
Investigating Population Diversity, Sex Ratio Dynamics, and Resource Utilization: Insights into Lamprey Species within the Multispecies Ecosystem of the Great Lakes

Abstract

In the current ecological environment of the North American Great Lakes region, the invasive alien species of lampreys has been posing a serious threat to the stability of the ecosystem. For a long time, the population size and sex ratio of the lampreys have shown a close relationship with ecological resources (e.g., food), and this phenomenon provides us with a new perspective to prevent and control the lamprey problem in the Great Lakes region of North America. In this study, by constructing three distinct hierarchical mathematical models, we thoroughly explored in depth the specific relationships between lamprey population size, sex ratio, and food abundance.

In Model 1, we first applied the **Fourier transform** method to analyze the patterns of food abundance over time in the Great Lakes waters of North America. Then, through the zero-sum **game theory**, we considered the female and male ratio of the lamprey population as opposites, and established a model based on differential equations to describe the variation of the sex ratio of the lamprey with the food abundance in the environment.

In Model 2, we focused on the variation pattern of the population size of lampreys under the ideal condition of no interference from other species. In this model, we improved the traditional **Logistic population growth model** by incorporating the different effects of food abundance and population sex ratio on the population growth rate, and explored the **feedback regulation mechanism** of the lamprey population under ideal conditions.

In Model 3, we constructed an ecosystem model for a localized system in the Great Lakes, and explored the population interrelationships among three species: lampreys, native fish, and parasitoids. We made corresponding adjustments to the Logistic model based on the characteristics of these species and built the model by incorporating cooperative and competitive game theory with varying degrees and influences. After 25 years of simulations, we described in detail the significant and remarkable role of lampreys in the ecosystem.

In the summary section, we revealed the interactions and constraints on the sex ratio and abundance of the lamprey population through a careful and detailed analysis of these three models, elucidating the unique patterns of the population dynamics of the lamprey. At the ecosystem level, we summarized and generalized the ecological effects of lampreys on the population size of other species.

Finally, in the Further Discussion section, we discussed how to control the population size of the lamprey by means of **proportional-integral-differential compensation**, based on the ecosystem model of Model 3 from the perspective of engineering control. This provides new ideas for the prevention and control of the lamprey.

Keywords: Fourier transform, game theory, Logistic population growth model, feedback regulation mechanism, proportional-integral-differential compensation

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1 Problem Restatement

Lampreys are typically either male or female, while some species exhibit a 1:1 sex ratio at birth, others deviate from this balance due to environmental factors. For example, the sex ratio of lampreys is influenced by their growth rate in the larval stage, which is in turn affected by food availability. In environments with limited food, the male proportion can be as high as 78%, while in environments with more food, the male proportion is around 56%. This variation in sex ratio has implications for lamprey populations and the larger ecosystem they inhabit.

Our research project focuses on understanding the effects of adaptive sex ratio variation in sea lampreys and its implications for the larger ecological system. We aim to develop mathematical models to analyze how the sex ratio of sea lampreys is influenced by environmental conditions, particularly food availability. By investigating the ability of lampreys to alter their sex ratios based on resource availability, we aim to shed light on the interactions within the ecosystem resulting from these variations.

Specifically, we will address the following key questions:

- a) What are the implications and effects on larger ecosystems when the sex ratio of lampreys can be altered? We will examine how changes in the sex ratio of lampreys can impact the overall ecological system, including the dynamics of other species and the stability of the ecosystem.
- b) What are the advantages and disadvantages of lamprey populations? We will explore the benefits and drawbacks of adaptive sex ratio variation for the lamprey population itself, which helps us understand the evolutionary advantages and potential challenges that come with altering sex ratios.
- c) How does the variability in lamprey sex ratios affect the stability of the ecosystem? This analysis will provide insights into the potential impacts on the balance and functioning of the ecosystem.
- d) Can ecosystems with variable sex ratios in lamprey populations provide advantages for other species, such as parasites? We can understand the broader ecological implications of sex ratio variations.

