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Impacts of Sea Lamprey Sex Ratio Variation Analysis based on L-V Model and P-P Model

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Abstract. As an important animal model for the study of biological evolution and disease, lamprey has attracted the attention of many scholars. Its variable sex ratio is also becoming the focus of studying because of the impact of ecological system. This paper utilizes mathematical method, and establishes the Lotka-Volterra Model to simulate the variations of the sex ratio among lamprey larvae populations. Additionally, Holling II function and Weak Alley Effect are adopted to establish a Predator-Prey Model of adult lampreys in three-tiered food chain, predicting the population dynamics of adult lamprey. The result of model simulation finds that low environmental capacity leads to a unexpectedly high ratio of male lampreys, which is up to 74.51% and proably causes population extinction. The study offers a novel insight into the interaction between ecosystems and fish species with variable sex ratios such as the lampreys.

Keywords: Lampreys, Lotka-Volterra Model, Allee Effect,Sex Ratio.

1. Introduction

Lampreys are often regarded as ancient parasites with significant ecological impacts in some habitats [1]. For instance, the fisheries in the Great Lakes region of North America have suffered significant declines due to the invasion of lampreys [2]. The food supply influences the sex ratio of sea lamperys, and in some circumstances where food is insufficient, the proportion of male sea lamperys probably increases. The variational ratio has a certain impact on the ecosystem.

Further study on the variable sex ratio of sea lamprey is beneficial to identifying the interactions between the population and the ecosystem. Johnson N.S found that the sex ratio was mainly influenced by larval growth rate [3], and the result of field study showed unproductive environments became increasingly male-skewed and productive environments became less male-skewed with time. The article of Erin Ross reiterated his conclusion [4]. The downside of Johnson's study was that Johnson was unable to use mathematical relationships to forecast the changes in the population of larval male and female lamprey. By profiling lasma metabolomic, Sonam Tamrakar found the sex- and maturation-dependent metabolic strategies in sea lamprey [5]. With the development of genetic technology, many scholars provide some new ideas for the reasons of sex ratio change in lampreys from the perspective of gene expression [6,7].

Considering the problems existing in the current research, the Lotka-Volterra Model and Predator-Prey Model incorporating Weak Alley effect are proposed in this paper. This article analyzes the effects of sex ratio changes on the environment of juvenile and adult sea lampreys respectively. It is expected that the study in this paper can provide a new way of thinking about the interaction between the ecosystem and fish with variable sex ratio such as sea lampreys.

2. The Model Establishment of Lotka-Volterra Model and Predator-Prey Model

2.1. The Lotka-Volterra Model Competition Model among Larval Lampreys

The sex ratio dynamics in lampreys is critically dependent upon juvenile growth rates, which is tightly linked to the availability of food resources. Based on previous research, in environments characterized by limited food resources, there is a markedly higher proportion of male lampreys compared to females. Therefore, the phenomenon above can be perceived as a result of intraspecific competition between sexes for food resources, with males exhibiting greater competitiveness.

Furthermore, it should be noted that plankton and organic debris constitute the primary sustenance of larval lampreys, ensuring a relatively stable supply, so intraspecific competition has a greater impact on population density than predation relationship during the juvenile stage.

In order to accurately elucidate the dynamics of larval lamprey population, a model is established for intraspecific competition among larval(hereinafter referred to as Model I) using the classical Lotka-Volterra framework.

The x_1 is represented as the population of female, while x_2 is the population of male, and the mathematical expression is as follows.

$$\begin{cases} \dfrac{dx_1}{dt} = r_1\left(1 - \dfrac{x_1 + \alpha_1 x_2}{K_1}\right)x_1 \\ \dfrac{dx_2}{dt} = r_2\left(1 - \dfrac{x_2 + \alpha_2 x_2}{K_2}\right)x_2 \\ x_1(0) = x_1^0, x_2(0) = x_2^0 \end{cases} \tag{1}$$

Table.1. Value of parameters mentioned in the model

Parameter	Value
$r_1 = r_2$	0.8
$\boldsymbol{x}_1^0 = \boldsymbol{x}_2^0$	30000
$\boldsymbol{\alpha}_1$	1
$\boldsymbol{\alpha}_2$	0.5

In resource-poor environments, the number of males exceeds that of females, suggesting stronger competitiveness for food resources among males. To accurately reflect this situation in above model, α_1 is set as 1 and α_2 is set as 0.5.

