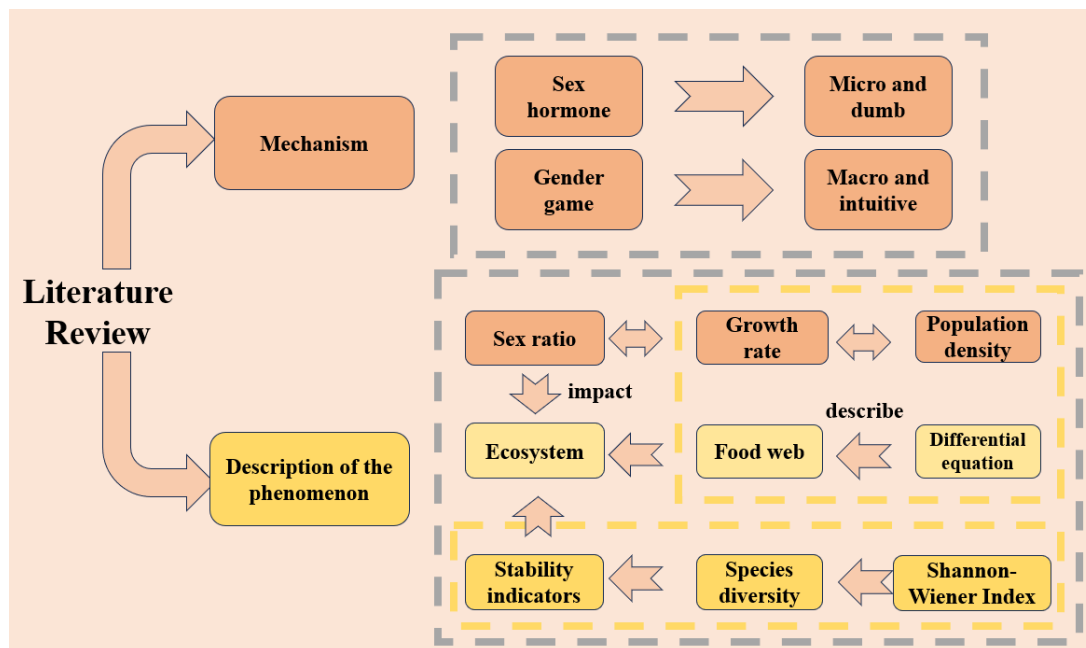


Figure 2: Literature Review Framework

1.4 Our Work

This task necessitates the development of a mathematical model to depict adaptive alterations in the sex differentiation of sea lampreys contingent upon resource availability. Consequently, we aim to evaluate the advantages and disadvantages associated with this ability. Our endeavor predominantly encompasses the following.

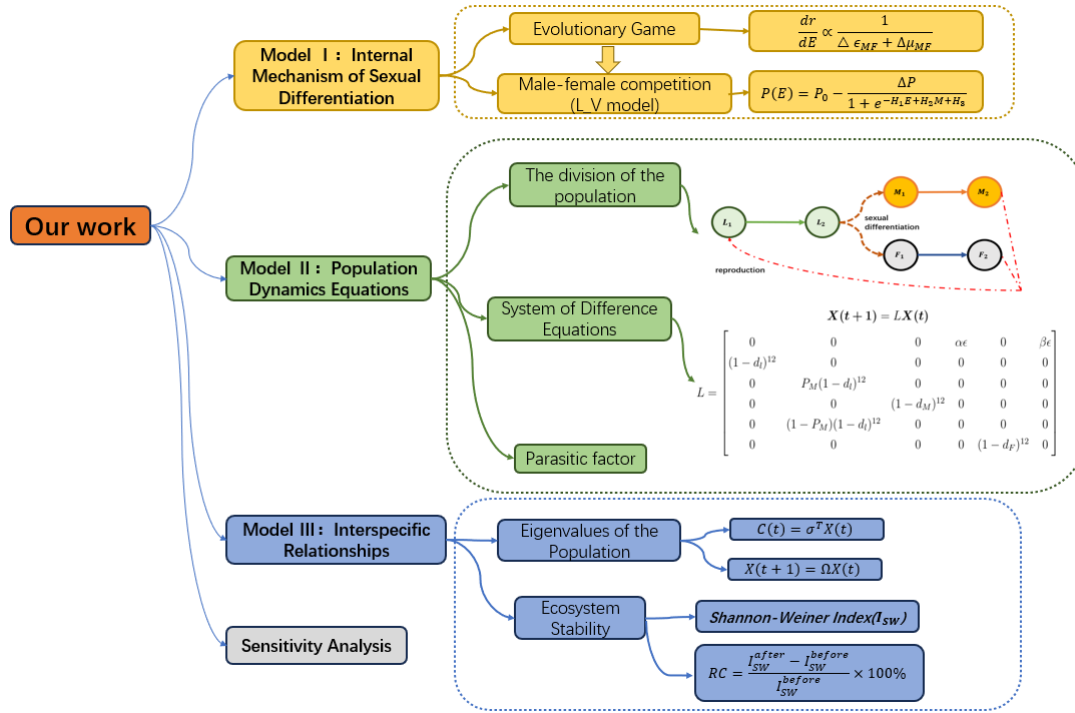


Figure 3: Flow Chart of Our Work

2 Notations

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

Table 1: Notations used in this paper

Symbol	Description
N_{total}	Total population of sea lampreys
P_M	Individual gender differentiation ratio(Male)
R_M	Population gender presentation ratio(Male)
$d_{L,M,F}$	Mortality rates for larvae, males, and females
$x_i(t)$	The population size of the i-th population at time t.
K	Carrying capacity of the environment
σ_i	Parasitic factors.
$C(t)$	Eigenvalues of population
CPE_n	Normalized energy
S_i	Inter-specific interaction factors

*Some variables are not listed here and will be discussed in detail in each section.

3 Model Preparation

3.1 Data Collection

The question did not provide us with data directly, so we need to consider which data to collect in the model building. Through the analysis of the problem, we need to collect the relevant information of sea lampreys, such as **their life cycle** and so on. The data sources are shown in Table 2.

Table 2: Data and Database Websites

Data content	Database Websites
Population Density Index	http://www.glfrc.org/
Physiology Introduction	https://www.noaa.gov/
Food Resources and Amount	https://www.fws.gov/
Literature	https://scholar.google.com/
Fishing Information	https://www.usda.gov/

3.2 Specific information about sea lampreys

This section summarizes the key physiological characteristics of the sea lampreys that are needed in model building.

- Sexual differentiation of sea lamprey is mainly determined by environmental factors (EDS), and the direction of sexual differentiation of sea lamprey larvae is directly determined by the growth rate [3]: energy-rich, fast growth rate, the larvae are more inclined to differentiate into females.
- Due to the different mortality rates of sea lamprey females and males and external environmental factors, the individual sex differentiation ratio and sex presentation ratio of sea lamprey population are different, and the model needs to distinguish between the two variations. In general, the ratio of males is greater than that of females.
- Sea lampreys' sex organs require more energy to develop into ovaries than testes, that is, more energy is needed for sex differentiation into females; females consume more energy to lay eggs than males consume to ovulate sperm, so females need more energy to survive and generally have more energy and larger body size.
- There are four stages in the life cycle of the sea lamprey: egg, larvae, juvenile, and adult. Each stage has different physiological characteristics
- Sea lampreys have a high number of viable eggs from a single breeding, and they die within a short period of time after completing their breeding activities.
- In the sea lamprey population, males are more aggressive, i.e., more predatory, more competitive, and less likely to be preyed upon.