2 Global Assumptions and Justifications

- a) Assuming that the following terms Lamprey, Sevegill eel, and Sea Lamprey are used interchangeably, and that the various species of the genus Sevegill eel will be considered only for their most representative *petromyzon marinus*.
- b) In order to reflect the typicality of the research object, this paper only discusses the geographical background of the Great Lakes region in North America, and other regions of the world will not be considered for the time being.

- c) In this paper, the term "ecosystem" is generally used to refer to the middle and lower reaches of rivers in the Great Lakes basin and the water bodies near the lake inlets, which are regarded as the whole of the water bodies.
- d) The simulations in this paper assume that the abiotic non-living portion of the ecosystem is stable and do not take into account the effects of extreme weather, climate warming, or catastrophic mutations.

3 Model Establishment and Solutions

3.1 Model 1: Model of Food Resource Abundance and Population

Sex Ratio Based on Fourier Transform and Zero-Sum Game Theory

3.1.1 Model Establishment

a. Establishment of the Fourier Transform Model

In the present establishment of this model, we intensively conducted an in-depth study of the sea lamprey population in the Great Lakes region of North America, with a particular focus on metamorphosis during its life cycle. Lampreys exhibit a remarkable two-stage lifestyle during their development: At the larval stage juveniles feed primarily by filter-feeding, while at the adult stage adults exhibit a parasitic nature and are accustomed to attaching to other fish bodies to feed on their blood. It is noteworthy that the gonadal development of the lamprey in its larval stage is unique as its gender is not yet clearly differentiated at this stage, and only becomes determined after it grows into an adult.

In our preliminary observations of this specialized organism, we found a significant correlation between the sex ratio at the adult stage (i.e., the proportion of males in the entire population) and the amount of food filtered during the larval stage (Yang, 2007). Specifically, when food resources are abundant in the aquatic environment, the overall growth cycle of sea lampreys accelerate and the sex ratio of the population tends to equalize. Conversely, when food resources are scarce, the growth cycle of sea lampreys is prolonged and the proportion of male individuals in the population is relatively higher. This phenomenon reflects the potential impact of food resource availability on the sex ratio of the sea lamprey populations, providing an important ecological basis for our modeling.

And in a study of seasonal changes in food quantity in the Great Lakes region of North America, special attention was given to the filter-feeding behavior of juvenile larval lamprey stages. Based on existing academic research, the primary sources of filter-feeding for larval lamprey are primarily associated with microorganisms and abiotic non-living organic matter in the water column (Evans, 2012). Further studies indicated that these filter-feeding sources mainly consisted of three categories: algae, bacteria and abiotic non-living organic matter, and

their abundance showed regular variations in different months throughout the year (Bowen., 1994).

In order to accurately characterize the seasonal variation patterns of total abundance of these organisms over time (months), we adopted a continuous Fourier transform method: by superimposing three sinusoidal functions with different periods, amplitudes, and phases to model and simulate the unique, yet similar variation patterns of these three types of organic matter. This method not only accurately reflects the seasonal trends of each type of various organic substances, but also reveals the interactions and relative importance among different organic matter.

