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The Ecological System Model of Lampreys with Variable Sex Ratios

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ABSTRACT: The sex differentiation process of lampreys is particularly unique, as gender is correlated with its growth and development rate. This article aims to investigate the fitness advantages and ecological implications of the gender determination mechanism of lampreys by constructing a species ecological model. Based on the Lotka-Volterra ecosystem simulation equations, a male-female competition model for species with variable sex ratios was proposed to enable the modeling of the process of sex ratio evolution in lamprey populations. Subsequently, a time-delayed logistic equation was introduced to modify the model and predicted oscillations in population size and sex ratio over time, which was consistent with the observed phenomenon. Then, a simplified multi-species ecosystem model containing producers and consumers at four trophic levels was developed, taking into account the growth and development cycle of lampreys and food chain relationships. The paper investigated the changes of various populations in the ecosystem under different sex ratios by numerical methods. The results show that increasing the proportion of male competitive advantage will increase the population of lampreys and have certain impacts on other species in the ecosystem.

KEYWORDS: Ecological Modeling; Lotka Volterra Model; Sex Ratios; Mathematical Modeling.

I. INTRODUCTION

Current research suggests that the determination of gender in lampreys may be closely related to their growth rate, which is a novel gender-influencing factor not observed in other species. From 2005 to 2007, scientists from the U.S. Geological Survey and the University of Michigan marked larvae of sea lampreys with coded wire tags and released them into the environment [1]. Some were released into fast-flowing streams and rivers with higher food quality and quantity, which flowed into Lake Huron and Lake Michigan, referred to as "high-productivity areas." Others were released into slower-moving waters, where streams converged with lakes, and food supply and quality were lower, termed "non-high-productivity areas."

Over the three years following release, sea lampreys had sufficient time to enter their parasitic phase. In "high-productivity areas," 56% of tagged sea lampreys were male, while in "non-high-productivity areas," this proportion was 78%. The mechanism by which growth rate determines lamprey gender is not yet fully understood. Existing research suggests that the energy required for gonadal development in female lampreys is higher than in males. Therefore, under harsh environmental conditions, male lampreys may gain a competitive advantage, resulting in a higher proportion within the population.

The mechanism of gender ratio variation in lampreys enhances the population's environmental adaptability, providing a new perspective for studying the ecological significance of lamprey sex determination mechanisms and their impact on ecosystems. In order to solve the 2024 Mathematical Contest in Modeling (MCM) Problem A [2], we have developed phenomenological models of lamprey sex determination mechanisms based on ecological models. These models are built upon the competitive advantage of males in environments with limited food resources. Specifically, we established a mathematical model of two-sex competition and cooperative reproduction, which also considers the age structure distribution of lampreys. This model provides an effective descriptive tool for studying lamprey gender ratios and the ecological impacts of lampreys on ecosystems.

II. COMPETITION MODEL OF LAMPREYS WITH VARIABLE SEX RATIOS

To investigate the effects of a lamprey population with variable sex ratio on its ecosystem. In this paper, we first constructed a species model of lampreys in which male lampreys exhibit competitive advantage during periods of food scarcity, simulating an equilibrium with a sex ratio close to 1:1 under food-rich conditions and an overall

population bias toward males under food-scarce conditions. On this basis, a multi-species interaction model of the food chain associated with lampreys was developed using the Lotka-Volterra dynamic system model to study the effects of changes in the sex ratio of lampreys on their ecosystems, taking advantage of the ecological niche relationships of lampreys.

Mathematicians have proposed several classical theories on how to study and characterize the behavior of complex biological communities. This paper primarily adopts the widely used Lotka-Volterra dynamical system model in ecology to investigate [3], as depicted by the following equations:

$$\dot{N}_i = \lambda_i + r_i N_i \left(1 - \frac{N_i}{K_i} - \sum_{j \neq i} \alpha_{ij} \frac{N_j}{K_j} \right), i = 1, 2 \dots S \quad (1)$$

For a community consisting of S species, we define N_i as the species density of the i -th species at a certain moment (normalized by K_i , i.e. $N_i = \frac{N_i}{K_i}$). The rate of change in species abundance at a given moment is primarily determined by the influx rate of external species, denoted as λ_i , as well as the reproductive and mortality dynamics of the species.