4 Assumptions and Explanations

Considering that practical problems always contain many complex factors, first of all, we need to make reasonable assumptions to simplify the model, each of which is properly justified.

- **Assumption 1: Merging parasitic and predatory behaviors of sea lampreys into predation for analysis**

Explanation: The parasitic behavior of sea lampreys is highly lethal; for most small fish, being parasitized leads to death. The energy of the prey is transferred

to the sea lamprey, resembling predation behavior. We can approximate parasitism as predation to simplify the inter-species interaction model.

- **Assumption 2: When analyzing the external environment, the primary focus is on the variations in energy levels.**

Explanation: The individual gender differentiation ratio of sea lampreys is mainly determined by the energy level.

- **Assumption 3: The impact of major disasters such as earthquakes and tsunamis on population numbers is not within the scope of our consideration.**

Explanation: These major disasters are rare events in reality. To simplify the problem, our model doesn't take them into consideration.

- **Assumption 4: Only consider the differences in age and gender of sea lampreys while neglecting other individual variations.**

Explanation: The key point of this paper is to understand the impact of sex differentiation on population behavior, and this assumption helps simplify the problem.

- **Assumption 5: The data in this research is accurate.**

Explanation: We assume the data we collect of lampreys is accurate so that we can base a reasonable mathematical model on it.

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

5 Internal Mechanism of Sexual Differentiation

5.1 Evolutionary Game

Guidelines for animal behavior: **The ultimate goal of all activities in a population of organisms is to bring the population to or towards its maximum size under the constraints of the limited energy.** To achieve this, life activities are rationally regulated according to energy levels, involving the trade-off between the organism's own survival and the reproduction of its offspring, which may result in changes in survival, reproduction, or sex ratios.

For the sea lamprey, we introduce the proportion of males in the population as a variable, discretize the population size of the biological population in a phased manner, and obtain the following equation for the evolution over time.

$$N(T+1) = rN(T)\epsilon_M + (1-r)N(T)\epsilon_F + rN(T)\mu_M + (1-r)N(T)\mu_F \quad (1)$$

Here $N(T)$, $N(T+1)$ denote the population size in the T th and $(T+1)$ st time period, respectively, r denotes the proportion of male individuals in the population, ϵ_M , ϵ_F denote the factors contributing to the reproductive behavior by males and females, respectively, and μ_M , μ_F denote the survival rates of male and female individuals, respectively. Divide both sides simultaneously by $N(T)$ to get the growth rate λ :

$$\lambda = \frac{N(T+1)}{N(T)} = r\epsilon_M + (1-r)\epsilon_F + r\mu_M + (1-r)\mu_F \quad (2)$$

Since $r, \alpha, \epsilon, \beta, \mu_M, \mu_F$ are all functions of the level of energy obtained by the population, E , it is possible to express λ as a function of E , i.e., $\lambda = \lambda(E)$. According to

animal behavioral guidelines, populations spontaneously choose the survival and reproduction mode that makes λ maximal, where we only consider the effect of energy, the impact equation is as follows:

$$\frac{d\lambda}{dE} = \frac{dr}{dE}\epsilon_M - \frac{dr}{dE}\epsilon_F + \frac{dr}{dE}\mu_M + r\frac{d\mu_M}{dE} - \mu_F\frac{dr}{dE} + (1-r)\frac{d\mu_F}{dE} \quad (3)$$

From the information in (4.4), **we assume that the contribution factors of females and males to reproductive behavior do not vary with energy level, whereas the proportion of males, and the survival rates of both females and males are affected by energy level**, in the form we will give in (5.3), (6.2.3).

For λ to reach its maximum value λ^* , the following differential expression needs to be satisfied:

$$\frac{d\lambda^*}{dE} = 0 \quad \frac{d^2\lambda^*}{dE^2} < 0 \quad (4)$$

Substituting Eqs. (2),(4) into Eq. (5) yields the following variation in the proportion of males with energy level when the population behavior is optimal:

$$\frac{dr}{dE} = \frac{-r\frac{d\mu_M}{dE} - (1-r)\frac{d\mu_F}{dE}}{\epsilon_M - \epsilon_F + \mu_M - \mu_F} \quad (5)$$

Since the survival of females and males is positively correlated with the level of energy levels and the proportion of males, r , varies between 0 and 1, the numerator less than 0 is constant:

$$0 < r < 1 \quad \frac{d\mu_M}{dE} > 0 \quad \frac{d\mu_F}{dE} > 0 \quad (6)$$

The sign in Eq.(6) is determined only by the denominator, which is related to energy levels and the magnitude of parameters. The choice of these parameters as a whole responds to the sensitivity of male and female individuals to resources in terms of increasing population size. If males are less sensitive to resource use than females, energy is reduced by an equal amount and the number of male individuals is reduced less than that of females, i.e., the proportion of males increases, just like sea lampreys.

The sex ratio of the sea lamprey is closely related to the growth rate v , which is directly determined by the energy level, i.e:

$$v \propto E \quad (7)$$

The higher the energy level, the faster the growth rate of individuals and the smaller the proportion of males in the population, further justifying **the gender game model**. Based on this, we can also transform all functions on growth rate into functions on energy, i.e., the parameters in this paper are only considered as functions of energy.

5.2 Gender differentiation ratio in the population.

In the previous section, we explained the correlation between the proportion of males in a population and energy levels **from an evolutionary perspective but did not obtain a display expression**. In this section, we seek to give a specific form for the proportion of males versus energy levels in populations of sea lampreys.

Assuming that within the population of sea lampreys, males and females represent two distinct subspecies primarily characterized by a competitive relationship, the

Lotka-Volterra model yields the following equations:

$$\begin{cases} \frac{dM}{dt} = r_1x(1 - \frac{M}{K_1} - S_2\frac{F}{K_2}) \\ \frac{dF}{dt} = r_2y(1 - \frac{F}{K_2} - S_1\frac{M}{K_1}) \end{cases} \quad (8)$$

Herein, M and F represent the quantities of male and female individuals, respectively. The parameters r_1 and r_2 denote the intrinsic growth rates of females and males, while K_1 and K_2 signify the environmental carrying capacities for females and males. Additionally, S_2 and S_1 represent the competition impact factors of females on males and males on females, respectively, within the Lotka-Volterra model.

The stable solutions for the system of equations (8) can be determined as follows: $M^* = \frac{S_1-1}{S_1S_2-1}K_1$ $F^* = \frac{S_2-1}{S_1S_2-1}K_2$ At equilibrium, the proportion of males in the sea lamprey population is given by $r = \frac{M^*}{F^*+M^*}$. According to the background of the study, this r corresponds to the gender presentation ratio R_M , which is related to the ease of external energy acquisition represented by E . In other words, $R_M = R(E)$, and its specific form is provided in Equation (6.3).

5.3 Individual gender differentiation ratio

For larvae, the ratio of gender differentiation does not exhibit a linear or unrestricted relationship with energy. In cases of significant deviations where there are either predominantly females or predominantly males, the rate of change is noticeably reduced. As the deviation diminishes, the rate of change gradually increases, showing an overall "S"-shaped trend. Therefore, based on the **Logistic Model**, we establish the following equation:

$$P(E) = P_0 - \frac{\Delta P}{1 + e^{-H_1E+H_2}} \quad (9)$$

Here, H_1 is a factor measuring the individual gender differentiation response, and H_2 represents the shift constant.

6 Population Dynamics Equations

In this section, we develop a modified **Difference Equation Model** describing the evolution of sea lamprey populations, taking into account the sex differentiation of sea lampreys as well as the effects of external energy levels. Using this model, together with data from the Great Lakes and related literature, we predicted the evolution of the sea lamprey population size over a long period under simple external conditions.

