The Impact of Biologically Adaptive Sex Ratio Variation in Lamprey Population on Ecosystem Stability: Based on Lotka-Volterra Model

Hanyi Zhao [†], Yuyao Chen [†,*], Danni Ma [†]

School of Mechanical Engineering and Automation, Harbin Institute of Technology (Shenzhen), Shenzhen, China, 518071

* Corresponding Author Email: cyy_hitsz@163.com

[†] These authors contributed equally.

Abstract. Lamprey has the characteristics of adaptive sex ratio variation and plays a complex role in the ecosystem. In order to study the impact of adaptive sex ratio variation on ecosystem stability, this paper establishes a differential equation group based on the Lotka-Volterra model, and uses the collected data to obtain unknown parameters. By solving these equations, it is found that the adaptive sex ratio variation of lamprey can regulate the imbalance of ecosystem. Then, the male and female lamprey populations were used as two variables. Based on the basic model and Fischer 's principle, an improved model was established. Considering the uncertainty of the ecosystem, two sets of data of high mortality and normal mortality were established. The results showed that the sex ratio of lamprey could optimize resource utilization. When resources are scarce and mortality increases, the sex ratio of lampreys becomes unbalanced, leading to the extinction of female fish.

Keywords: Lotka-Volterra Model, Adaptive Sex Ratio Variation, Lamprey Population, Dynamic Model.

1. Introduction

The lamprey is an ancient jawed fish that lives in lakes or oceans. Its gender is determined by the availability of food and growth rate in its youth. This characteristic has a significant impact on the species abundance and ecosystem of the lamprey itself. As a parasitic animal, improper handling of lampreys can lead to serious disruption of ecosystem balance and significant economic losses.

The sex determination mechanism of fish can be changed from completely genetic determination to completely environmental determination. Certain research provides an opportunity to understand how physiology and environment interact to determine sex [1].

In recent years, adaptive sex ratio variation phenomenon is widely discovered and analyzed in many species. The research of Hagen R et al. provides strong evidence for a male-biased sex ratio in a large herbivore and weak evidence for variations in the secondary sex ratio owing to environmental conditions [2]. The work by Wang YB et al., for the first time, conclusively demonstrates that two intracellular symbionts affect sex ratios in their whitefly hosts by regulating fertilization and supplying B vitamins. Their results reveal that both symbionts have the convergent function of regulating reproduction in phylogenetically-distant whitefly species [3]. Joaquim Casellas et al. do evidential segregation analysis for offspring sex ratio in rabbit and sheep populations [4]. Using experimental evolution, Yin D et al. show that a gene family with a historical role in sperm competition plays a large role in regulating male frequency after self-fertility evolves [5].

Fish can also exhibit environmental reversals, such as social structure and feeding temperature, which can cover the main genotypic sex and lead to phenotypic sex reversals, which are usually fixed [6]. Environmentally induced sex determination and reversal (here referred to as sex determination) can lead to highly variable population sex ratios and are important when considering management strategies for valuable, invasive, and hatched fish.

There are still little studied in basal fishes such as lamprey, despite their tremendous potential value for comparative study and the economic and cultural value in real life [7]. Presently, the sex ratio of adult lampreys on the Great Lakes is estimated to be 55% male. The sex ratio of the least brook lamprey population also varies greatly, and high-density populations are more likely to be male-prone than low-density populations. However, the factors contributing to the varying sex ratio are still not clear. By using mathematical modeling methods, we can efficiently recognize the widespread impact of the sex ratio of lampreys on the ecological environment, and thus develop better ecosystem management strategies.

