

Biomass prediction of sea lamprey population based on dynamic feature matrix composite differential equation system

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Abstract. This article presents a mathematical model to predict sea lamprey biomass, addressing the species' impact on the Great Lakes fishery. The model, comprising a Dynamic Age Pyramid and a Multi-species Lotka-Volterra system, captures the complex life stages and behaviors of sea lampreys. It simulates their diet, habits, and growth parameters across different ages, considering their adaptive sex ratio variation. Key findings include the model's ability to dynamically update sea lamprey population characteristics annually in response to environmental changes. Simulations show that populations with dynamic sex ratios reach equilibrium faster, with an increasing female proportion over time in resource-rich environments. However, these populations exhibit less resilience to rapid environmental shifts compared to those with stable sex ratios. The study concludes that the model offers a valuable tool for understanding complex organism-environment interactions and enhances traditional ecological models by providing a dynamic, biologically meaningful population feature matrix. This innovation aids in managing invasive species like sea lampreys without harming native ecosystems.

Keywords: Sea Lamprey, Adaptive sex ratio variation, Lotka-Volterra Model, Ecosystems.

1. Introduction

Sea lampreys (*Petromyzon marinus*) are parasitic vertebrates native to the Atlantic Ocean. They have remained largely unchanged for more than 340 million years. In their native Atlantic Ocean, sea lampreys are parasites that typically do not kill their host^[1]. However, sea lampreys act as predators in the Great Lakes where no such co-evolutionary link exists. Sea lampreys have had an enormous negative impact on the Great Lakes fishery. Each individual is capable of killing more than 20 kilograms of fish over their parasitic feeding period. Host fish in the Great Lakes are often unable to survive sea lamprey parasitism, either dying directly from over-bleeding or infections in the wound. Sea lampreys jeopardize nearly all large Great Lakes fish species such as brown trout, lake sturgeon, ciscoes, burbot, walleye, and Pacific salmonids^[2].

The U.S. government faces significant challenges in managing the sea lamprey population in the Great Lakes. Annually, the U.S. and Canadian governments spend at least \$15 million on sea lamprey control measures, which include mechanical barriers, electrical barriers, and chemical treatments.^[3] However, these control measures, including the use of lampricides, have also impacted native species, leading to a decrease in their occupancy both in treated and untreated streams. These challenges highlight the complexity of controlling an invasive species without causing harm to native ecosystems^[4].

Among the many studies of sea lamprey habits, one phenomenon worth noting is that sea lamprey is a species with adaptive sex ratio variation, which means the sex ratio of sea lamprey populations can change according to environmental conditions^[5]. Their feeding habits and habitat can also change dramatically during their complex life history. This article will focus on the living habits of sea lampreys and establish mathematic model to describe their unique life cycles. Based on this model, government can make more accurate annual estimates of sea lamprey population and adjust the intensity of population control measures to minimize the impact on native species.

2. Research ideas and methods

2.1. Overall research ideas

The life history of the sea lampreys is very complex, with specific feeding and behavior patterns at different stages of its life and discrete periods of reproduction. Sea lamprey larvae feed mainly on plankton, while juvenile and adult sea lampreys feed on the blood and body fluids of other fish^[6]. Based on the life history of sea lampreys in Literature Review, a multi-species Lotka-Volterra model with dynamics population updates was established.

This model is composed of the Dynamic Age Pyramid Model and the Multi-species Lotka-Volterra Model. The aim is to achieve an accurate modelling of the dietary habits, behavior patterns, and growth-related parameters of sea lampreys in different quantities for each age group. The Age Pyramid with the Population Characteristic Matrix of the sea lampreys is shown in Fig 1. In the Population Characteristic Matrix, the numbers I to X denote the sea lamprey populations of the corresponding age groups.