2.2. Downstream Migration Success Rate

Lampreys spawn upstream, and their juveniles descend to the habitat after reaching adulthood. The downstream migration success rate is namely the proportion of migrating from upstream to downstream and successfully arriving at suitable habitat. Lampreys and grass carps are both anadromous fishes, so the downstream migration success rate of grass carps can be used as a substitute, and the success rate of descending is 78.6% [8]. The population of juveniles is obtained from the intraspecific competition model of Model I and is represented as Z_0, while the number of successful migrant is Z.

$$Z = 78.6\% Z_0 \tag{2}$$

2.3. The Predator-Prey Model of Adult Lampreys in Three-Tiered Food Chain

Lampreys exert a significant ecological impact in specific habitats, and particularly sea lampreys parasitize various large fish species, such as trout and salmon, and display strong aggression. Consequently, they can be regarded as apex consumers within the food source-host-lamprey trophic chain model. The predator-prey model was employed to clarify the dynamics of adult lamprey population growth and its ecosystem-wide effects, and each link is shown in the Figure 1.

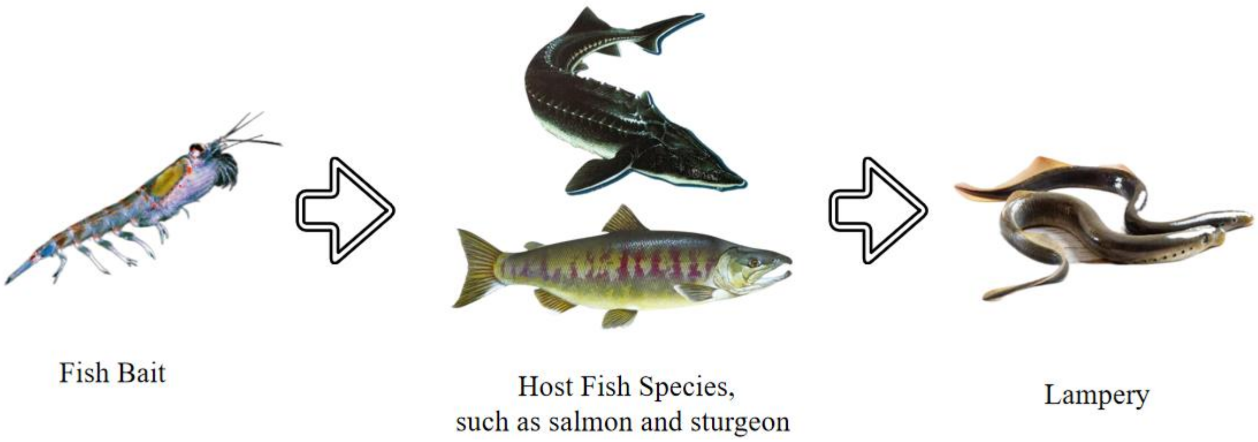


Figure 1. The three-tiered food chain of adult lampreys

The classical model of the food chain is summarized as follows:

$$\begin{cases} \dfrac{dx}{dt} = rx\left(1 - \dfrac{x}{K}\right) - G_1(x)y \\ \dfrac{dy}{dt} = -d_1 y + c_1 G_1(x)y - G_2(y)z \\ \dfrac{dz}{dt} = -d_2 z + c_2 G_2(y)z \end{cases} \tag{3}$$

In this equation, K represents the environmental capacity of the prey, r denotes the intrinsic growth rate of the prey, d_1 and d_2 respectively denote the natural mortality rates of host fish and the sea lamprey, c_1 and c_2 respectively denote the effective conversion rates of host fish and lamprey, and $0 < c_1 < 1, 0 < c_2 < 1$· $x(t), y(t), z(t)$ respectively refer to the population numbers of the prey, host fish and lamprey at time t.