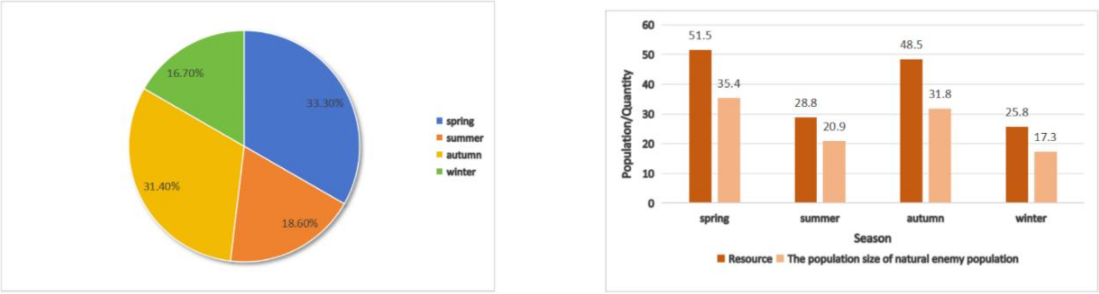
To study the impact of adaptive sex ratio variation on ecosystem stability, this paper establishes two models: Sex ratio-Resource Model and Improved Sex ratio-Resource Model. The values of key parameters such as mortality rate and resource consumption rate are determined by data from relevant literature. From the results obtained by solving the equations, the relationship between sex ratio of lampreys and resource availability as well as ecosystem stability can be analyzed.

2. Establishment of the model

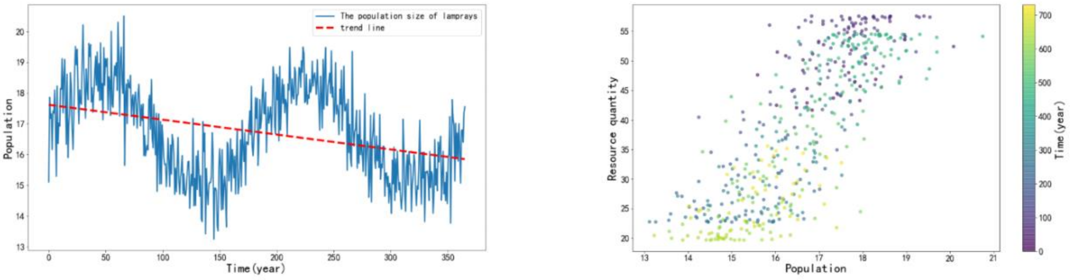
2.1. Data acquisition and visualization

This paper refer to some data including the population of lampreys and trout Lakes as well as the natural enemy populations in the Great in recent years [8, 9]. Based on the data, the resources can be quantified. In this paper, the definition of resources is all external factors that affect the survival of lamprey populations. Resources are determined by the amount of food that sea lampreys eat, the appropriate sand and gravel needed for breeding, etc. Here, the unit of resources is defined as the amount of resources needed to survive a lamprey. We remove outliers with significant deviations based on the 3σ principle and replace missing values with the average of the data before and after. And in this paper, the default unit for variables is ten thousand.

The obtained data can be visualized as follows. Firstly, we visualize the resource levels and natural enemy populations, as shown in Figure 1(a) and Figure 1(b). In addition, a line graph of population size over time and conducted linear regression analysis is plotted. The relationship between population size and resource quantity can be observed through scatter plots. It can be seen in Figure 1(c) that the population size shows periodic changes and overall shows a downward trend. The relationship between population size and resource quantity generally follows a positive linear relationship shown in Figure 1(d).



(a) The proportion of resources (b) Natural Enemy - Resource



(c) Population size change trend (d) Population - Resource

Figure 1. Data visualization diagram

2.2. Original model

In the natural environment, the number of predators and the number of prey often exhibit regular periodic changes. The *Lotka-Volterra* model describes this fluctuation pattern through a system of differential equations [10, 11]. Assuming there are two species living in the same space, namely species 1 and species 2. According to the model, there are the following relationships:

$$\frac{\mathrm{d}N_1}{\mathrm{d}t} = r_1 \cdot N_1 \cdot \left(1 - \frac{N_1}{K_1} - \alpha \cdot \frac{N_2}{K_1}\right) \tag{1}$$

$$\frac{\mathrm{d}N_2}{\mathrm{d}t} = r_2 \cdot N_2 \cdot \left(1 - \beta \cdot \frac{N_1}{K_2} - \frac{N_2}{K_2}\right) \tag{2}$$