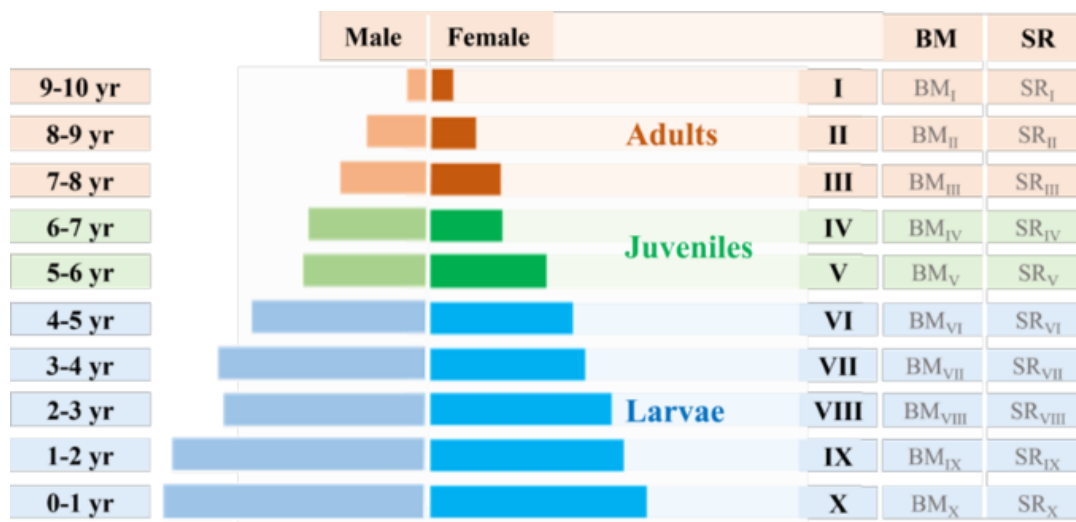


Fig. 1 The Age Pyramid and the Population Characteristic Matrix.

2.2. Model description on dynamic population characteristics of sea lampreys

Unlike most animals, the sex ratio of sea lampreys varies in each age group. In most cases, the sex determination of sea lampreys is irreversible^[7]. Therefore, it can be inferred that the sex ratio of sea lampreys in any age group depends solely on the resource availability when they are in their second to third year of the larval period Fig 2.

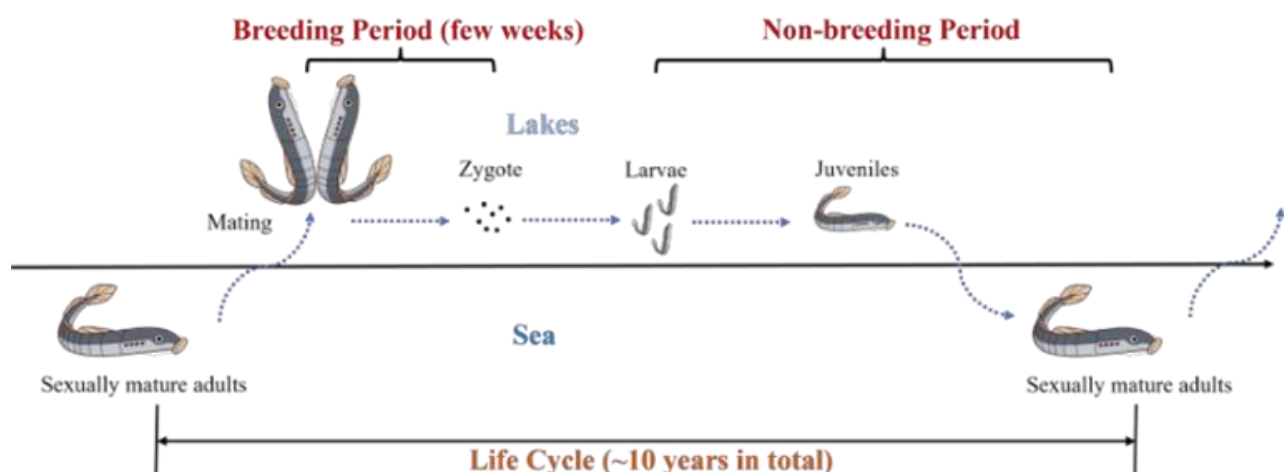


Fig. 2 the life cycle of sea lampreys

During each breeding period, adult sea lampreys at the top of the Age Pyramid mate randomly, producing fertilized eggs before dying. A portion of these eggs hatch into larvae, converting the adults' biomass (BMI) into the initial biomass of new larvae (BMX) proportionally. Fig 3 illustrates the annual changes in the Population Characteristic Matrix. The scale factor η for this conversion is linked to the sex ratio (SRI) as per Formula 1.