The migration rate λ_i here can be understood as the exchange between an open ecological system and external species. For instance, microorganisms entering the gut through food, seabirds migrating between islands, or the exchange of species between a unit volume of seawater and external seawater. This migration rate is crucial for maintaining the stability of an ecosystem, as certain ecological systems may experience extinction of a particular species due to transient anomalies, thereby affecting the stability point of the entire system.

The term $r_i N_i$ represents the intrinsic growth of an individual species in the absence of any environmental pressure, manifesting as a positive correlation with the current species abundance. The term following the growth rate accounts for mortality due to intraspecific and interspecific competition, representing a corrected growth rate. Here, K_i denotes the carrying capacity of the environment when species i exists independently, which also accounts for this term. Interactions between different species can be coupled using the interaction matrix α_{ij} , where different values can represent biological relationships such as competition, predation, parasitism, cooperation, etc. Although the entire LV equation is nonlinear, we still model the interactions between species as being proportional to the linear relationship between the densities of the two species.

Therefore, based on the Lotka-Volterra equation, male and female lampreys are considered as two species competing with each other. In terms of competition, the parameters for males are set higher than females to simulate a higher competitive rate. Sea lampreys (*Petromyzon marinus* L. 1758) primarily employ a polygamous mating system. A study by Dhamelincourt et al. [4] have shown that each male mates with 2.33 ± 2.13 females. Consequently, for lampreys, fertilization success is high, and each female lamprey can produce a large number of eggs. Thus, for both male and female lampreys, their intrinsic growth terms are determined by the density of females. In traditional two-species competition models, without introducing other mechanisms, the competitively disadvantaged species tends to gradually extinct. However, in our model, females undertake the reproductive task, so their population size will not decrease to zero but will be maintained at a small value. Therefore, the Lotka-Volterra model for the population growth of lampreys with competition between sexes is as follows:

$$\begin{cases} \dot{N}_1 = N_2 - N_1(\alpha_{11}N_1 - \alpha_{12}N_2) \\ \dot{N}_2 = N_2 - N_2(\alpha_{21}N_1 - \alpha_{22}N_2) \end{cases} \quad (2)$$

Where population density has been normalized using environmental capacity, and since $r_i = 1.0$, this is equivalent to taking the unit time as the time required for the population to naturally grow by a factor of 1 (equivalent to one generation). For the interaction strength matrix α_{ij} , we set a parameter α greater than 1 to construct it, controlling the relative competition coefficients between males and females. The specific construction method is as follows:

$$[\alpha_{ij}] = \frac{1 + \alpha}{1 + \alpha^2} \begin{bmatrix} 1 & 1 \\ \alpha & 1 \end{bmatrix} \tag{3}$$

For the stable state with a time derivative of 0, we can solve for the normalized quantities of both sexes using equations (2) and (3):

$$\begin{cases} N_1(\infty) = \frac{\alpha}{1 + \alpha} \\ N_2(\infty) = \frac{1}{1 + \alpha} \end{cases} \tag{4}$$

The sex ratio is given by $\frac{N_1}{N_2} = \alpha$, with $N_1 + N_2 = 1$. Therefore, as the male's competitive advantage α increases, the model in this paper can reflect the increase in the proportion of males in the population (while the total population remains constant). Taking $\alpha = 1.0, 2.0, 3.0, 4.0$, the numerical solution results are as follows:

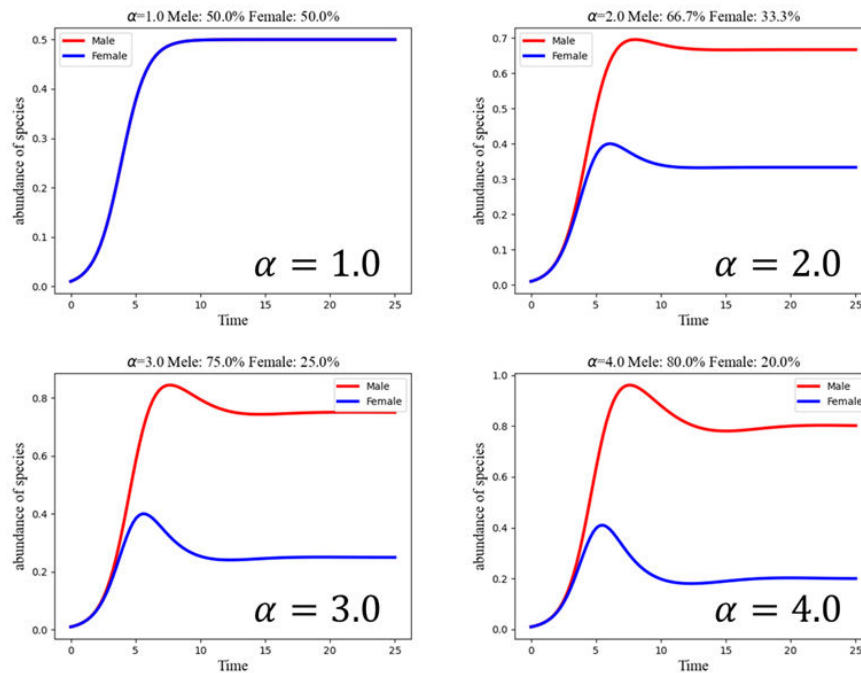


Figure 1: The Numerical Results of the Model of Sexual Competition

III. DELAYED MODEL OF INTERSEX COMPETITION IN LAMPREYS

The foundation of the Lotka-Volterra (LV) dynamical system is the Logistic equation, wherein the population growth rate is an instantaneous response to the population density N_i . However, in many practical scenarios, this response exhibits a lag effect. For instance, if the average lifespan of lampreys is denoted as T , then the population growth rate at time t should be related to the population density at time $t - T$, as lampreys hatched at time $t - T$ will contribute to reproduction at time t . Therefore, the normalized Logistic equation should be modified as follows:

$$\dot{N}(t) = N(t)[1 - N(t - T)] \tag{5}$$

Therefore, based on the time-delayed Logistic equation, this paper establishes the delayed model of intersex competition in lampreys with variable sex ratios within a single species as follows:

$$\begin{cases} \dot{N}_1(t) = N_2(t) - N_1(t)(\alpha_{11}N_1(t - T) - \alpha_{12}N_2(t - T)) \\ \dot{N}_2(t) = N_2(t) - N_2(t)(\alpha_{21}N_1(t - T) - \alpha_{22}N_2(t - T)) \end{cases} \quad (6)$$

The settings of the interaction strength matrix α_{ij} are the same as in the model described in Section 4.1. Due to the substantial number of eggs laid by lampreys during each spawning event, the time required for the population to double naturally is relatively short. Assuming a lifespan of $T = 1.5$ time units, we consider values of $\alpha = 1.0, 2.0, 3.0, 4.0$. The numerical solutions of the delayed model are as shown in the Figure 2.

After introducing the time-delay effect, the growth of the lamprey population exhibits significant oscillations. This is attributed to the mismatch between the delayed regulation of the population and the instantaneous (competitive) resource changes. However, eventually, the population converges to a stable solution. Furthermore, it is observed that with an increase in the proportion of males, the oscillation period lengthens, and the amplitude of oscillations decays more rapidly. This implies that an increase in the proportion of males contributes to the stability of the population.

In reality, oscillations in population numbers are a common ecological phenomenon. A study conducted by Docker [5] investigated male sex ratio data spanning 80 years from 1946 to 2016 in the Great Lakes region. This dataset includes the male percentage before and after lamprey control measures in the upstream regions of three Great Lakes (Superior, Michigan, and Huron), the downstream regions of two Great Lakes (Ontario and Erie), and Lake Champlain, as shown in the Figure 3.

