

Dynamics of Sea Lamprey Populations in Marine and Lake Environments: An Analysis of Sex Ratio Impacts and Predatory Behavior

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Abstract. Understanding the population dynamics of lamprey under the influence of human activities and environmental changes is essential for ecosystem balance and biodiversity conservation. In this paper, a lamprey population dynamics model is constructed. Besides, changes in lamprey populations in different ecosystems and the impacts of lamprey on different ecosystems are explored. Specifically, after analyzing the intraspecific stage structure, the Lotka-Volterra predation model is introduced, and then the lamprey population dynamics model of lamprey is obtained. Moreover, a valuation index system for ecosystems is constructed. Subsequently, the Runge-Kutta method is cited to perform differential equation numerical solutions. The simulation results show that in marine ecosystems, the lamprey population will fluctuate initially and gradually reach stability. However, when in lake ecosystems with high food availability, the lamprey population will first decrease and then increase over a short period. In contrast, when the food availability of the lake ecosystems is low, the lamprey population decreases but does not tend to zero.

Keywords: Population Dynamics, Lotka-Volterra Predator Model, Runge-Kutta Method, Lamprey.

1. Introduction

Lampreys are one of the few survivors of an ancient jawless vertebrate lineage that is of great research value[1]. For example, germline genomic studies of sea lampreys have helped to understand the evolution and development of genome structure in lampreys and other vertebrates[2]. However, lamprey is an invasive species in some regions (such as the Great Lakes region of North America), which seriously affects the ecological balance[3]. So it is crucial to understand and predict the population dynamics of the lamprey population under different environmental conditions.

The differential equation model and the Lotka-Volterra model are two common and key models for studying the population dynamics of one specific species[4-6]. After analyzing the life cycle of green sea turtles, Wei et al constructed a differential stage-structured model to study the population dynamics of green sea turtles[7]. Xu et al constructed a demographic model for blue crab population dynamics which consists of two ordinary differential equations(ODEs), one for adult crabs and a second for juvenile crabs[8]. Georgiev et al proposed some differential equation models to investigate the honeybee population dynamics[9]. Nurrohman et al used Lotka-Volterra and Competitive Lotka-Volterra models to predict the population dynamics of owl and rice-field rats[10]. Iordanka N et al utilized the Lotka-Volterra model to study the population dynamics with the harvesting of the Atlantic Menhaden as prey and the Striped Bass as a predator[11].

In this paper, the intraspecific stage structure of lampreys is analyzed and a four-compartment differential dynamical model is proposed. Furthermore, the Lotka-Volterra model is utilized to improve the differential model. Then, the Runge-Kutta method is used to solve this problem. Consequently, the lamprey population dynamics are analyzed.