6.1 The establishment of the model

6.1.1 Delineation of populations

In order to simulate the evolution of the sea lamprey population more realistically, we first attempted to divide the entire population into several groups with different physiological parameters based on the biological characteristics of sea lampreys in (4.4).

Sexual differentiation in sea lampreys generally occurs when juveniles are 2 years old, before which the gonads are immature and sexless. Accordingly, we tentatively classified the sea lamprey population into three parts: juveniles, males, and females.

Further, in context, sex differentiation occurs only in 2-year-old individuals at each stage in the juvenile cohort, so the juveniles are divided into two age groups in terms of years, with the same physiological parameters except for the occurrence or not of sex differentiation.

After differentiation, male and female individuals have different mortality rates, and each period is characterized by the reproductive activity of age-appropriate male and female individuals; to reflect this actual process, we divide the male and female groups equally into two periods each measured in years. **The first period consists of females and males who have just completed differentiation, and the second period consists of females and males who are about to give birth and die immediately after giving birth.** The transition from the early to the late stages is subject to a process of natural selection, which is reflected in the mortality rate.

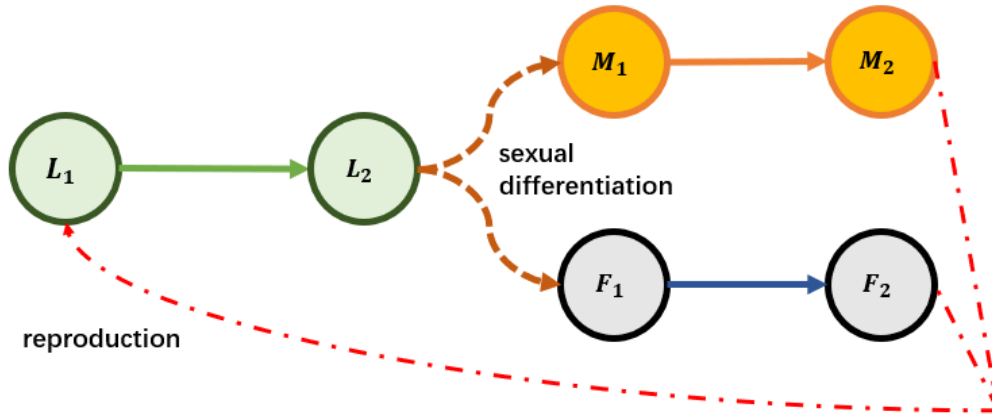


Figure 4: Division of populations

6.1.2 Specific form of the model

We denote by $x_1(t), x_2(t), x_3(t), x_4(t), x_5(t), x_6(t)$ the number of individuals in the $L_1, L_2, M_1, M_2, F_1, F_2$ groups in the graph at time period t , which satisfy the following evolutionary equation:

$$\begin{cases} x_1(t+1) = [\alpha x_4(t) + \beta x_6(t)] \cdot \epsilon \\ x_2(t+1) = (1 - d_l)^{12} x_1(t) \\ x_3(t+1) = P_M (1 - d_l)^{12} x_2(t) \\ x_4(t+1) = (1 - d_M)^{12} x_3(t) \\ x_5(t+1) = (1 - P_M) (1 - d_l)^{12} x_2(t) \\ x_6(t+1) = (1 - d_F)^{12} x_5(t) \end{cases} \quad (10)$$

Using $\mathbf{X}(t) = [x_1(t), x_2(t), x_3(t), x_4(t), x_5(t), x_6(t)]^T$ to denote the distribution of the number of the population at the time of period t , the system of equations (10) can be written as

$$\mathbf{X}(t+1) = L\mathbf{X}(t) \quad (11)$$

$$L = \begin{bmatrix} 0 & 0 & 0 & \alpha\epsilon & 0 & \beta\epsilon \\ (1 - d_l)^{12} & 0 & 0 & 0 & 0 & 0 \\ 0 & P_M(1 - d_l)^{12} & 0 & 0 & 0 & 0 \\ 0 & 0 & (1 - d_M)^{12} & 0 & 0 & 0 \\ 0 & (1 - P_M)(1 - d_l)^{12} & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & (1 - d_F)^{12} & 0 \end{bmatrix} \quad (12)$$

where α, β denote the contribution factors of males and females to the number of reproductive behaviours, respectively, ϵ denotes the number of viable eggs in a single reproductive behaviour, P_M is the proportion of hatchlings that differentiate into males, and d_l, d_M, d_F are the monthly mortality rates of hatchlings, males, and females, respectively. All are functions of energy level, the exact form of which is given in (6.2).

6.2 The parameters

In order to solve the model, specific parameter values or parameter expressions are required. In this subsection, we first analyzed the energy level E , which gives a range of variation in food availability based on the relative abundance of the main food (lake trout) for the sea lampreys in the Great Lakes, and then normalized the energy level. Based on this, the remaining parameters in the model with energy level as the independent variable were considered, their functions on energy level E were specifically given, and the parameters in the functions were fitted to the available data.

6.2.1 Measurement of energy levels

From the relative abundance and CPE index of lake trout in the Great Lakes, it is reasonable to assume that the maximum energy level provided by lake trout is $CPE = 8$, defining the energy level in this maximum food supply scenario as 1, whereby the level of food supply for sea lampreys in real-world scenarios can be mapped to the level of energy between $[0,1]$ to eliminate the effect of different magnitudes.

6.2.2 Individual Gender Differentiation Ratio: P_M

Introducing the effect of population size on the basis of (5.2): the change in the sex ratio of the population with energy gives the sex differentiation ratio as a function of energy level as:

$$P_M = P_0 - \frac{\Delta P}{1 + e^{-H_1 E + H_2 - H_3 M}} \quad (13)$$

Where H_3 responds to the magnitude of the effect of the existing population size on the proportion of sex differentiation, P_M indicates the proportion of sex differentiation of the population, and the rest of the parameters have the same significance as in equation (13).

6.2.3 Mortality Rate: d

We found that energy levels, in addition to affecting population sex in sea lampreys, can alter population sex ratios by affecting mortality rates of both males and females, as well as undifferentiated juveniles. The effect of energy level on mortality was small

within the given energy range, and we approximated this as a **linear relationship**. Taking into account the differences in energy requirements for survival and energy utilization capacities of juveniles, males, and females, the mortality function for the three species was obtained in the following form:

$$\begin{cases} d_l = a_l - b_1 \times E \\ d_M = a_2 - b_2 \times E \\ d_F = a_3 - b_3 \times E \end{cases} \quad (14)$$

Combined with a short-term numerical indicator for the Great Lakes population of sea lampreys, we fitted, and parameter values were obtained:

a_1	a_2	a_3	b_1	b_2	b_3
0.126	0.125	0.143	0.027	0.009	0.018

As can be seen from the parameters, the mortality rate of females was always higher than that of males, and the difference between the two increased with higher energy. Overall, all three mortality rates increased with decreasing energy, but all varied within a small range.

6.2.4 Environmental Capacity: K

The eigenvalue modulus length of the system of difference equations (11) corresponding to the iterative matrix (12) will be greater than one under some given parameter conditions, affecting the convergence of the iteration results, which is not in line with the reality of nature. Considering the effects of energy supply level and intra-population competition, in reality, we rationally introduced the environmental capacity to limit the growth of population size. Due to the difference in energy requirements between female and male individuals, **the environmental capacity is also affected by the sex ratio**, whereby the expression is given as follows:

$$K = (a + bE) \cdot \frac{1}{1 + e^{c-dP_M}} \quad (15)$$

where a, b, c, and d are constants to be found. Combined with the data in the related literature [4], the specific expression was fitted to obtain the following:

$$K = 20000 \cdot \frac{(2 + E)}{1 + e^{3(1-2P_M)}} \quad (16)$$

6.3 The results and further analysis

Combining the model and parameters given in (6.1) and (6.2), adjusting the initial value and energy level, we find that **under the condition of a given energy level, the population parts converge to the same value when the initial value does not change very much**, which indicates that the model is robust to the selection of the initial value. At steady state, the relationship between the number of population components and the energy level is shown in Fig. 5.