In which, N_1 and N_2 are the population numbers of two species respectively; K_1 and K_2 are the environmental carrying capacities of two species respectively; r_1 and r_2 are the population growth rates of two species respectively. α is the competition coefficient between species 2 and species1, which means that the space occupied by each N_2 individual is equivalent to the space occupied by αN_1 individuals. β is the competition coefficient between species 1 and species 2. In the model, $\frac{N_1}{K_1}$ is the space already utilized by the species 1 themselves, while $\alpha \cdot \frac{N_2}{K_1}$ represents the occupation of space by the N_2 population, which together constitute the utilized space term. Then $\left(1 - \frac{N_1}{K_1} - \alpha \frac{N_2}{K_1}\right)$ can be understood as unused space term.

When the environmental capacity of species 1 is K_1, the inhibitory effect of each individual in the population on their own population growth is $\frac{1}{K_1}$, and the impact of each individual in the N_2 population on the N_1 population is $\frac{\alpha}{K_1}$. The same applies to species 2.

This model can be extended to situations with larger populations:

$$\begin{gathered}
\frac{\mathrm{d}x_1}{\mathrm{d}t} = r_1 x_1 \left(1 - \frac{x_1 + \alpha_{12} x_2 + \alpha_{13} x_3 + \cdots}{K_1}\right) \\
\frac{\mathrm{d}x_2}{\mathrm{d}t} = r_2 x_2 \left(1 - \frac{x_2 + \alpha_{21} x_1 + \alpha_{23} x_3 + \cdots}{K_2}\right) \\
\frac{\mathrm{d}x_3}{\mathrm{d}t} = r_3 x_3 \left(1 - \frac{x_3 + \alpha_{31} x_1 + \alpha_{32} x_2 + \cdots}{K_3}\right)
\end{gathered} \tag{3}$$

This is a set of equations used to describe the interaction between predator and prey in a closed system. Although primarily used in predator-prey models, the rationale of these equations can be applied to the study of any population dynamics. In this paper, the mutual inhibition and promotion relationships between various groups are considered and the *Lotka-Volterra* model is extended.

2.3. Sex ratio-resource model

The growth rate of the lamprey population is determined by both birth and death rates in the natural state. Furthermore, considering the female ratio and population survival rate of lamprey, it can be seen that the factor that increases the population of lamprey is $B \cdot \left(1 - P_{\text{male}}(t)\right) \cdot S\left(N(t), R(t)\right) \cdot N(t)$. Then the factor that decreases the population is $D\left(N(t), R(t)\right) \cdot N(t)$. And then we can get the first equation.

$$\frac{\mathrm{d}N}{\mathrm{d}t} = B \cdot \left(1 - P_{\text{male}}(t)\right) \cdot S\left(N(t), R(t)\right) \cdot N(t) - D\left(N(t), R(t)\right) \cdot N(t) \tag{4}$$

The growth rate of resources is determined by the total consumption rate of lampreys and the rate of resource regeneration. Therefore, the second equation is obtained.

$$\frac{\mathrm{d}R}{\mathrm{d}t} = G\left(R(t)\right) - C\left(N(t)\right) \cdot N(t) \tag{5}$$

Considering the constraints of the natural environment, the amount of resources will not increase infinitely, and the growth of resources will gradually decrease with the increase of resources.

Therefore, a discrete block growth model is introduced here to make the resource growth rate linearly decrease.

$$G\big(R(t)\big) = G \cdot R(t) \cdot \left(1 - \frac{R(t)}{R_{\max}}\right) \tag{6}$$

Where G is the daily growth rate of resources and $R_{\max}$ is the environmental carrying capacity of resource quantity.