The functional response functions of host fish and lamprey are denoted with $G_1(x)$ and $G_2(y)$ respectively. This model adopts the widely used Holling II function as the functional response function, with its initial expression being:

$$G_1(x) = \frac{m_1 x}{1 + \alpha_1 x}\ ,\quad G_2(y) = \frac{m_2 y}{1 + \alpha_2 y} \tag{4}$$

The semi-saturation constants of the fish bait and host fishes, represented by α_1 and α_2 respectively, along with the search rates of the host fishes and lampreys, represented by m_1 and m_2 respectively.

In the actual situation, what is noteworthy is that the bait of host fish may be small fish, which have a certain ability to avoid being preyed. Therefore, to improve the functional response function $G_1(x)$ of the fish bait, the effect of prey refuges is needed. If the prey shelter coefficient is δ, then $x-\delta xy$ represents the number of the preys that fail to take refuge in time and are captured by the host fish. The improved $G_1(x)$ can be obtained as follows:

$$G_1(x)=\frac{m_1 x(1-\delta y)}{1+\alpha_1 x(1-\delta y)}, \quad \delta\in\left[0,\frac{1}{y}\right] \tag{5}$$

The phenomenon of low birth rate due to a lower population density is called the Allee Effect [9], and Figure 2 makes it more clearly. The per capita growth rate is negative in strong Allee Effect while it remains positive in weak Allee effect.

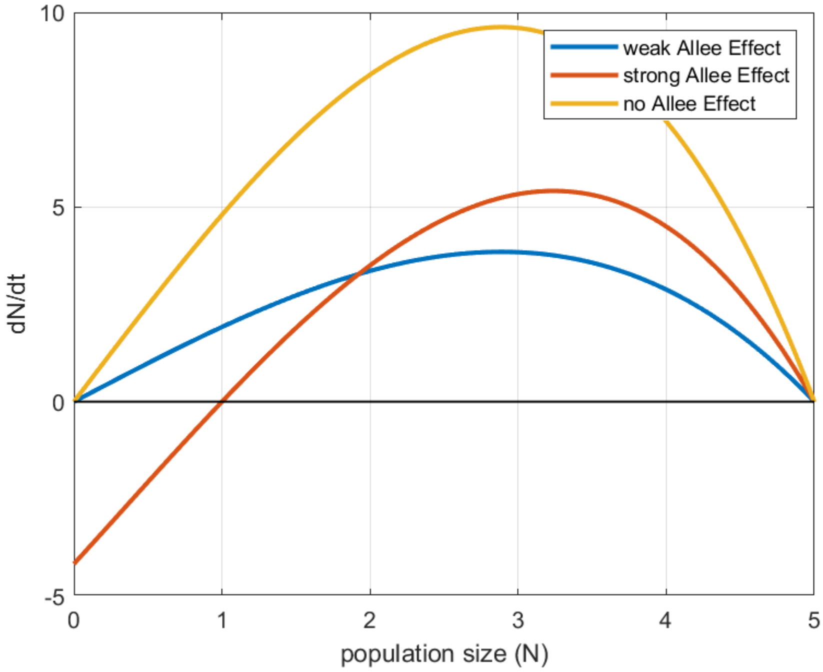


Figure 2. The impact of Allee Effect on population growth rate

Lampreys are very vulnerable when facing environmental influences due to their backtracking characteristic, and the sex ratio may be unbalanced due to the barren environment, and then reducing the population reproduction rate. But it is well known lampreys are ancient creatures, and the main reasons for the endangerment of lampreys in some regions are human activities and pollution caused by human activities. Lampreys in general natural environments have experienced a long time, so it is believed that lamprey populations will not experience negative growth or even extinction under natural conditions. Therefore, only the multiplicative Weak Allee Effect is introduced in the model.

The function of the Weak Allee Effect is as follows:

$$A(z)=\frac{z}{z+h} \tag{6}$$

The Allee Effect Constant is represented by h, $h>0$, and the larger h is, the more remarkable the Allee Effect is.

Considering the relatively smaller size of lampreys in comparison to other analogous apex predators, the number of lampreys is expected to be several times larger than that of their counterparts when both predators receive an equivalent amount of energy.