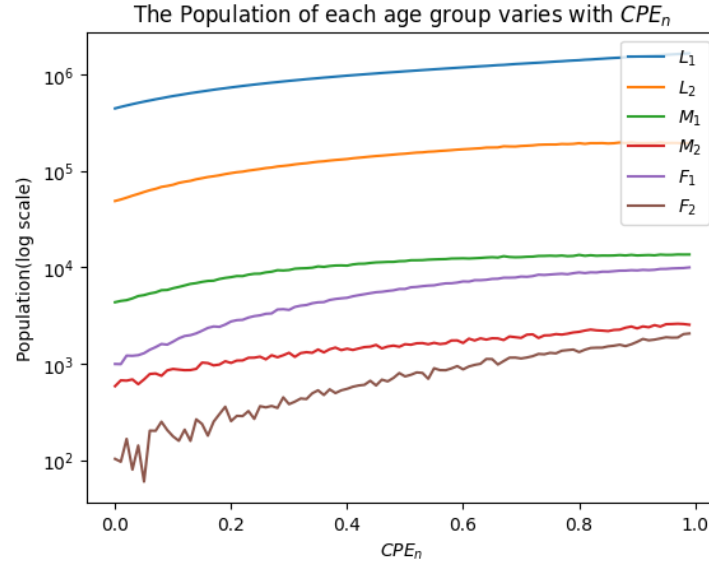


Figure 5: The population of each group varies with CPE_n

According to Figure 5, the number of larvae in the population is significantly larger than the number of adults because the sea lamprey has a high number of viable eggs from a single spawning and undergoes a mortality screening at each stage of age, which is in line with the actual situation. On the other hand, the number of females and males tended to be the same as the energy level increased, and **the lower the energy level, the higher the sex ratio of males in the population.**

The specific number of different groups were intercepted at $CPE_n=0.97$ and $CPE_n=0.0101$, respectively, and represented in a bar chart as in Figure 6.

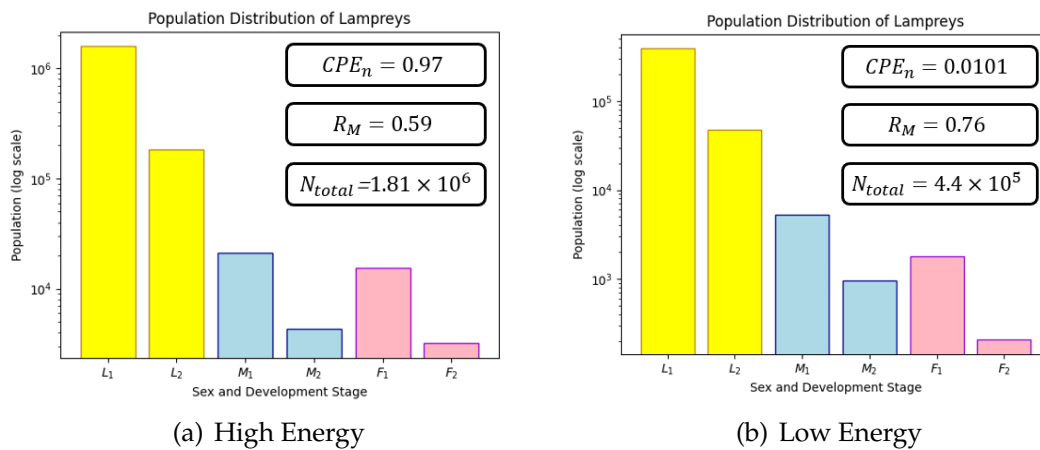


Figure 6: The population of each group under certain CPE_n

As can be seen from the figure, as the energy level decreased from 0.97 to 0.0101, on the one hand, the population size of the sea lamprey at equilibrium decreased significantly, which was mainly due to the decrease in the environmental capacity caused by the decrease in energy; on the other hand, **the proportion of males in the population increased significantly**, which was attributed to two main reasons: (1). **With lower energy, the ratio of males to P_M in the L_2 sex differentiation is elevated**; (2). The mortality rate of both males and females increases with decreasing energy, but the value of increased mortality rate of males is smaller than that of females, i.e., **males are less**

negatively affected by decreasing energy.

At the same time, **lower energy** leads to a higher proportion P_M of sex differentiation in the population, which in turn leads to **an increase in the environmental capacity K** , alleviating the pressure of lower energy on the population to a certain extent, which reflects the fit between the model and the actual behavior of the population.

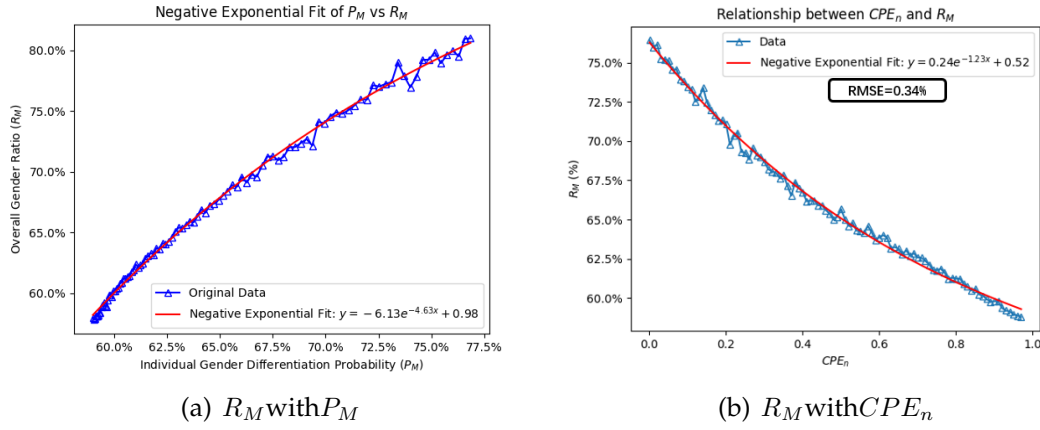


Figure 7: Model results fitting

The corresponding sex ratio in the model output was obtained by varying the value of the energy level CPE_n in the model parameters with a fixed step size. This gives (a) **the proportion of population sex presentation with individual sex differentiation**, (b) **the proportion of population sex presentation with energy supply level**. The explicit relationship is as follows

$$R_M = 0.24e^{-123CPE_n} + 0.52 \quad (17)$$

$$R_M = -6.13e^{-4.63P_M} + 0.98 \quad (18)$$

Considering the specific values, $H_1 = 0.97$, energy supply is abundant and the proportion of males in the population = 0.59, and $CPE_n = 0.0101$, energy supply is scarce and the proportion of males in the population = 0.76, which is in high agreement with the data of the title, which proves the reasonableness of the model.