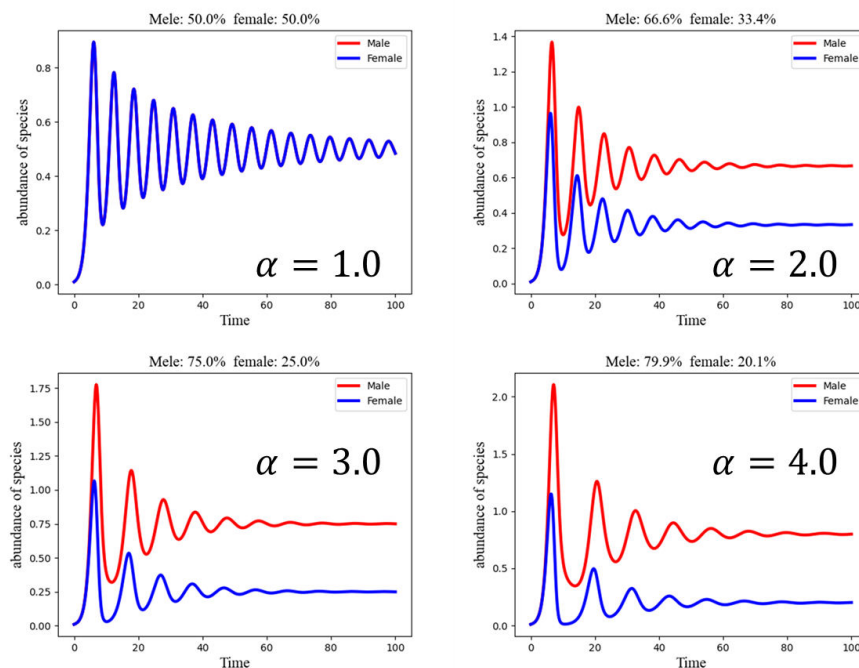


Figure 2: The numerical solutions of the delayed model of intersex competition

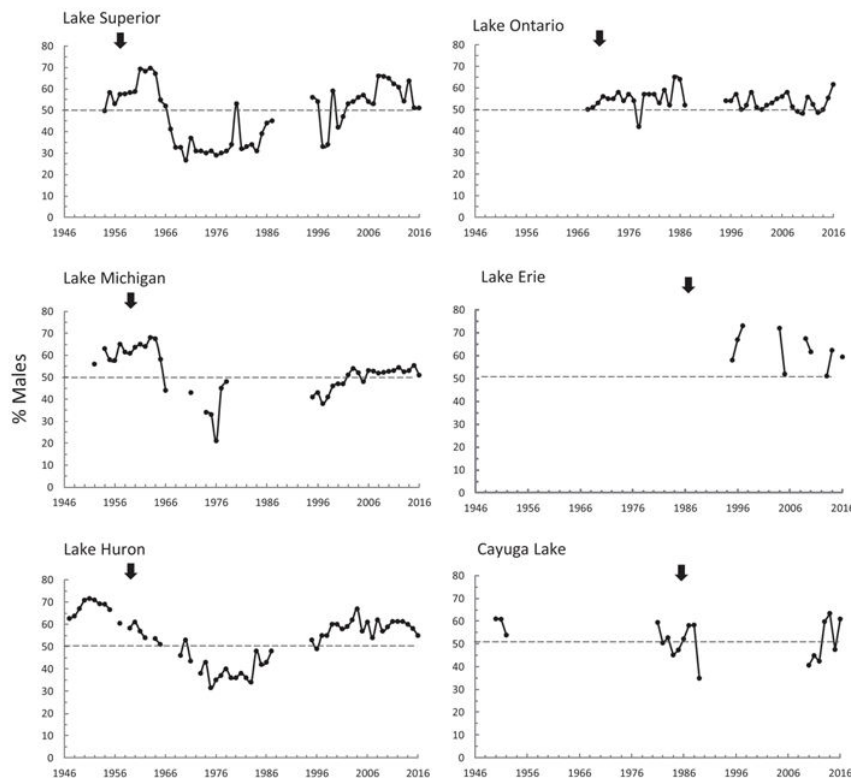


Figure 3: The gender ratio changes before and after the introduction of the lampricide [5].