Ultimately, an optimized model has developed considering the three-tiered food Chain of adult lampreys (hereinafter referred to as Model II).

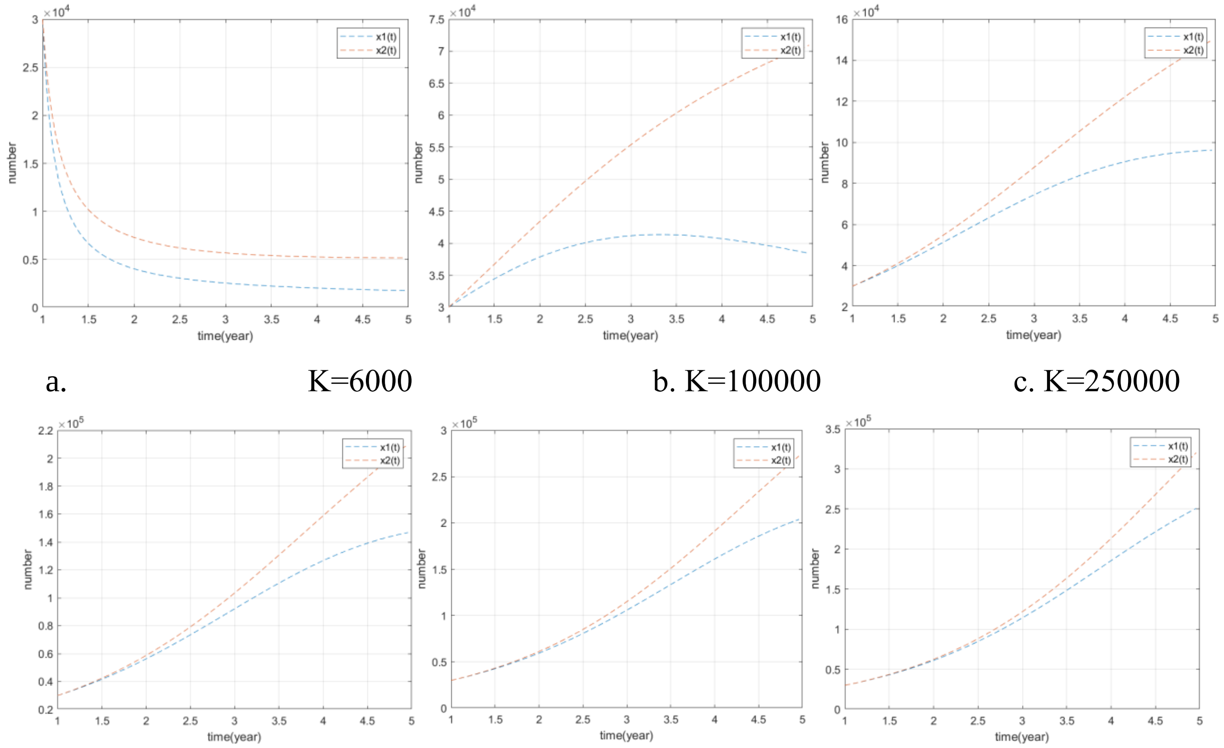
$$\begin{cases} \dfrac{dx}{dt} = rx\left(1-\dfrac{x}{k}\right)-\dfrac{m_1x(1-\delta y)y}{1+\alpha_1x(1-\delta y)} \\ \dfrac{dy}{dt} = -d_1y+c_1\dfrac{m_1x(1-\delta y)y}{1+\alpha_1x(1-\delta y)}-\dfrac{m_2yz}{1+\alpha_2y} \\ \dfrac{dz}{dt} = -d_2z+c_2\dfrac{m_2yz^2}{(1+a_2y)(z+h)} \end{cases} \tag{7}$$

$$Z_{lamprey} = 2z \tag{8}$$

3. Results

3.1. The changes in sex ratio with environment in Model I

The value of K is changed and the theoretical trend is consistent with the actual curve:



a. K=6000 b. K=100000 c. K=250000

d. K=400000 e. K=600000 f. K=800000

Figure 3. The curve of x_1 and x_2 with varying K values

As can be seen from the Figure 3, with the environmental capacity increasing, the population density increases, and the sex ratio of males to females gradually approaches 1:1. This is consistent with the natural phenomenon described in previous researches.