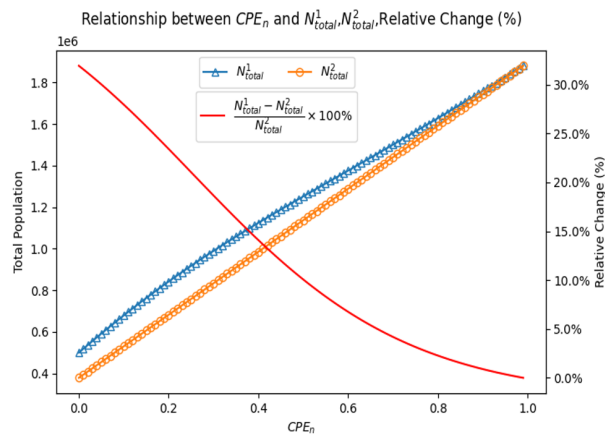


Figure 8: The relative change of N_{total} with CPE_n

In order to compare the advantages and disadvantages of sex differentiation on population development, the changes in population size with the level of energy availability at steady state, with and without sex differentiation, were made separately as

in Figure 7.

The trend of relative growth with energy is also plotted. (N_{total}^2 , P_M is fixed at 0.56, and N_{total}^1 , P_M varies with energy level according to the above equation). It can be seen that **sex differentiation leads to a larger population size of the sea lampreys population at the same energy level**. The relative change showed a decreasing trend with more energy, and was **higher than 30%** when the energy supply was extremely short, and when the energy supply was very abundant, the sex differentiation had basically no effect on the population size. This indicates that sex differentiation is beneficial to the survival and development of populations in times of energy shortage.

On the basis of the above discussion of the steady state, in order to further analyse the role of sex differentiation, we make a plot of the change in population over time for a given energy level as follows

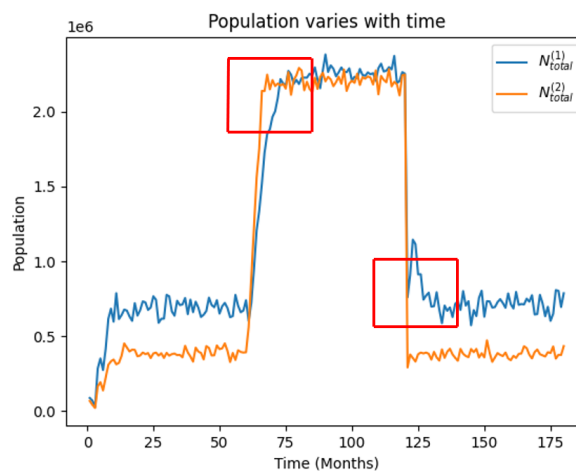


Figure 9: N_{total} with Time

$N_{total}^{(1)}$ denotes populations of sea lampreys with changeable sex differentiation ratios, $N_{total}^{(2)}$ denotes populations with fixed sex differentiation ratios, and the rest of the parameters are the same. To give a clearer impression of the sex differentiation ratio, we introduce a dramatic change in energy. We **increase the energy level from 0.1 to 0.9 at $t=60$, and dial back the energy level from 0.9 to 0.1 at $t=120$** , and observe the changes in the two population curves.

It can be seen that populations with changeable sexual differentiation have **significantly higher populations at low level of energy**, while there is no advantage when energy is sufficient. This suggests that the phenomenon of changeable sex differentiation can improve the tolerance of populations to the harsh environment of low energy. When the external environment improves and the energy suddenly rises, $N_{total}^{(1)}$ **rise more slowly**, mainly because changeable sex differentiation leads to an uncoordinated sex ratio of the populations, which is not conducive to the development of reproductive behaviour and leads to a slower increase in population size; while when the external environment deteriorates and the energy suddenly falls, $N_{total}^{(1)}$ **decline more slowly**, which is because by increasing the proportion of males, the population can **slow down the overall mortality rate and the reduction of environmental capacity**, thus relieving the environmental pressure and favoring the survival and development of the population.

In summary, the phenomenon of sex differentiation is conducive to the maintenance of higher population sizes in unfavourable external environments (when energy levels are low) and **increases the stability of the population's resistance to environ-**

mental degradation, but when external environments are improving (when energy levels are high), the uneven sex presentation ratio resulting from the sex differentiation **reduces the stability of the population's resilience**.

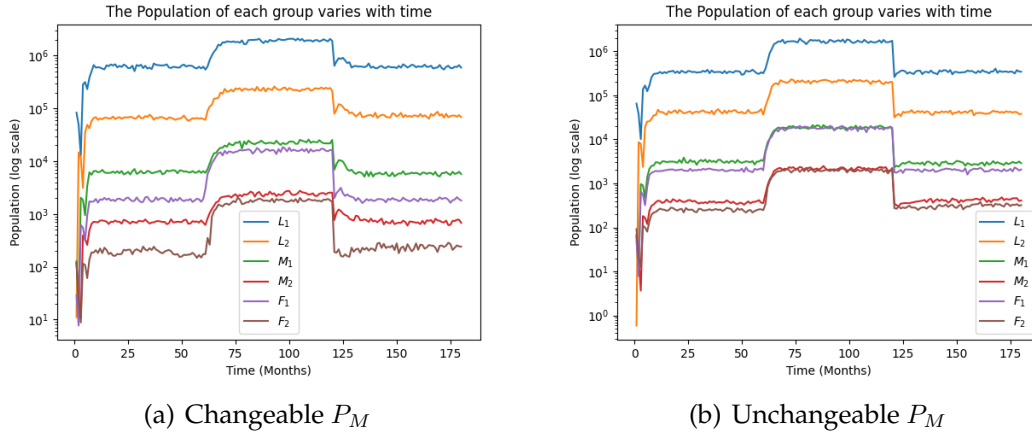


Figure 10: The population of each group with time

From Figure 10.(a), when the energy is lower, the proportion of males presenting in the population is significantly higher than that of females, and when the energy level increases, the number of female and male individuals tends to be the same, which is consistent with the actual situation.

Based on the above discussion of the changes in the population size of the sea lampreys, we hypothesize a species that parasitizes the sea lampreys, the parasite depends on the lampreys for its survival and reproduction, and the changes in the number of the lampreys will have a direct effect on the population size of the parasite. Different sexes of lampreys may have different resistance to the parasites, which will change the infection and dispersal pattern of the parasites, and thus the population size of the parasitic species, so we can get:

$$N_P \propto \sum_{i=1}^6 \sigma_i x_i(t) \quad (19)$$

Where N_P represents the population size of the parasitized species, and σ_i **denotes the average parasitism capacity of the i th group of sea lampreys, depending on the physiological characteristics of sea lampreys in each group**. Since females are more susceptible to parasitism and have a larger parasitism-holding capacity, $\sigma_{5,6} > \sigma_{3,4}$.

When the energy decreases, the decrease in the population size of sea lampreys will lead to a decrease in the number of parasitic species, and the decrease in the proportion of females will exacerbate the decrease in the number of parasitic species; when the energy increases, the increase in the population size of sea lampreys will lead to an increase in the number of parasitic species, and the increase in the proportion of females will promote a further increase in the number of parasitic species. Taken together, the sex differentiation of sea lampreys will lead to **a more drastic change in host species in response to external energy**, which will harm the stability of the host species.

7 Model:Population eigenvalues

7.1 The Establishment of the model

As in the study of hypothetical parasitic populations in the previous section, in reality, individuals of different ages and sexes of the sea lamprey interact with the environment and the rest of the species in different ways and to different extents, but at the same time function as a population as a whole in the food chain and even in the whole ecosystem. In order to describe this phenomenon in more detail, based on the previous difference equation model and grouping, this part **extends the parasitism factor σ_i to different interspecies relationships** and creatively introduces the concepts of **population eigenvalue** and population eigenvectors as tools for describing the interactions between the sea lamprey population and the ecosystem.