2. Intraspecific Stage Structure Analysis in Lampreys

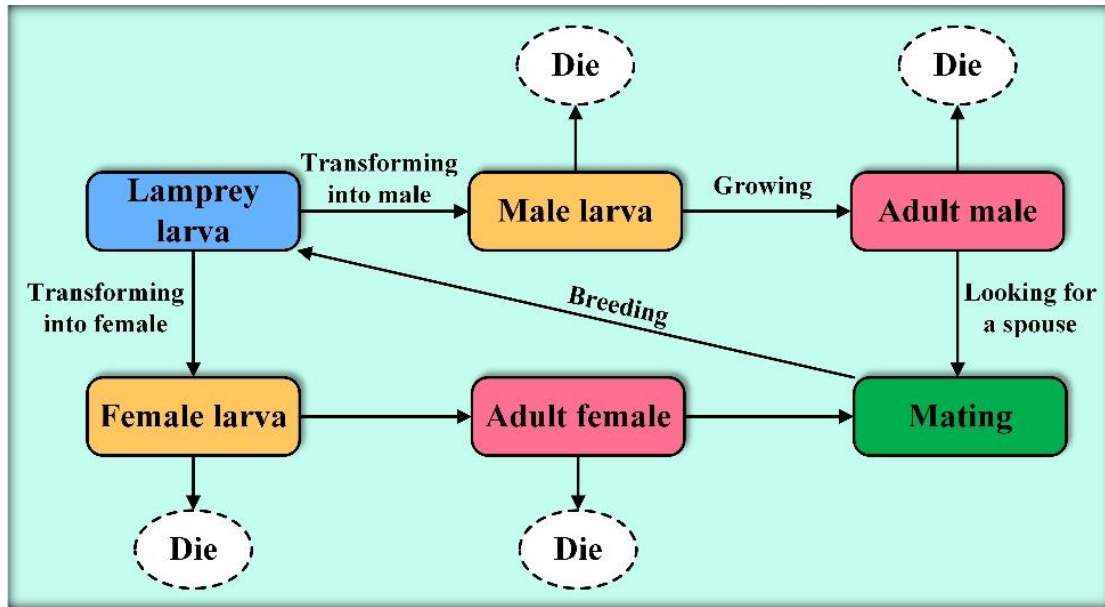


Figure 1. Schematic diagram of lampreys' life cycle

Sea lampreys become male or female depending on how fast they grow during the larval stage. The growth rates of these larvae are influenced by the availability of food. In environments with low food availability, growth rates will be lower and the percentage of males can reach about 78% of the population. However, in environments where food is more readily available, the proportion of males is about 56 percent of the population [12].

The life cycle of lampreys is shown in Figure 1. When modeling the lamprey population, the lamprey population is simplified into two stages: larva stage and adult stage. According to the essential purpose of this study, this paper clearly distinguishes between the males and females across the stages. The larva stage here refers to the stage at which the sex of lamprey larvae is determined and also includes the stage of the fertilized egg. Let $A_M(t) + A_F(t)$ denote the total population of adult lampreys of a focal colony at time t , where $A_M(t)$ denotes the population of adult male lampreys at time t , and $A_F(t)$ for females. Similarly, let $E_M(t) + E_F(t)$ denote the population of lamprey larvae at time t , where $E_M(t)$ denotes the population of male lamprey larvae at time t , and $E_F(t)$ for females.

Then, a four-compartment dynamical model to describe the stage-structured dynamics of the lamprey population is developed.

$$\begin{cases} \frac{dA_M}{dt} = \alpha_M E_M - \beta_A A_M \\ \frac{dA_F}{dt} = \alpha_F E_F - \beta_A A_F \\ \frac{dE_M}{dt} = G(P) \cdot r \left(1 - \frac{A_M + A_F}{K}\right) \cdot \frac{m \left(\frac{A_F}{A_M}\right)^2}{a^2 + \left(\frac{A_F}{A_M}\right)^2} A_M - \beta_E E_M - \alpha_M E_M \\ \frac{dE_F}{dt} = (1 - G(P)) \cdot r \left(1 - \frac{A_M + A_F}{K}\right) \cdot \frac{m \left(\frac{A_F}{A_M}\right)^2}{a^2 + \left(\frac{A_F}{A_M}\right)^2} A_M - \beta_E E_F - \alpha_F E_F \end{cases} \quad (1)$$

where model parameters α_M , α_F , β_A , β_E , r , K , a and m are both positive constants. Table 1 gives a detailed description of all the parameters in the model.

Table 1. Parameters descriptions and values

Parameter	Description
α_M	Maturity rate of lamprey larvae that become adult males
α_F	Maturity rate of lamprey larvae that become adult females
β_A	Adult lamprey mortality
β_E	Lamprey larvae mortality
r	Maximum average number of eggs per successful interaction
K	Carrying capacity of adult lampreys

The ecological justifications for this model are summarized as follows:

Adult males A_M

The population of adult male lampreys A_M is determined by one inflow and one outflow:

(a) The inflow population is modeled as $\alpha_M E_M$, which gives the new adult male lampreys, where α_M is the maturity rate of male lamprey larvae. It is quite difficult for each lamprey larva to reach adulthood because many lamprey larvae are killed by birds or other predators as they emerge from their eggs, which makes α_M very small.

(b) The outflow population, namely the population of dead adult male lamprey, is modeled as $\beta_A A_M$, where β_A is adult lamprey mortality.