$$BM_X = BM_I \times \eta(SR_I) \quad (1)$$

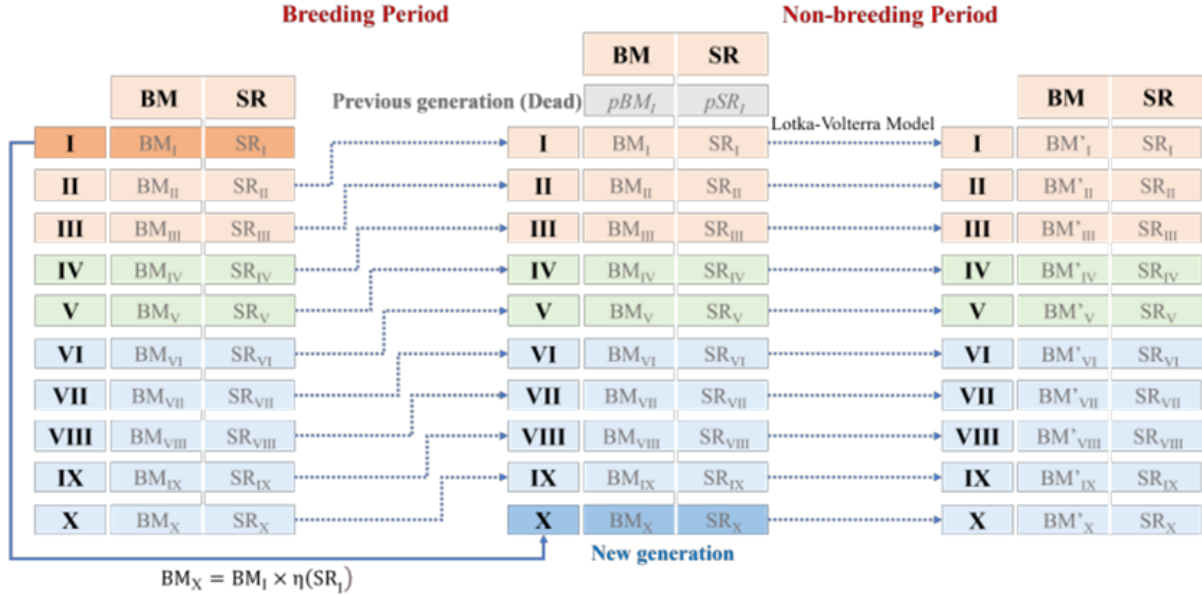


Fig. 3 Breeding and non-breeding period in the life history of sea lampreys.

Statistic results of multi-year survey data from 74 collection sites in the Great Lakes region indicate that the proportion of females in the sea lamprey population ranges from 15% to 62% in natural environments and is usually between 20% and 50% [8]. Based on these data and the anatomical data of the sea lampreys, the functional relationship between sex ratio and η is shown in Formula 2.

$$\eta = -0.8SR_I^2 + 0.8SR_I, \quad SR_I \in [0,1] \quad (2)$$

Newborn larvae are asexual because their gonads have not yet developed. Sex determination occurs in the second to third year (Stage VII in the Age Pyramid). In summary, the relationship between the sex ratio and environmental resources is shown in Formula 3.

$$\frac{SR_{VII}-0.2}{1-0.2} = \frac{BM_M-0.2}{N_M-0.1N_M} \quad (3)$$

Solving for:

$$SR_{VII} = \frac{BM_M}{3N_M} + \frac{1}{6} \quad (4)$$

By repeating the above steps annually, the Population Characteristic Matrix in this model can be dynamically updated in response to changes in external conditions.

2.3. Model description on interspecific interaction

Juvenile sea lampreys are parasitic, feeding on the blood of various fish species in the lake, effectively acting as apex consumers. The adults spend most of their lives in the Atlantic Ocean and are not considered part of the lake ecosystem [9]. Fig 4 illustrates the food chains in the lake and ocean ecosystems. In order to simulate this situation better, a Multi-species Lotka-Volterra Model was established.