Define the population eigenvalue as follows:

$$C(t+1) = \sum_{i=1}^6 \sigma_i x_i(t) \quad (20)$$

Where $C(t)$ characterizes the effect of the role of the population as a whole in the ecosystem, e.g. interactions with the rest of the population such as competitors, food, natural enemies, etc., which both unifies the population's effect on the outside world and can also be used to measure the effect of the outside world on the population. σ_i **denotes the contribution factor of the i th subgroup to $C(t)$** , which is determined by the physiological characteristics of each group and the **populations interacting with sea lampreys**, here we do not provide specific numerical values at the moment.

Accordingly, we can incorporate information about the effects of sea lampreys of different ages and sexes on the external environment into the same variable, and thus consider the interaction of the sea lamprey population as a whole with another population, with the following set of difference equations:

$$\begin{cases} x_1(t+1) = [\alpha x_4(t) + \beta x_6(t)] \cdot \epsilon + \gamma^{(1)} \Delta C(t) \\ x_2(t+1) = (1 - d_l)^{12} x_1(t) + \gamma^{(2)} \Delta C(t) \\ x_3(t+1) = P_M (1 - d_l)^{12} x_2(t) + \gamma^{(3)} \Delta C(t) \\ x_4(t+1) = (1 - d_M)^{12} x_3(t) + \gamma^{(4)} \Delta C(t) \\ x_5(t+1) = (1 - P_M) (1 - d_l)^{12} x_2(t) + \gamma^{(5)} \Delta C(t) \\ x_6(t+1) = (1 - d_F)^{12} x_5(t) + \gamma^{(6)} \Delta C(t) \\ C(t+1) = \sigma^T X(t) = \sum_{i=1}^6 \sigma_i x_i(t) \\ \Delta C(t+1) = \varepsilon_1 C(t) (1 - S_1 \frac{H(t)}{K_2}) + \varepsilon_1 \end{cases} \quad (21)$$

$$H(t+1) = H(t)(1 - \alpha) + \varepsilon_2 H(t) (1 - \frac{H(t)}{K_2} - S_2 \frac{C(t)}{K_1}) + \varepsilon_2 \quad (22)$$

Where H denotes another population interacting with the sea lamprey, $\gamma^{(i)} = \frac{\sigma_i}{\sum_{i=1}^6 \sigma_i}$, S_1, S_2 denote the factors of influence of the population H on the population of sea lamprey, and the population of sea lamprey on the population H , respectively (predation, competition, etc.), and K_1, K_2 denote the maximum value of the characteristic quantity of the sea lamprey population and the environmental capacity of population H , respectively. Due to the uncertainty in nature, we introduced the **stochastic factors** $\varepsilon_1, \varepsilon_2$

to simulate the effects of stochastic fluctuations in nature on the population and the ecosystem. Using S_1, S_2 to characterise different interspecific relationships

Using S_1, S_2 to characterise different interspecific relationships

Table 3: Information about S_i

Impact Factor	Interspecific Relationships
$S_1 > 0, S_2 > 0$	H:Competitor
$S_1 > 0, S_2 < 0$	H:Predator
$S_1 < 0, S_2 > 0$	H:Prey

Combine $X(t), C(t)$ and $\Delta C(t)$ to introduce population eigenvectors:

$$\chi(t) = [x_1(t), x_2(t), x_3(t), x_4(t), x_5(t), x_6(t), C(t), \Delta C(t)]^T \quad (23)$$

The system of equations () can be rewritten as:

$$\chi(t+1) = \Omega \chi(t) \quad (24)$$

$$\Omega = \begin{bmatrix} 0 & 0 & 0 & \alpha\epsilon & 0 & \beta\epsilon & 0 & \gamma^{(1)} \\ (1-d_l)^{12} & 0 & 0 & 0 & 0 & 0 & 0 & \gamma^{(2)} \\ 0 & P_M(1-d_l)^{12} & 0 & 0 & 0 & 0 & 0 & \gamma^{(3)} \\ 0 & 0 & (1-d_l)^{12} & 0 & 0 & 0 & 0 & \gamma^{(4)} \\ 0 & P_F(1-d_l)^{12} & 0 & 0 & 0 & 0 & 0 & \gamma^{(5)} \\ 0 & 0 & 0 & 0 & (1-d_l)^{12} & 0 & 0 & \gamma^{(6)} \\ \sigma_1 & \sigma_2 & \sigma_3 & \sigma_4 & \sigma_5 & \sigma_6 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & \rho(1-s_1 \frac{H(t)}{K_2}) & 0 \end{bmatrix} \quad (25)$$

Population eigenvectors are clear and easy to use, and contain not only the quantitative information of each subgroup in the current period, but also the characterisation of the degree of interaction between the population as a whole and the outside world, $C(t)$, and the result of the interaction, $\Delta C(t)$, i.e., it includes information on the external interaction of the population and the prediction of the next period, which contains a wealth of significance.

7.2 Results under different conditions.

In this section, we explore the interactions between the two populations by considering another population H as a competitor or predator of the sea lampreys, respectively. (The interactions of the H as food population are similar to those of the predator population.)

7.2.1 Competitor

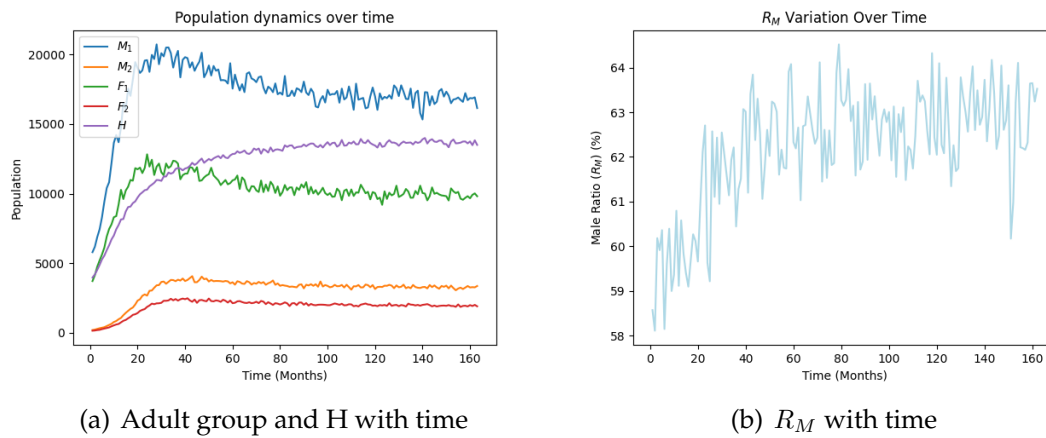


Figure 11: Competitor(changeable P_M)

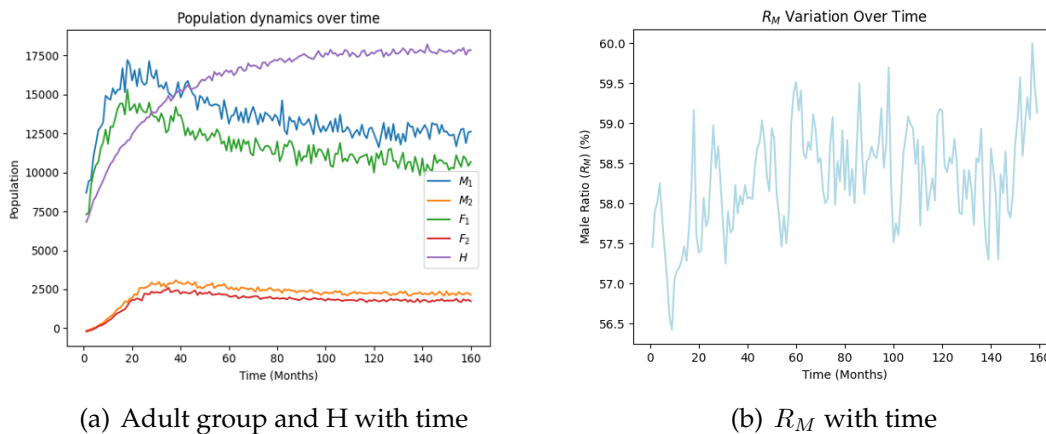


Figure 12: Competitor(unchangeable P_M)