To summarize, we have

$$\frac{dA_M}{dt} = \alpha_M E_M - \beta_A A_M \quad (2)$$

Adult females A_F

The population of adult female lampreys A_F is determined by one inflow and one outflow:

(a) The inflow population is modeled as $\alpha_F E_F$, which gives the new adult female lampreys, where α_F is the maturity rate of female lamprey larvae.

(b) The outflow population, or the population of dead adult female lamprey, is modeled as $\beta_A A_F$, where β_A is adult lamprey mortality.

Similarly, we have

$$\frac{dA_F}{dt} = \alpha_F E_F - \beta_A A_F \quad (3)$$

Male larvae E_M

The population of male lamprey larvae is determined by one inflow and two outflows:

(a) The inflow population is the population of lamprey larvae that transform into male lamprey larvae, which is mainly determined by the proportion of male larvae in total larvae $G(P)$, spawning biomass NE , fertility rate NM , and population of adult male lampreys A_M .

(1) For the proportion of male larvae in total larvae $G(P)$, $G(P)$ will be higher (in this case, it will be higher than 0.5) under conditions of insufficient food, so a logistic function is considered to characterize this process, i.e.

$$G(P) = \frac{1}{1 + e^{\frac{-1}{s}(P_0 - P)}} \quad (4)$$

where $G(P)$ is the proportion of male larvae in total larvae, P is food quantity, s is a parameter that can be solved, and P_0 is the food quantity that corresponds to half of the male population.

(2) For spawning biomass NE , NE is affected by its population. In a given environment, when there are too many adult lampreys, the survival environment is more severe due to interspecific competition, so NE will be reduced. Similar to the intraspecies competition model, we have

$$NE = r(1 - \frac{A_M + A_F}{K}) \quad (5)$$

where NE is spawning biomass, r is the maximum average number of eggs per successful interaction, and K is the carrying capacity of adult lampreys.

(3) For fertility rate NM affected by sex ratio, lampreys reproduce sexually, and the female produces many eggs in a reproductive mode similar to that of sea turtles. When the sex ratio is fixed, the fertility rate NM is directly proportional to the number of adult males, so we have

$$NM = f(\frac{A_F}{A_M}) \cdot A_M \quad (6)$$

where NM is the fertility rate, and f is a function whose independent variable is the sex ratio. The lamprey courtship process is very similar to the predator-prey process. So we have

$$f(\frac{A_F}{A_M}) = \frac{m(\frac{A_F}{A_M})^2}{a^2 + (\frac{A_F}{A_M})^2} \quad (7)$$

where m and a are both parameters.

(b) Two outflows are $\alpha_M E_M$ and $\beta_E E_M$ respectively, where $\alpha_M E_M$ is the inflow population of adult male lampreys and $\beta_E E_M$ is the population of lamprey larvae that go dead.

$$f(\frac{A_F}{A_M}) = \frac{m(\frac{A_F}{A_M})^2}{a^2 + (\frac{A_F}{A_M})^2} \quad (8)$$

To summarize, we have

$$\frac{dE_M}{dt} = G(P) \cdot r(1 - \frac{A_M + A_F}{K}) \cdot \frac{m(\frac{A_F}{A_M})^2}{a^2 + (\frac{A_F}{A_M})^2} A_M - \beta_E E_M - \alpha_M E_M \quad (9)$$

Female larvae E_F

The population of female lamprey larvae is determined by one inflow and two outflows like male lamprey:

(a) The inflow population is the population of lamprey larvae that transform into female lamprey larvae, which also is mainly determined by the proportion of male larvae in total larvae $G(P)$, spawning biomass NE , fertility rate NM , and population of adult male lampreys A_M .

(b) Two outflows are $\alpha_F E_F$ and $\beta_E E_F$ respectively, where $\alpha_F E_F$ is the inflow population of adult male lampreys and $\beta_E E_F$ is the population of lamprey larvae that go dead.