Table.2. Density and male sex ratio in relation to environmental capacity

K	Sum	Male%
6000	6.9388×10^3	74.51%
100000	1.0934×10^5	64.87%
250000	2.4591×10^5	60.90%
400000	3.5687×10^5	58.86%
600000	4.7594×10^5	57.19%
800000	5.7111×10^5	56.08%

It can be clearly seen from Table 2 that, in general, the larger the male proportion is, the lower the population density is, and an excessive male proportion will lead to gender imbalance, further affecting the reproductive rate.

In real ecosystems, based on the Logistic model, the value of K can be obtained according to the level of the ecosystem. The ecosystem is divided into six levels, and the higher the level is, the larger the K is [10]. The corresponding relationship is shown in Figure 4.

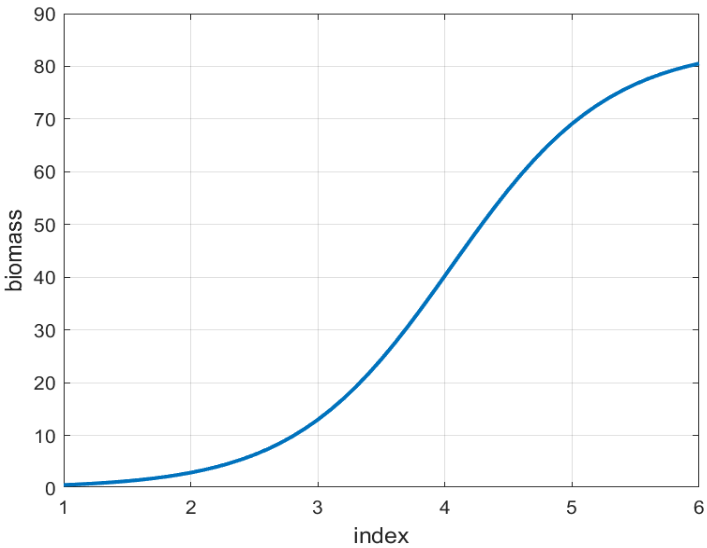


Figure 4. Diagram of biomass variation with grade

According to the level of ecosystem, the curve can be used to roughly judge the environmental capacity of the ecosystem. The first level of ecosystem is called primary bare area with no botany, and the final level is climax community with dynamic stability. The advanced level has higher biomass and the trend is initial fast followed by slow in the rate of biomass growth. Their relationship approximates the Logistic model. So the level of ecosystem can be used to estimate the value of biomass K.

3.2. The positive impact on ecological system

In response to a slight decrease in environmental capacity, the sea lampreys exhibit the ability to adjust the sex ratio by reducing the proportion of resource-consuming females and increasing the proportion of males, which optimizes utilization of environmental resources and maintaining population stability.