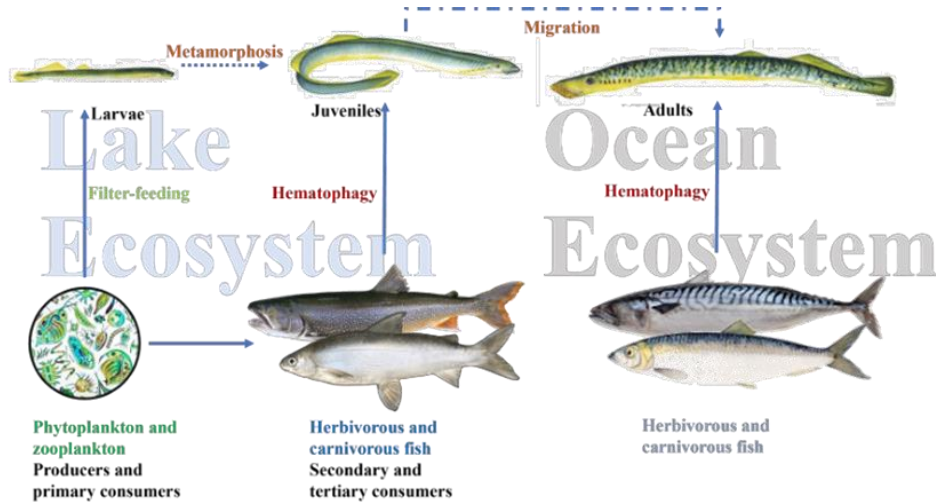


Fig. 4 Food chains in the lake and ocean ecosystem.

In the ocean, due to the abundance of resources far exceeding that of lakes, the self-regulation ability of the ecosystem is also stronger. Interactions between species are weak. The rate of change of their biomass can be described by Formula 5.

$$\frac{dBM_A}{dt} = \gamma_A B_M \left(1 - \frac{BM_A}{N_A}\right) \quad (5)$$

When there are only two species in the system, the interactions between the two species can be represented by the Lotka-Volterra equation (Formula 6).

$$\begin{cases} \frac{dX}{dt} = X(a_{10} + a_{11}X + a_{12}Y) \\ \frac{dY}{dt} = Y(a_{20} + a_{21}X + a_{22}Y) \end{cases} \quad (6)$$

The change in biomass of plankton can be described using a modified Logistics model (Formula 7):

$$\frac{dBM_M}{dt} = BM_M \left[a_{10} \left(1 - \frac{BM_M}{N_M}\right) + a_{12}BM_F + a_{13}BM_L \right] \quad (7)$$

The biomass of other fish in the lake can also be described using the Lotka-Volterra model, which is shown in Formula 8:

$$\frac{dBM_F}{dt} = BM_F (a_{20} + a_{21}BM_M + a_{23}BM_L + a_{24}BM_J) \quad (8)$$

Larvae form a competitive relationship with other fish that feed on plankton. The modified Lotka-Volterra model for the larvae is shown in Formula 9.

$$\frac{dBM_L}{dt} = BM_L (a_{30} + a_{31}BM_M + a_{32}BM_F) \quad (9)$$

The biomass of juveniles depends on their food, which is the biomass of other fish. The change in biomass of juveniles is shown in Formula 10.

$$\frac{dBM_J}{dt} = BM_J (a_{40} + a_{42}BM_F) \quad (10)$$

The biomass of all sea lampreys (BMT) in the lake over a full year can be described by the following equation

$$BM_T = BM_L + BM_J \quad (11)$$

$$\begin{cases} BM_L = BM_{VI} + BM_{VII} + BM_{VIII} + BM_{IX} + BM_X \\ BM_J = BM_{IX} + BM_X \end{cases} \quad (12)$$

Combining the above models, the interaction coefficient matrix was constructed ,as shown in Fig 5 to describe the interactions between these organisms within the ecosystem.