The whole dynamic model of female larvae E_F is derived similarly as Male larvae E_M , so the final model is given directly as

$$\frac{dE_F}{dt} = (1 - G(P)) \cdot r(1 - \frac{A_M + A_F}{K}) \cdot \frac{m(\frac{A_F}{A_M})^2}{a^2 + (\frac{A_F}{A_M})^2} A_M - \beta_E E_F - \alpha_F E_F \quad (10)$$

The schematic diagram of the constructed lamprey population dynamics model is shown in Figure 2.

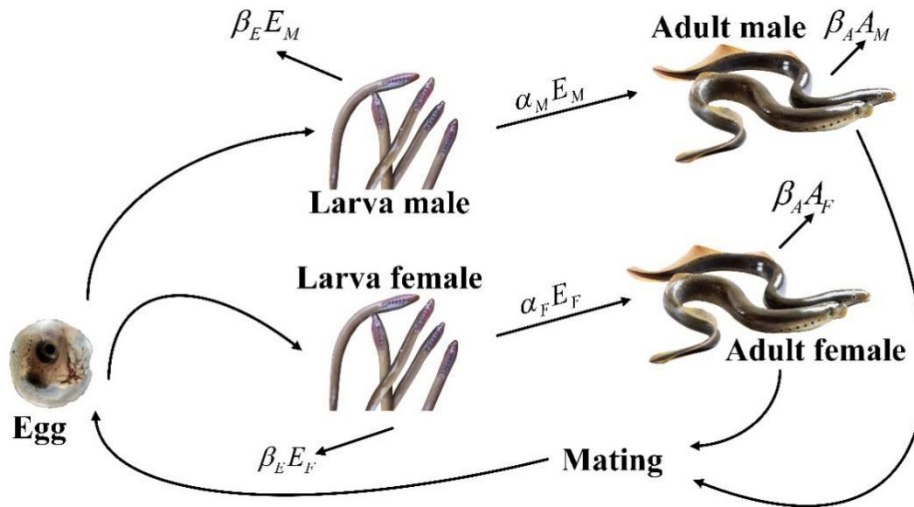


Figure 2. Schematic diagram of lamprey intraspecific population dynamics model

3. Study on Lampreys' Impact on Ecosystems

3.1. Population dynamics model for lampreys

Previously, the relationships within the lamprey population have been analyzed. The biodynamic model without the participation of other species was obtained. But in fact, the impact of other components on lamprey populations in an intact ecosystem can not be ignored. Here species that prey on lampreys as well as species that are preyed upon by lampreys are considered, and the effects of lamprey predators on lampreys are already included in lamprey mortality, so hereby this paper focuses on species that are preyed upon by lampreys. Given such a classical predation relationship, the Lotka-Volterra model is introduced which demonstrates that the population size of predators and prey varies depending on the number and interaction of both parties. With the introduction of the Lotka-Volterra model, we have

$$\begin{cases} \frac{dA_M}{dt} = \alpha_M E_M - \beta_A A_M + \mu_{A_M} \chi P \cdot A_M \\ \frac{dA_F}{dt} = \alpha_F E_F - \beta_A A_F + \mu_{A_F} \chi P \cdot A_F \\ \frac{dE_M}{dt} = G(P) \cdot r \left(1 - \frac{A_M + A_F}{K}\right) \cdot \frac{m \left(\frac{A_F}{A_M}\right)^2}{a^2 + \left(\frac{A_F}{A_M}\right)^2} A_M - \beta_E E_M - \alpha_M E_M \\ \frac{dE_F}{dt} = (1 - G(P)) \cdot r \left(1 - \frac{A_M + A_F}{K}\right) \cdot \frac{m \left(\frac{A_F}{A_M}\right)^2}{a^2 + \left(\frac{A_F}{A_M}\right)^2} A_M - \beta_E E_F - \alpha_F E_F \\ \frac{dP}{dt} = \alpha_P P - \chi P (A_M + A_F) \end{cases} \quad (11)$$

where P is the prey population quantity namely food quantity, χ is the probability of predation by adult lampreys, μ_{A_M} is the predation efficiency of adult male lamprey, and μ_{A_F} is the predation efficiency of adult female lamprey.