After the introduction of TFM in the upstream regions of the three Great Lakes (Superior, Michigan, and Huron), the male proportion initially declined. This decrease can be attributed to the control of the lamprey population, resulting in reduced intraspecific competition and a greater tendency for each lamprey to develop into a female. However, subsequently, the gender ratio began to rise, exhibiting certain oscillatory patterns. This phenomenon shares similarities with the population oscillations predicted by the time-delay model proposed in this paper.

IV. THE IMPACT OF LAMPREYS ON LARGE ECOSYSTEMS

The life cycle of lampreys consists of four stages, typically spanning 18 months but can extend up to 5 years. The first of these stages is the spawning phase, which usually occurs in spring and early summer. From April to June, lampreys seek suitable nesting sites in freshwater streams. Once an area is selected, male lampreys construct nests, typically by moving rocks, forming a large depression or basin on the river or lakebed. Subsequently, female lampreys lay 30,000 to 100,000 eggs, which are externally fertilized by the males. After spawning, both male and female adult lampreys quickly perish. Adult lampreys do not feed during the spawning period. In the second stage, fertilized eggs settle into sand or gravel and begin to develop. Weeks later, the eggs hatch, and the larvae further burrow into the substrate. Larvae feed by filtering algae and other aquatic organic matter. This larval stage can last for over three years. In the third stage, known as the transformation phase, the larvae undergo metamorphosis into adult lampreys. During this stage, lampreys develop mouths, teeth, and eyes. They also migrate to larger bodies of water, such as the ocean or freshwater systems like the Great Lakes. In the fourth stage, lampreys reside in habitats for 12 to 18 months as mature adults, beginning to feed by attaching to fish and sucking blood, often causing excessive bleeding or wound infections, leading to the death of many parasitized fish. This stage is known as the parasitic phase, during which the lampreys' reproductive organs mature.

Newly hatched larval lampreys are freshwater filter feeders, consuming detritus, algae, and other organic matter from the riverbed. Once they enter a saline environment (or enter the Great Lakes), lampreys develop parasitic capabilities, attaching to fish and feeding on their blood and skin. Lampreys can attach to various fish species and appear to have no preferred host species. Lampreys in the parasitic phase remain prey for other predators, such as certain fish and birds.

Large numbers of sea lampreys preyed upon by albatrosses have been found on South Georgia Island in Argentina [6]. The biological network involving parasitism, predation, and competition among sea lampreys is depicted in the reference [7].

Considering the ecological niche shift of lampreys from larvae to adults, we can simplify an ecosystem relationship containing lampreys as follows. This system encompasses producers, lamprey parasitism, competition between lampreys and co-equal consumers, predation by higher-level consumers, and other interactions. It represents a relatively comprehensive system of relationships:

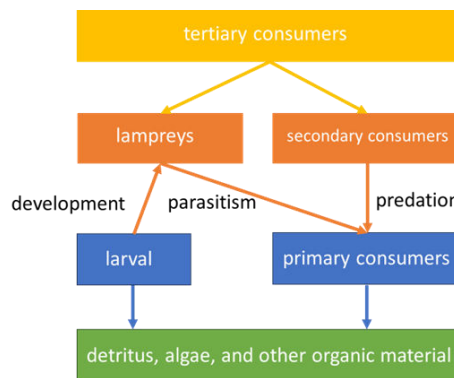


Figure 4: Ecosystem network including lamprey larvae and adults

In reference [8], it was found that 5%-15% of lake trout caught in the Great Lakes region had been parasitized by lampreys. Considering that individuals that have died due to lamprey parasitism cannot be caught, we can estimate the intensity of predation-parasitism interaction to be approximately between 0.1 and 0.2. In question 1, we uniformly set it to 0.15. Then, we can establish the following Lotka-Volterra dynamic system. The LV equations of the ecosystem are as follows:

$$\dot{N}_i = \lambda_i + N_i \left(1 - \sum_{j=1}^5 \alpha_{ij} N_j \right), i = 1, 2 \dots 5 \tag{7}$$

where $N_0 \sim N_6$ represent the abundance of producer, Male lampreys, Female lampreys, primary consumers, secondary consumers, tertiary consumers, respectively. And $\lambda_i = 1 \times 10^{-6}$, is used to prevent accidental extinction of species during computation, and the interaction matrix α_{ij} takes the following values:

$$\alpha_{ij} = \begin{cases} 1 & \text{if } i = j \\ \pm 0.15 & \text{if predatory or parasitic relationship between } i \text{ and } j \\ \alpha_{12} = \alpha & \alpha_{21} = \frac{1}{\alpha} \end{cases} \tag{8}$$