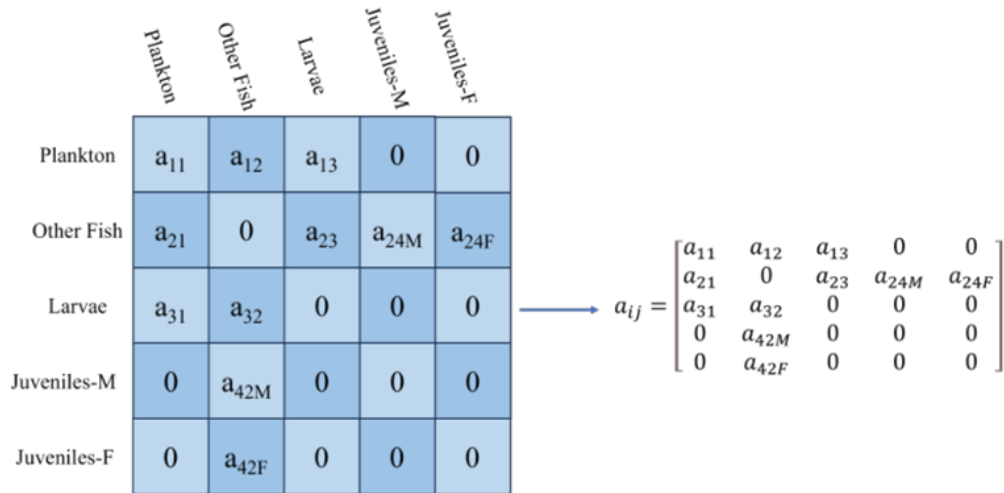


Fig. 5 Interaction coefficient matrix.

3. Results

3.1. The establishment of simulation model

In order to test the model, an ideal lake ecosystem with a simplified food chain was established, which is shown in Fig 6. This ecosystem consists of plankton, sea lampreys of different age groups and other fish. Based on the statistical data about the Great Lakes from 1985 to 2018 ^[10], the parameters were set for different species of the ecosystem. The parameters are also shown in Fig 6.

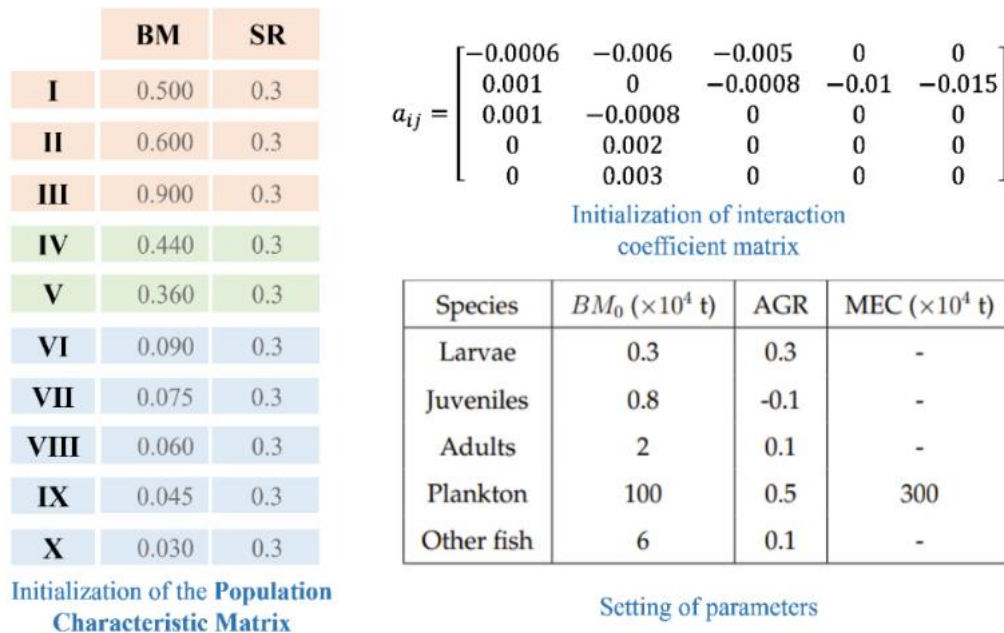


Fig. 6 Initialization of the sea lamprey populations and the ecosystem.