Regard the change of sex ratio as a result driven by multiple biological and environmental factors. To describe the male proportional function of lampreys $P_{\text{male}}(t)$, two variables $F\big(N(t), R(t)\big)$ and $G\big(N(t), R(t)\big)$ are introduced here, which indicate the factors that cause the sex ratio to be skewed in favor of males of females respectively. Consequently, the third equation can be got.

$$\frac{\mathrm{d}P_{\text{male}}}{\mathrm{d}t} = F\big(N(t), R(t)\big) \cdot \big(1 - P_{\text{male}}(t)\big) - G\big(N(t), R(t)\big) \cdot P_{\text{male}}(t) \tag{7}$$

In the above equations, there are several important parameters set as follows.

For lampreys usually lay 80000 to 100000 eggs at once, take the average and set the value of B (Number of eggs laid by female individuals) to 9 [8].

The natural mortality rate of fish populations under different white noise levels is found and fishing mortality rates are obtained through Monte Carlo simulation [12]. Due to the fact that lampreys are a food source in some areas, we assume a fishing mortality rate of 1%, resulting in a natural mortality rate of approximately 40%.

The number of lampreys in the Great Lakes is currently less than 100000, so we take 10 as the initial population size reasonably. It is assumed that the resource quantity and population quantity are of the same order of magnitude, and here it is set to 50. Meanwhile, due to the abundance of resources, the initial male proportion is set as 56%.

2.4. Improved sex ratio-resource model

In the above sex ratio-resource model, the lamprey population is regarded as a whole. Now, in order to analyze the advantages and disadvantages of sex ratio variation in the lamprey population, it is reasonable to consider the different roles of male and female individuals in the ecosystem during their lifecycle, thus the impact of sex ratio on population reproductive ability, survival rate, and long-term stability can be analyzed.

Assuming that between male and female lampreys, there are differences in resource dependence and consumption rates. The reproductive rate and the death rate are influenced as well. Based on the above definitions and assumptions, a differential equation model can be constructed to obtain the changes in the resource and the number of male and female lampreys over time.

The growth rate is the difference between birth rate and mortality rate. Based on equation (4), we can easily get the dynamic equation of male and female lampreys:

$$\frac{\mathrm{d}N_{\mathrm{m}}}{\mathrm{d}t} = B\big(N_{\mathrm{m}}(t), N_{\mathrm{f}}(t)\big) \cdot S\big(N(t), R(t)\big) \cdot N_{\mathrm{m}}(t) - D_{\mathrm{m}}\big(N(t), R(t)\big) \cdot N_{\mathrm{m}}(t) \tag{8}$$

$$\frac{\mathrm{d}N_{\mathrm{f}}}{\mathrm{d}t} = B\big(N_{\mathrm{m}}(t), N_{\mathrm{f}}(t)\big) \cdot S\big(N(t), R(t)\big) \cdot N_{\mathrm{f}}(t) - D_{\mathrm{f}}\big(N(t), R(t)\big) \cdot N_{\mathrm{f}}(t) \tag{9}$$

The survival rate of lampreys is directly proportional to the amount of resources and inversely proportional to the population size, and can be expressed as follows:

$$S\big(N(t), R(t)\big) = \frac{R(t)}{N(t)+K} \tag{10}$$

Where K is a constant used to regulate the impact of resources on individual survival rates.

According to Fisher's principle, when one gender dominates the population, genes from the other gender are more easily transmitted, and a 1:1 ratio of male to female offspring is a stable strategy for natural evolution [13]. Therefore, by modifying the established model and incorporating equation (10), The following equations can be obtained:

$$\frac{\mathrm{d}N_{\mathrm{m}}}{\mathrm{d}t} = B \cdot \frac{R(t)}{N(t)+K} \cdot N_{\mathrm{f}}(t) - D_{\mathrm{m}} \cdot N_{\mathrm{m}}(t) \tag{11}$$

$$\frac{\mathrm{d}N_{\mathrm{f}}}{\mathrm{d}t} = B \cdot \frac{R(t)}{N(t)+K} \cdot N_{\mathrm{m}}(t) - D_{\mathrm{f}} \cdot N_{\mathrm{f}}(t) \tag{12}$$