3.2. Evaluation index system for ecosystems

To obtain the quantity of various groups in the evolution of the preliminary ecosystem, a numerical scheme to explain how they evolve is needed. Since this is a first-order ordinary differential system, which does not contain higher-order terms and high-dimensional networks, the Runge-Kutta method is utilized to solve this system, obtaining numerical results for the preliminary ecosystem evolution.

To characterize the impact on the ecosystem, the following indicators are introduced uniformly into the analysis:

$N(t)$: The total quantity of all species at time t .

$Q_i(t)$: The total quantity of species i at time t .

$Q_i(0)$: The initial total quantity of species i .

$R_i(t_1, t_2) = \frac{\max_{t \in (t_1, t_2)} Q_i(t) - \min_{t \in (t_1, t_2)} Q_i(t)}{Q_i(0)}$: The ratio of the amplitude of the quantity of species i between time

t_1 and t_2 to the initial total quantity of species i which can describe the stability of species in the evolutionary process.

When $0 \leq |R_i(t_1, t_2)| \leq 4$ the species is developing stably.

When $|R_i(t_1, t_2)| \geq 4$ there are large fluctuations in the development of species.

$U_i(t) = \frac{Q_i(t) - Q_i(0)}{Q_i(0)}$: The ratio of the quantity of species i at time t to the initial total quantity of

species i which can describe the growth of one species during its evolution in the ecosystem.

When $U_i(t) \leq -0.5$ the quantity of species decreases in evolution. In other words, species develop poorly.

When $2 > U_i(t) > -0.5$ the quantity of species is controlled within a reasonable range and the species develops well.

When $U_i(t) \geq 2$ the species grow too fast in their evolution. That is the species overrun the ecosystem.

3.3. Impacts on Lake Environments

In lake environments where the resource availability is relatively low, the lamprey population is 78% male. A preliminary ecosystem population evolution diagram is displayed in Figure 3.

According to Figure 3, $|R_1(30, 50)| = 10.75 \geq 4$ $|R_2(30, 50)| = 4.65 \geq 4$ which indicates that various groups are very unstable in the evolution process, the ecosystem is relatively fragile, highly sensitive to internal and external changes, and the quantity of species within fluctuates greatly.

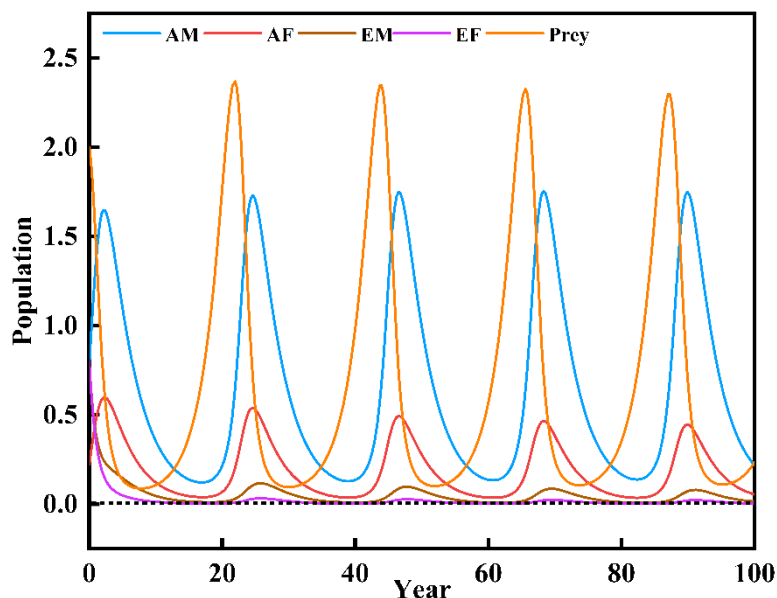


Figure 3. Diagram of population evolution in preliminary lake environments

Specifically, according to the fact that female lampreys need more nutrients and food during growth, the population tends to expand the proportion of male lampreys when the food supply is insufficient. In addition, the lamprey population is dominated by males in the breeding stage, reproducing and increasing rapidly in the case of a large proportion of males, thus forming a predation relationship with prey with greater fluctuation in the number of species.