These parameters were used to find numerical solutions to the equations in the Dynamic Age Pyramid Model and illustrate the change in the biomass of plankton, other fish and sea lampreys (larvae and juveniles) in the lake over time for 100 years. Random perturbations are added to better simulate the real situation. The results of the change in biomass of each species over time in the ideal ecosystem under the different condition of the fixed SR (=0.3) or SR changes with the availability of resources at the larval period was shown in the following Figs 7, respectively.

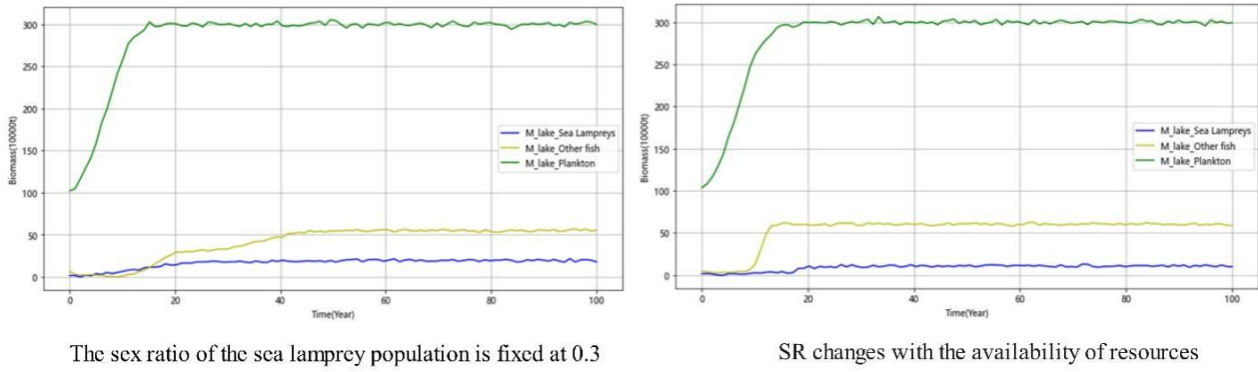


Fig. 7 Change in biomass of each species over time.

To better understand the role of the sex ratio in the sea lamprey population, the paper analysis the change in sex ratio over time, which is shown in Fig 8. The sex ratio of sea lampreys in the I and II stages are randomly generated since they are technically asexual at those periods.