Then, based on equation (5), the improved resource dynamic equation can be got:

$$\frac{\mathrm{d}R}{\mathrm{d}t} = G\big(R(t)\big) - \big(C_{\mathrm{m}} \cdot N_{\mathrm{m}}(t) + C_{\mathrm{f}} \cdot N_{\mathrm{f}}(t)\big) \tag{13}$$

Where C_{m} and C_{f} are the resource consumption rates of male and female individuals respectively.

On the basis of sex ratio-resource model, the key parameters and further set different mortality rates and resource consumption rates are retained and further set respectively. In addition, considering the uncertainty of the natural environment such as sudden natural disasters, a set of data with higher mortality rates is set up for comparison.

The physiological structure of male and female lampreys is different, and males often develop more strategies to avoid predators. Therefore, we bias the mortality rates of males and females downwards and upwards by 5% respectively, based on the baseline natural mortality rate.

3. Results

By visualizing the numerical solution of the differential equation system including equations (4)-(7), the following graph is obtained.

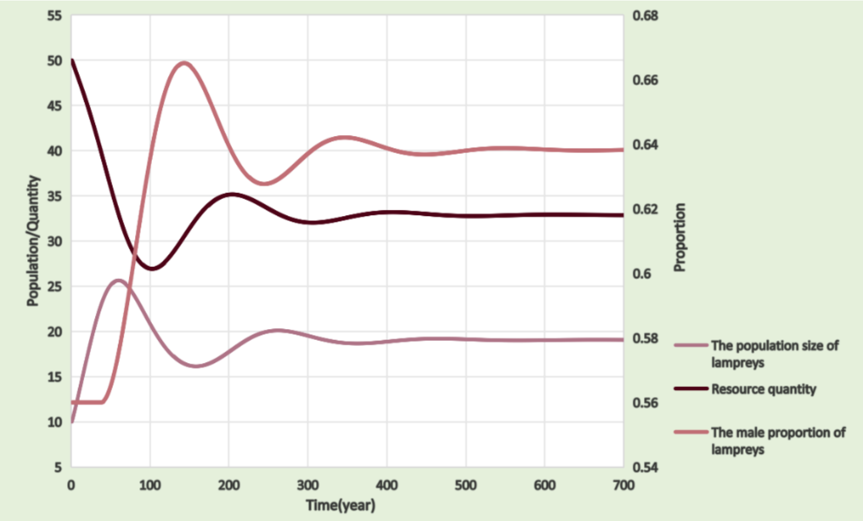


Figure 2. The impact of adaptive sex ratio variation of lampreys on ecosystem

From Figure 2, it can be seen that over time span of 700 years, the proportion of males in lampreys first increased, then fluctuated locally within a certain range, and finally stabilized at around 64%. The trend of changes in the proportion of males is consistent with the population size, but opposite to the resource quantity. It can be clearly seen that in the case of insufficient resource supply, the proportion of males increases, and vice versa, it decreases to a lower level. Its changes are slightly lagging behind the changes in resource levels.

From this result graph, we can conclude that the amount of resources decreases with the increase of population size. The amount of resources determines the growth rate of lampreys, leading to a change in the proportion of males. As the proportion of males increases and the proportion of females decreases, it can be inferred from equation (5) that the population size decreases, further leading to an increase in resource availability. The process of impact generation is summarized in following Figure 3.