As can be seen from the figure.11,12, populations with variable sex differentiation ratios exhibit the following characteristics in relation to their competitors when the rest of the conditions are the same: (1)The range of variation in the sex presentation ratio of the populations is greater and more dramatic over time: (2)**Sea lamprey populations are larger than the other group;**

When competing, competitors cause the sea lamprey population to receive less energy, which in turn causes the proportion of males presenting in sea lampreys to increase through sex differentiation, and males are more competitive than females, which causes the population's trait volume to increase, and the maximum value of the trait volume to increase, i.e., **the population develops better, whereas its competitors are suppressed.**

In addition to this, a clear **temporal sequence** is reflected in the figure, with the larvae group growing rapidly first as the population develops, and after some periods the population growth of juveniles is passed on to the perennial male and female groups, so that **the adult group trends slightly later in number than the larvae.**

7.2.2 Predator

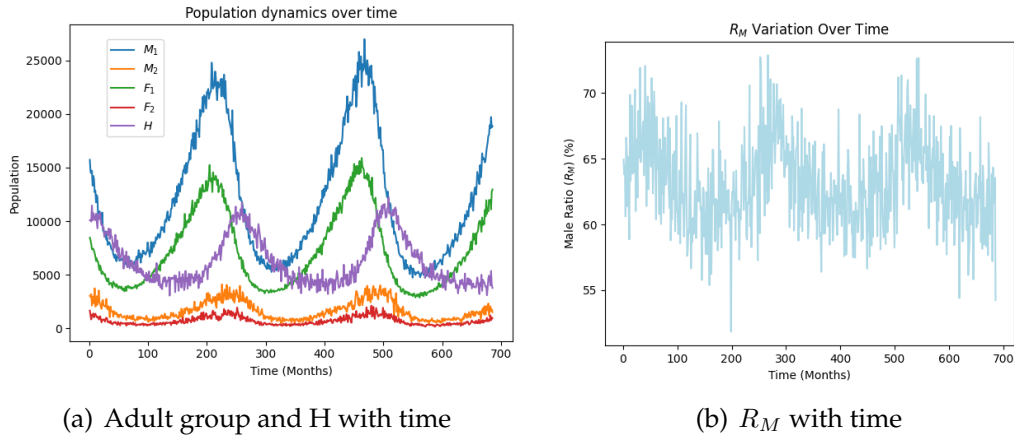


Figure 13: Predator(changeable P_M)

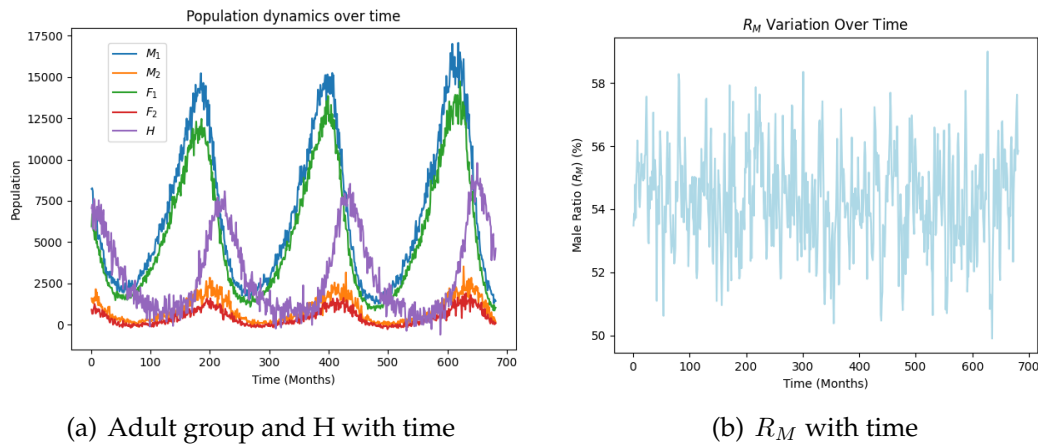


Figure 14: Predator(unchangeable P_M)

As can be seen from the figure.13,14, populations with variable sex differentiation ratios exhibit the following characteristics with predators when the rest of the conditions are the same: (1)The total sex-presentation ratio **fluctuates cyclically** and the overall level is higher than that of populations with fixed sex differentiation ratios; (2)**Higher levels of both predator and population numbers**; (3)**greater periodicity in population size fluctuations**

Predator predation on sea lampreys causes the sea lamprey population to decrease in size through direct predation, while the restriction of the activities of sea lampreys reduces their energy gain levels, **causing sea lampreys larvae to tend to differentiate into males**, relatively increasing the population level, and although males are lower in energy and difficult to prey upon, the overall increase in numbers overall compensates for and increases the predator's access to food, which in turn improves the population of predators. As can be seen from the results of Model 2, for populations with variable sex differentiation ratios, **the increase and decrease in numbers will be slower**, making for a greater period of fluctuation in that predation process.

7.3 Ecological System Stability

In this section, we examine the impact of lampreys as invasive species on the stability of lake ecosystems similar to the Great Lakes. We then investigate whether the gender differentiation characteristics of lampreys contribute to the exacerbation of disruptions to the stability of lake ecosystems. According to relevant literature, **ecosystem stability is positively correlated with species diversity**[8]. Therefore, we utilize the Shannon Diversity Index as a metric for assessing the biological diversity of the ecosystem, providing insights into the strength of ecosystem stability. The Shannon-Wiener Index employs information theory, where higher values indicate greater species diversity. It is defined as follows:

$$I_{SW} = - \sum_{i=1}^S p_i \ln(p_i) \quad (26)$$

Here, S represents the number of species in the ecosystem, and P_i denotes the relative abundance of the i -th species in the entire ecosystem. This can be calculated by dividing the number of individuals of that species by the total number of individuals in the entire ecosystem:

$$p_i = \frac{n_i}{N} = \frac{n_i}{\sum_{k=1}^S n_k} \quad (27)$$

We assume a lake ecosystem \mathcal{Z} that initially lacks lampreys. The lampreys will occupy the k -th trophic level in the ecosystem \mathcal{Z} . To simplify the model, we only consider the impact of lamprey invasion on the relative abundance of prey (at the $k - 1$ trophic level), competitors (at the k trophic level), and predators (at the $k + 1$ trophic level), while disregarding the influence on other trophic levels. Thus, in the ecosystem \mathcal{Z} , we examine the simplified community as follows:

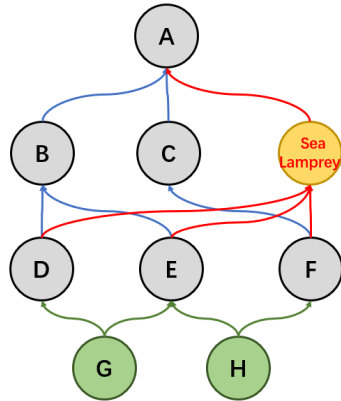


Figure 15: Food Web

According to the relevant literature, we consider the ecosystem depicted in the above figure to be stable when the population and relative abundance of each species follow the table below (sourced from data statistics of a specific lake[9]). This represents the ideal lake ecosystem before the invasion of lampreys.