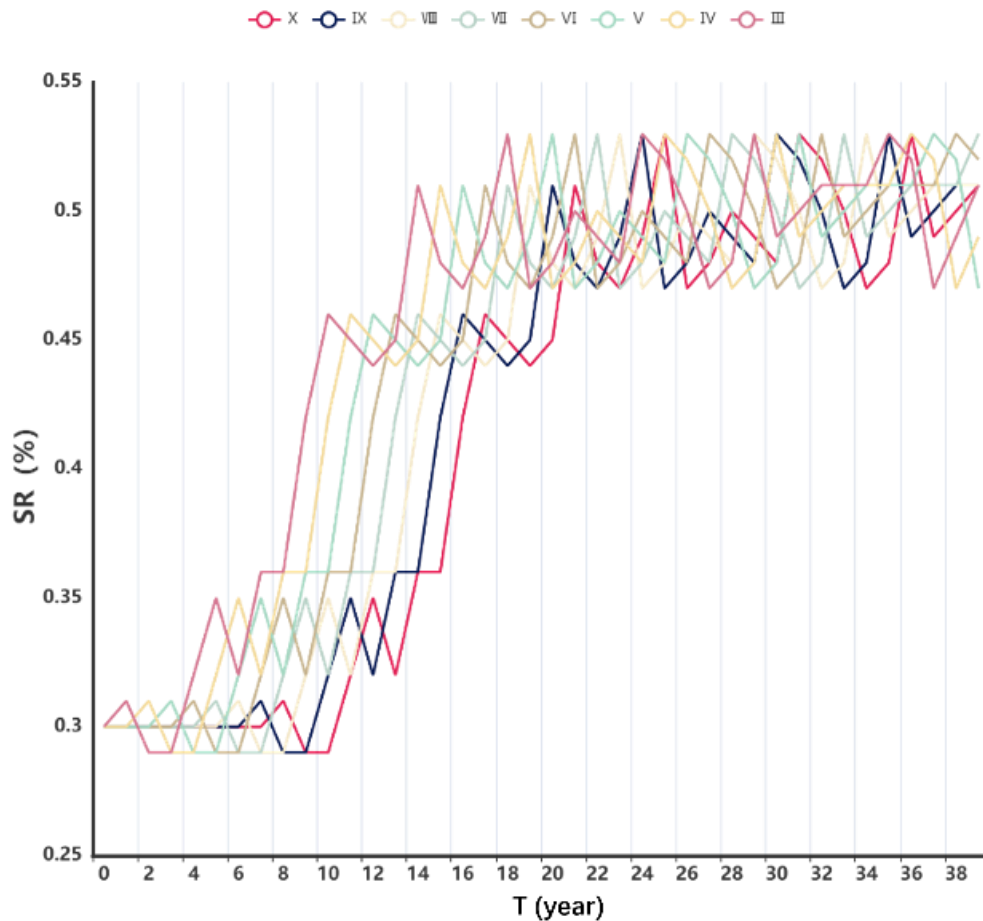


Fig. 8 The change in sex ratio over time in the sea lamprey population.

3.2. Analysis of the influences of adaptive sex ratio variation for the sea lamprey population.

The parameters for three different ecosystems are set as follows: (1) a stable and resource-rich ecosystem, the maximum environmental capacity of plankton is set as 3,000,000 ton and does not change over time. (2) a resource-declining ecosystem, the decline coefficient of the maximum environmental capacity of plankton is set to decrease by 60,000 tons per year. (3) an ecosystem with drastic ecological changes, we half the maximum environmental capacity of plankton when the three populations are at the same level to better observe the differences in biomass changes of the three different populations. The simulation results are shown in Fig 9.