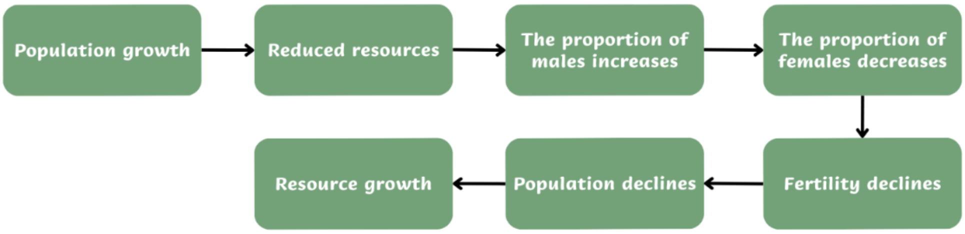


Figure 3. The influencing mechanism of sex ratio variation

Similarly, the numerical solution of the differential equation system including equations (11)-(13) is visualized in the following graph.

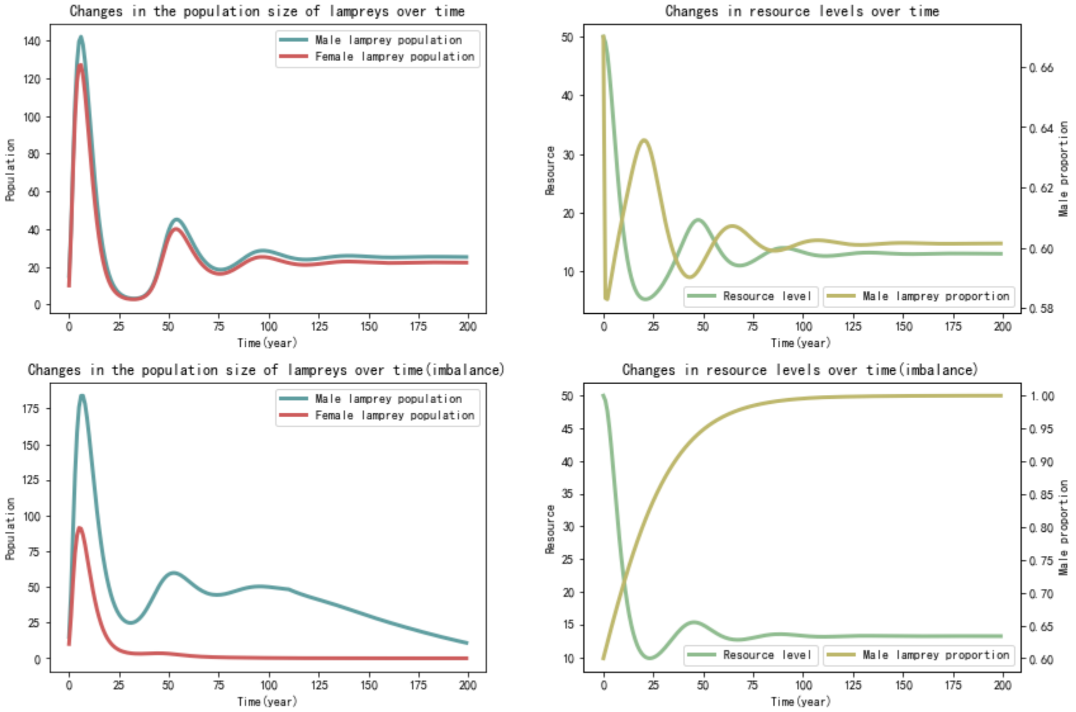


Figure 4. Changes in the population size and resources levels over time

It can be observed from Figure 4 that:

1) Under normal circumstances:

The numbers of female and male individuals increase and decrease synchronously, ultimately stabilize at around 200000. What's more, the relationship between population size, male proportion, and resource quantity is consistent with the results obtained from sex ratio-resource model, and the male proportion fluctuates between 58%-67%, ultimately stabilizing at around 60%. Thus, it can be concluded that adaptive sex ratio can optimize resource utilization and reduce pressure on specific resources. What's more, changes in environmental conditions, such as human fishing, may have varying impacts of different genders. Being able to change the sex ratio can make the population more flexible in adapting to environmental changes.