Although the slight resilience and stability of the ecosystem are reflected in Figure 3, when the external environment changes, the ecological imbalance of the whole ecosystem may occur, as shown in Figure 4.

According to the image, $U_1(100) = -0.83 \leq -0.5$ and $U_2(100) = -1 \leq -0.5$, which indicates that during the evolution of each species population, the quantity of all species decreases greatly and the development situation is poor in the ecosystem. Even prey species are endangered.

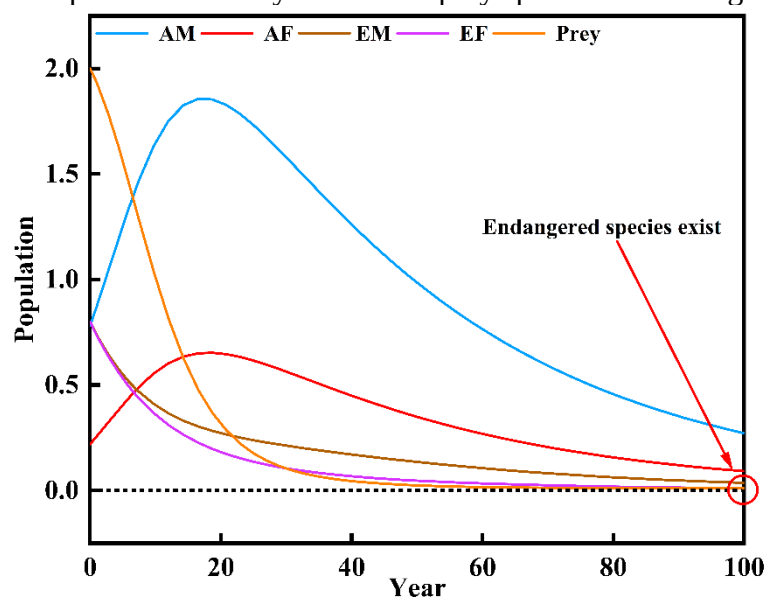


Figure 4. Diagram of ecological imbalance

3.4. Impacts on Marine Environments

In marine environments where the resource availability is relatively high, the lamprey population is 56% male. A preliminary ecosystem population evolution diagram is displayed in Figure 5.

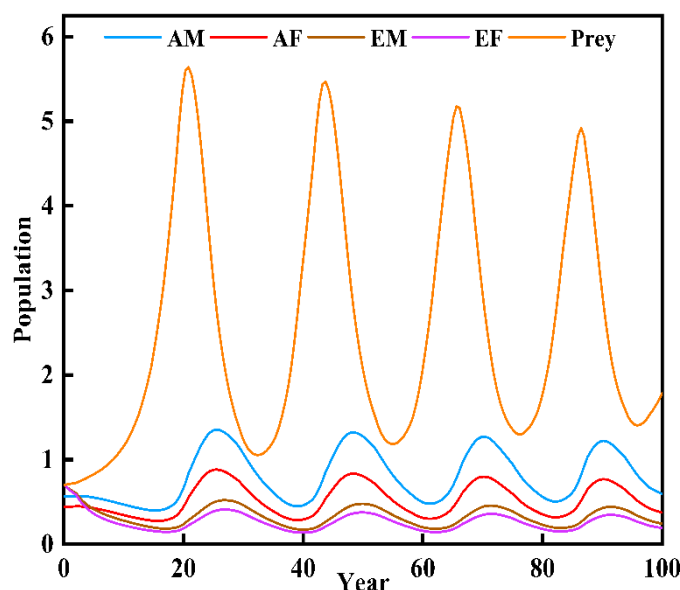


Figure 5. Diagram of population evolution in preliminary marine ecosystems

It can be easily calculated that when $0 \leq t_1 \leq t_2 \leq 100$, two following equalities always hold: $0 \leq |R_1(t_1, t_2)| = 3.1 \leq 4$ and $0 \leq |R_2(t_1, t_2)| = 3.3 \leq 4$, which indicates that the ecosystem is developing soundly and is relatively stable. Besides, lampreys and their prey form a periodic predation relationship and this relationship remains stable, and the prey population develops well.