This is a 6-element system of differential equations, solved using numerical methods. We solve the ecological system model with α values of 1.0, 2.0, 3.0, and 4.0. The results of the solution are as follows. Please note that the densities plotted in the figure below are normalized by the carrying capacity and do not represent absolute quantities:

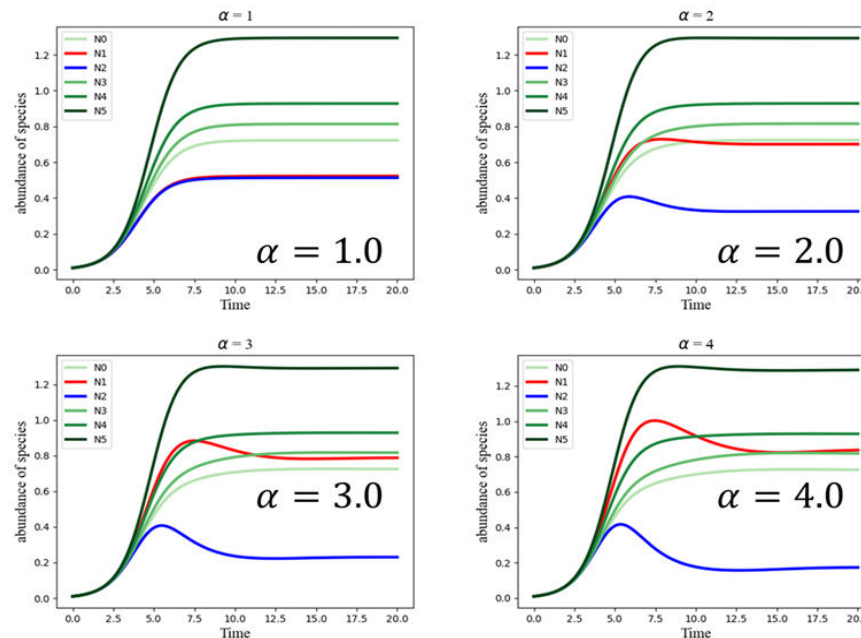


Figure 6: Results of a multi-species ecological system model under different lamprey sex ratios

In the above figure, the shades of green from light to dark represent consumer trophic levels from low to high, while red and blue represent male and female lampreys, respectively. From the figure, it can be observed that with an increase in the proportion of male lampreys, the relative density of the lamprey population increases (with the relative density of females remaining around 0.2 while that of males continuously rising), indicating a better adaptation of the population in the ecosystem. Additionally, due to the increase in the lamprey population, there is an increase in the nutrients consumed in the ecosystem. The number of lamprey parasitic hosts and co-equal consumers in competition decreases, while the number of higher-level consumers preying on lampreys increases. These findings align with our understanding. Therefore, the lamprey ecosystem model established in this paper can reflect the impact of lamprey sex ratios on their own population and the larger ecosystem.

V. CONCLUSION

This paper proposed a competition model for males and females in a species with variable gender ratios based on the Lotka-Volterraecological system model equations. Through skillful construction of interaction matrices, the evolution of gender ratios in the lamprey population was modeled. The model utilized a tunable parameter, α , to represent male competitive advantage. Subsequently, a logistic equation with time delay was introduced to amend the model, incorporating delayed effects into consideration. The model predicted population oscillations over time, including gender ratios, which aligned with empirical observations. Furthermore, considering the lamprey's growth and development cycles along with food chain relationships, a simplified ecosystem model with four trophic levels of producers and consumers was established. Through numerical methods, the paper investigated population changes in lampreys under different gender ratios. The results indicated that an increase in the proportion of competitive advantage among males would elevate the lamprey population and exert certain impacts on other species within the ecosystem.

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