2) Under high mortality rates:

The balance of sex ratio is disrupted, and the number of individuals rapidly declines to zero. The number of male individuals fluctuates and increases in the short term, but begins to decline after a period of time and eventually approaches zero. It shows that in some special environments, gender conversion is not fully adapted to environmental conditions, which may lead to gender imbalance and affect the long-term stability and reproductive ability of the population. And changing gender may require the consumption of additional energy and resources, making it unsuitable for survival activities such as foraging and evading predators.

4. Conclusion

In this paper, sex ratio-resource model and improved sex ratio-resource model are established to study the interactions between lamprey and the ecosystem. Three variables are defined for the rudimentary model. Based on the idea that growth rate equals growth factors minus inverse growth factors, a system of differential equations is established in this paper. Then the unknown parameters are determined by collected data. After solving the equations, it is found that the adaptive sex ratio variation of lamprey can regulate imbalances in ecosystems. Furthermore, we take male and female lamprey populations as two variables. On the basis of the rudimentary model, the improved model is established by combining Fisher's principle and the key parameters are retained. Considering the uncertainty in the ecosystem, two sets of data of high mortality and normal mortality are set up. This paper analyze the data for both two outcomes and conclude the advantages and disadvantages of lampreys. The variable sex ratio of lamprey can optimize resource utilization. Meanwhile, lamprey can adapt to the environment change flexibly. However, sex ratio variation is not without its drawbacks. When resource is scarce and mortality increases the sex ratio of lampreys becomes unbalanced, leading to the near extinction of females.

References

[1] Devlin RH, Nagahama Y. Sex determination and sex differentiation in fish: an overview of genetic, physiological, and environmental influences [J]. Aquaculture, 2002, 208 (3-4): 191-364.

[2] Hagen R, Ortmann S, Elliger A, et al. Evidence for a male-biased sex ratio in the offspring of a large herbivore: The role of environmental conditions in the sex ratio variation [J]. Ecology and Evolution, 2022.

[3] Wang YB, Ren FR, Yao YL, et al. Intracellular symbionts drive sex ratio in the whitefly by facilitating fertilization and provisioning of B vitamins [J]. The ISME Journal, 2020, 14 (12): 2923-2935.

[4] Joaquim Casellas, Marta Vázquez-Gómez, Samir Id-Lahoucine, Melani Martín de Hijas-Villalba. Evidential segregation analysis for offspring sex ratio in rabbit and sheep populations [J]. Livestock Science, 2023.

[5] Yin D, Haag ES. Evolution of sex ratio through gene loss [J]. Proceedings of the National Academy of Sciences, 2019, 116 (26): 12919-12924.

[6] Nakamura M. The mechanism of sex determination in vertebrates-are sex steroids the key-factor? [J]. Journal of Experimental Zoology Part A: Ecological Genetics and Physiology, 2010, 313A (7): 381-398.

[7] Mattes WP, Kitson JC. Sea lamprey control in the Great Lakes: A Tribal/First Nations Representative's perspective [J]. Journal of Great Lakes Research, 2021: S796-S799.

[8] Robinson KF, Miehls SM, Siefkes MJ. Understanding sea lamprey abundances in the Great Lakes prior to broad implementation of sea lamprey control [J]. Journal of Great Lakes Research, 2021: S328-S334.

[9] Young B, Allaire B, Smith S. Achieving Sea Lamprey Control in Lake Champlain [J]. Fishes, 2021, 6 (1): 2.

[10] Song Jie. Study on Some Lotka-Volterra Predator-prey Models [D]. Shanxi University, 2011.

[11] Lemos-silva M, Torres DFM. The Lotka-Volterra Dynamical System and its Discretization [M] In Advanced Mathematical Analysis and its Applications. 2023: 327-342.

[12] Lytle D, Tonkin J. Matrix community models for ecology and evolution [J]. npj Biodiversity, 2023. 5.2.

[13] Contreras-Reyes JE. Fisher Information and Uncertainty Principle for Skew-Gaussian Random Variables [J]. Fluctuation and Noise Letters, 2021, 20 (05): 2150039.