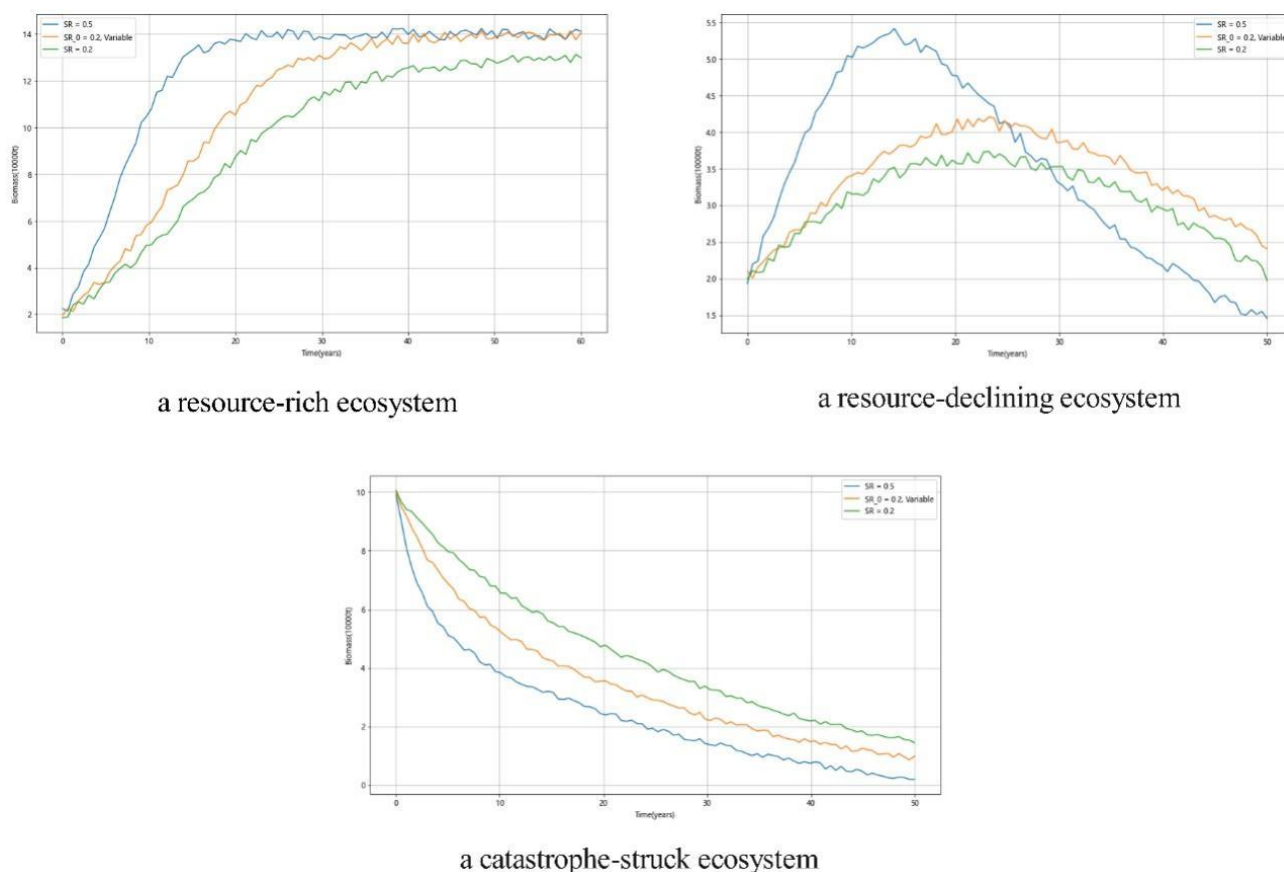


Fig. 9 Change in biomass of the three kinds of sea lampreys with different sex ratio characteristics in three kinds of ideal ecosystems.

4. Conclusions

The paper established the Dynamic Age Pyramid Model to describe the unique life cycles of sea lampreys, which updates the Population Characteristics Matrix according to environmental resources annually across different age groups throughout their life cycle. Based on this model, a Multi-species Lotka-Volterra Model was established, which studies the interaction between lampreys at different life stages and other organisms in the ecosystem and is described by building separate sets of differential equations. By combining these two models, the paper can reveal how changes in environmental resources affect the biomass and sex ratio variation of sea lampreys across various age groups.

The model was first to stimulate the changes in biomass of lamprey populations with constant and dynamic sex ratios in a resource-rich lake ecosystem and find that populations with dynamic sex ratios reach equilibrium faster, and the female proportion in the population gradually increases.

A series of oscillatory folds equally spaced parallel to each other was observed in Fig 8. The average sex ratio of sea lamprey populations gradually increases from the initial setting of 0.3 to around 0.5 and oscillates around 0.5 after the ecosystem reaches equilibrium. This suggests that in an environment with sufficient resources, the sea lamprey population will gradually and progressively update the sex ratio of each age group within the population, and eventually converge to a theoretically optimal ratio. By observing the performance differences of populations with fixed sex ratios and dynamic sex ratios in three environments with different resource distribution patterns, to find the advantages and disadvantages of this unique mechanism and found that adaptive sex ratio variation enhances the population's resilience when resources are limited but may not perform well in some environments where resources change rapidly (Fig 9).

In summary, adaptive sex ratio variation enables the sea lampreys to expand their population by increasing the proportion of females when there are sufficient resources available in the environment

and to reduce their population by decreasing the proportion of females when there are fewer resources available or when the environment is deteriorating gradually. This strategy of controlling population size to reduce energy consumption makes sea lampreys more adaptable to different environments. However, results showed that species with adaptive sex ratio variation are less resilient to more dramatic environmental changes than species with conservative sex ratios (e.g., species with a high proportion of males in this thesis). This is mainly because there is a time lag in sex ratio change, with sex determination occurring during the second to third year of the larval period, and the larvae must wait until they are sexually mature to regulate the rate of population growth.

The model exhibits high innovation and transferable value, which offers a method for describing the interaction mechanisms between organisms with complex life histories and behavior patterns and other organisms in the environment. By establishing a dynamically updatable population feature matrix and providing biologically meaningful descriptions of the information stored in each row and column of the matrix, the model significantly enhances traditional models in describing the life history of unconventional organisms.

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