In specific, according to the biological characteristics of the lamprey population, such as male promiscuity and polygamy, 56% of the male population enables the sex structure of the whole lamprey population to sound, and the number of lampreys fluctuates periodically within a reasonable range.

4. Results and Discussion

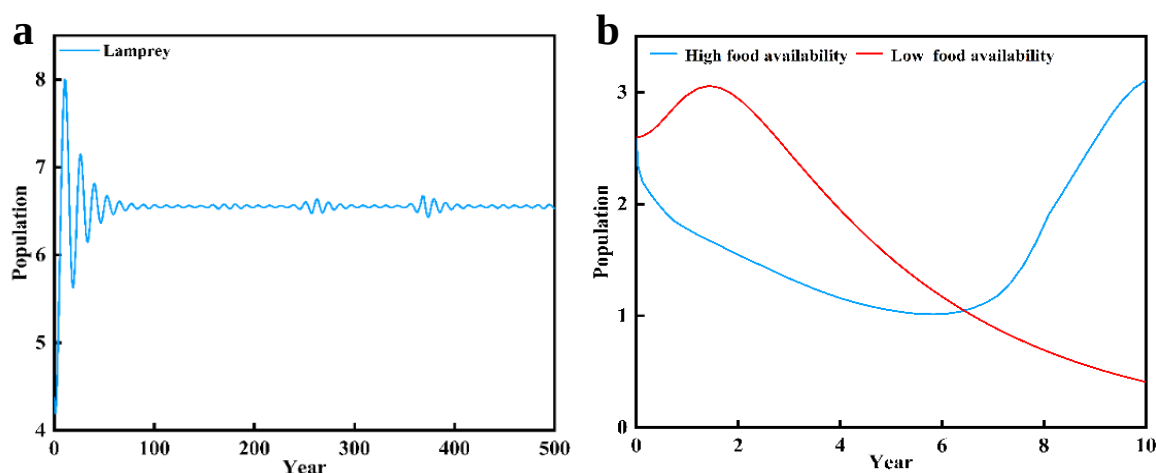


Figure 6: (a) Diagram of lamprey population evolution in marine ecosystems. (b) Diagram of contrast in lamprey population evolution in lake systems with different food availability

Figure 6 respectively gives diagrams of lamprey population evolution in marine ecosystems and lake ecosystems with different food availability.

In marine ecosystems, after experiencing large oscillations in quantity in the early stage, we have $0 < |R_1(80, 500)| = 0.001 \leq 4$, which indicates that the lamprey population tends to be stable and the population develops well. In lake ecosystems, however, the lamprey population presents different development tendencies depending on the food availability of lake ecosystems. When the food

availability of the lake ecosystem is high, the lamprey population is dominant. It is calculated that $2 > U_1(10) = 0.3 > -0.5$ which indicates that the population of lamprey grows steadily with reasonable periodic oscillations. Whereas, when the food availability of the lake ecosystem is not sufficient, it is calculated that $U_1(10) = -0.84 < -0.5$, which shows that the lamprey population is decreasing, having a risk of extinction.

5. Conclusions

In this paper, the growth trends of lampreys in Marine and lake ecosystems are analyzed and an evaluation index system for ecosystems is built. In marine ecosystems, the lamprey population fluctuates greatly initially and gradually gets into a stable stage. Besides, the population of other species in lake ecosystems shows stable periodic oscillation. However, in lake ecosystems, the lamprey population decreases first and then increases for a short time if the food availability is high. But when the food availability of the lake ecosystems is low, the lamprey population decreases but does not tend to zero.

This paper provides a research idea and framework that can be applied to the evaluation of different ecosystems, that is, to construct a differential equation model of species growth, namely population dynamics, and to analyze the growth trend of species and the changing trend of the environment by using the numerical solution method of the differential equation.

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