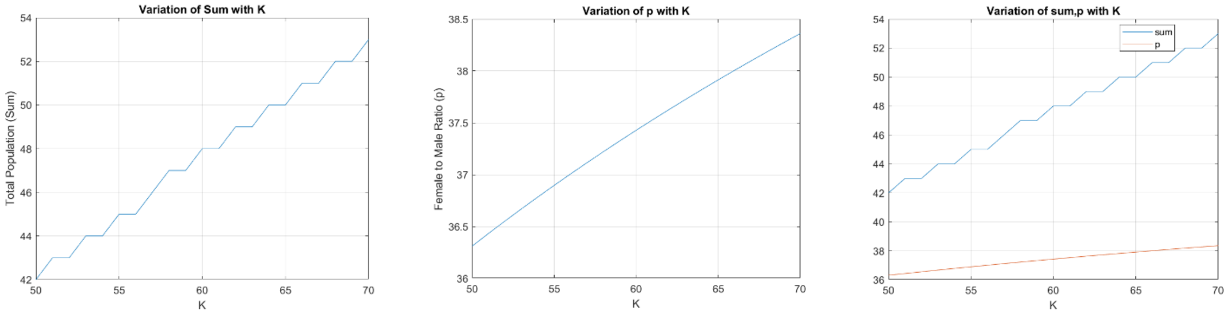


Figure 5. Density and sex ratio changing with environmental capacity

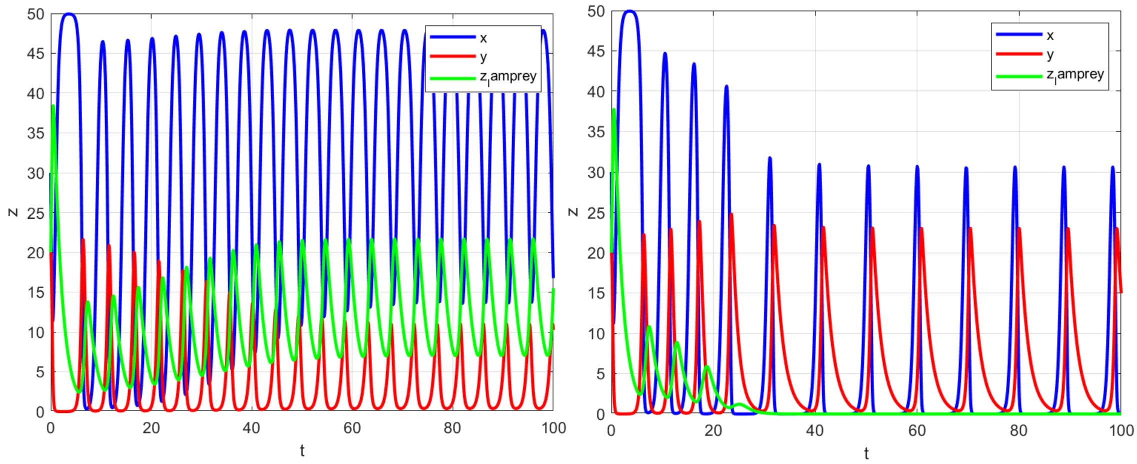
As can be seen from the Figure 5, the sex ratio of female to male slowly decreases with the decrease of K value, indicating that the proportion of female decreases and the proportion of male increases. In addition, when the population density curve decreases, there are multiple small platforms, indicating that the population can be maintained stable in a small range.

It is worth noting that in order to clearly see the change of the proportion of males and females, the proportion is processed to be 50 times of the original one when drawing the figure.

3.3. The negative impact on ecological system

3.3.1. The damage on the population of the sea lampreys

Unfavorable environmental conditions can result in an imbalanced sex ratio, subsequently leading to a decline in the reproductive rate and intensity, which has aggravated the Allee Effect.



a. h=0.6 b. h=1

Figure 6. The variation of population with different Allee Effect constants

The Figure 6 indicates that as h increases, the lamprey population will experience a rapid decline and fail to sustain stability. Finally, the population with high Allee Effect constant is heading for extinction. According to the definition of Allee Effect, an unbalanced sex ratio probably causes h to increase, which means the population at its breaking point.

3.3.2. The disruption of food chain

In the case of the inadequate resource within the adjustable range, the regulation of lamprey population can be partially achieved by changing the sex ratio. However, if other components in the food chain do not have the characteristics of regulating the sex ratio, population decline possibly occurs. Therefore, predators typically possess greater capabilities than their prey in Model II, this could lead to excessive fluctuations in species populations within the food chain and disrupt ecosystem dynamics.

4. Conclusions

The unique variable sex ratio of sea lampreys is in the spotlight, but there is a lack of mathematical characterization. Based on the above background, the paper adapts the Lotka-Volterra Model to address the intraspecific competition, and finds that when the value of environmental capacity K is 800000, meaning sufficient food, the ratio of male sea lampreys is 56.08%, which is almost balanced with the females. While K is 6000 and resource is scarce, the ratio of males is up to 74.51% and a sharp gender imbalance appears. Furthermore, the low value of K is often accompanied by the high value of Allee Effect constant h, which means population extinction of sea lampreys. The study does not only give the mathematical expression of changes in the sex ratio of sea lampreys, and comprehensive analyses on environment impacts of sex ratio variation are conducted from the positive and negative aspects, which enriches the research on the interactions between species and ecosystem.

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