Table 4: Information about the lake ecosystem

Relative Trophic Level	Species	Abundance	p_i^{before}	Ecological Parameters (Table 3)
Predator	A	100	0.00017	$S_1 = 0.0013, S_2 = -0.0017$
Competitor	B	1570	0.00260	$S_1 = 0.0038, S_2 = 0.0059$
	C	1230	0.00204	$S_1 = 0.0027, S_2 = 0.0073$
Prey	D	14000	0.02322	$S_1 = -0.0058, S_2 = 0.0062$
	E	11000	0.01825	$S_1 = -0.0035, S_2 = 0.0044$
	F	15000	0.02488	$S_1 = -0.0052, S_2 = 0.0039$
Producer	G	36000	0.59711	
	H	200000	0.33173	

Species C has gone extinct due to competition with sea lampreys.

The Shannon-Wiener Index at this point can be calculated as follows:

$$I_{SW}^{before} = - \sum_{i=1}^8 p_i^{before} \ln(p_i^{before}) = 0.9558 \quad (28)$$

Based on the previous analysis of the Population Eigenvalues Model (7.1), the ecological indicators of each species at equilibrium, under conditions of variable and fixed gender differentiation ratios, can be determined after the invasion of lampreys into the lake ecosystem:

Table 5

Species	Abundance	$p_i^{after(1)}$	Abundance*	$p_i^{after(2)}$
A	91	0.00016	95	0.00016
B	357	0.00061	578	0.00098
C	0	0	0	0
Sea Lamprey	2873	0.00491	2586	0.00440
D	7387	0.01263	8034	0.01368
E	4348	0.00743	4909	0.00836
F	9826	0.01680	11049	0.01881
G	36000	0.61551	36000	0.61303
H	20000	0.34195	20000	0.34057

The Shannon-Wiener indices can be calculated separately under conditions of variable and fixed gender differentiation ratios:

$$I_{SW}^{after(1)} = - \sum_{i=1}^9 p_i^{after(1)} \ln(p_i^{after(1)}) = 0.8580 \quad (29)$$

$$I_{SW}^{after(2)} = - \sum_{i=1}^9 p_i^{after(2)} \ln(p_i^{after(2)}) = 0.8724 \quad (30)$$

The invasion of lampreys (with a changeable gender differentiation ratio) has the following impact on the stability (species diversity) of the lake ecosystem:

$$RC^{(1)} = \frac{I_{SW}^{after(1)} - I_{SW}^{before}}{I_{SW}^{before}} \times 100\% = -10.24\% \quad (31)$$

The invasion of lampreys (with a fixed gender differentiation ratio) has the following impact on the stability (species diversity) of the lake ecosystem:

$$RC^{(1)} = \frac{I_{SW}^{after(2)} - I_{SW}^{before}}{I_{SW}^{before}} \times 100\% = -8.73\% \quad (32)$$

Furthermore, the enhancement ratio of the population's impact on the stability of the ecosystem under conditions of variable gender differentiation can be derived:

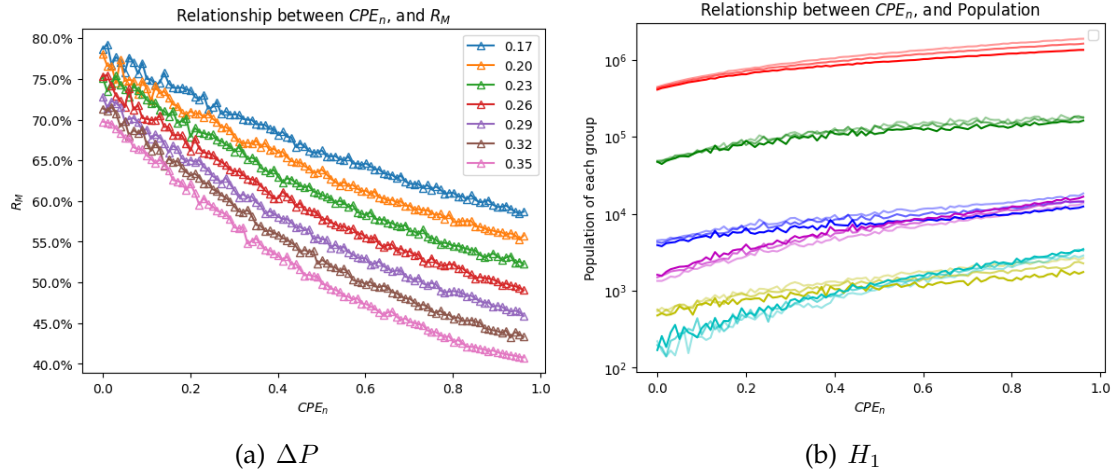
$$RC^{(3)} = \frac{RC^{(1)} - RC^{(2)}}{RC^{(2)}} \times 100\% = 17.3\% \quad (33)$$

In summary, **the invasion of lampreys leads to a decrease in the stability of the lake ecosystem by 10.24%**. This is attributed to the substantial competition pressure imposed by lampreys on species within the same trophic level. They compete for resources such as food and space, impacting the survival and reproduction of local species. Lampreys exhibit strong predatory capabilities, posing a significant threat to species at lower trophic levels, as evidenced by the data in Table 5.

Simultaneously, **its gender differentiation characteristics can increase its disruptive impact on stability by 17.3%**. This might be due to the overall competitive advantage of male lampreys over females, coupled with their lower energy requirements. The ability of lampreys to adjust their gender ratio based on external factors (energy levels) allows them to better ensure population size and overall competitiveness under extreme conditions, enhancing their destructive impact as an invasive species.

8 Sensitivity Analysis

Some key parameters of our model do not change during the simulation, such as ΔP fixed at 0.23 and H_1 fixed at 4. Therefore, based on the figure and figure, we adjust both the parameters ($\Delta P: 0.17 - 0.32, H_1: 3.9, 4, 4.1$) and rerun the model. The results are shown in figure 14 and table 6. We choose specific points at $CPE_n = 0.061, 0.321, 0.601, 0.931$ to analyse. The data in the table are the relative change of R_M and the population of each group.

Figure 16: Sensitivity analysis on ΔP and H_1 Table 6: Specific fluctuations with ΔP

ΔP	E=0.061	E=0.321	E=0.601	E=0.931
0.17	0.067	0.073	0.109	0.119
0.2	0.029	0.038	0.051	0.055
0.26	-0.030	-0.045	-0.047	-0.069
0.29	-0.037	-0.077	-0.090	-0.093
0.32	-0.065	-0.081	-0.094	-0.099

As shown in Figure 16 and Table 6, under given energy level conditions, the fluctuations in R concerning ΔP , and the changes in the population sizes of various groups with H_1 remain within a small range. This has little impact on the model's output and analysis, reflecting the robustness of the model.

9 Model Evaluation

9.1 Strengths

- The population of sea lampreys is grouped, and by utilizing difference equations, their evolution is simulated. This approach allows for a more detailed description of changes in different age groups and gender ratios within the population.
- The introduction of population characteristics integrates information about the overall population and allows for a simple and effective analysis of the interactions between sea lampreys and other populations, extending to the entire ecosystem.
- The utilization of Shannon information entropy provides a simple and effective measure for assessing the stability of the ecosystem, facilitating ease of use.

9.2 Weaknesses

- The calculation of difference equations is complex, and adjusting the parameters can be challenging.
- When calculating the ecosystem, the need for repeated computation of the difference equations makes it challenging to describe the interactions among multiple populations effectively.

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