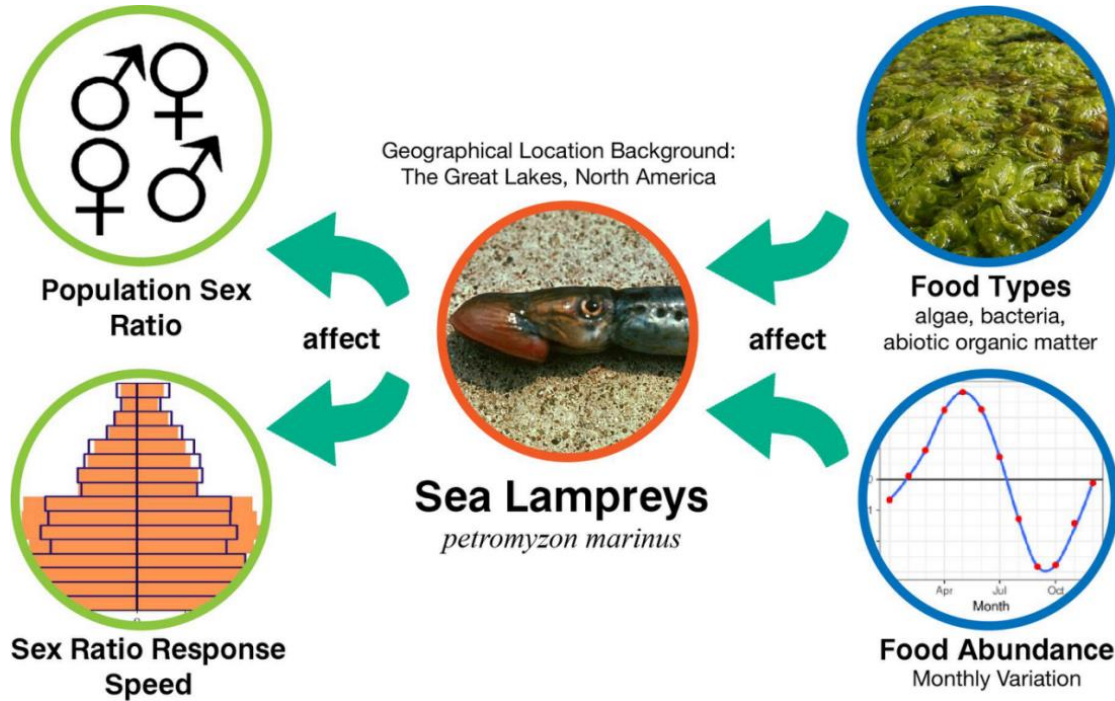


Figure 1 Basic factors affecting the sex ratio of sea lampreys

The following expression of Fourier transform model is used to define and study of the monthly variation of food abundance in the Great Lakes of North America:

$$F_t = \sum_{i=1}^3 (k_i \sin(m_i t + n_i) + p_i) \quad (1)$$

In equation (1), t is the time in months, k_i ($i = 1, 2, 3$), m_i ($i = 1, 2, 3$), n_i ($i = 1, 2, 3$) are the fitted parameters obtained. F_t is the fluctuation of food abundance over time t .

b. Establishment of the Zero-Sum Game Model

Based on the preliminary understanding of the changes in sex ratio of the lamprey populations under different levels of food abundance, we use a zero-sum game model to explain this phenomenon. In the model setting, we define the genes affecting the development of male

and female lampreys as Y and X, respectively, which are assumed to be "selfish" and capable of adopting independent strategies to gain advantages in response to changes in external environmental conditions. In order to better model and simulate the female genes' advantageous performance in times of abundant food and their disadvantageous position in times of scarce food, we add a "selfishness modification formula" to the female gene expressions in the zero-sum game model.

In this model, the two sides of the game are the female ratio x_t and the male ratio y_t at time t , with the sum of both being 1.0 at any given moment. And this dynamic game process is represented by the change in the values of x_t , y_t and as time t varies.

Given the food abundance and the sex ratio of the population at the initial moment, the sex ratio of the population will gradually change over time with a certain damping effect, eventually stabilizing to more accurately simulate the real-world scenarios. The rate of change of the population sex ratio is described by a differential equation in the form of a rate directly proportional to the total amount of food, which simulates the effect of the amount of food on the growth cycle, especially in the rate and speed of sex ratio changes. The final steady-state sex ratio achieved accurately and precisely reflects the state of the male-female ratio under different food quantity conditions.

The following are the expressions of the zero-sum game model we have defined:

$$\begin{aligned}\frac{\partial x_t}{\partial t} &= F_t x_t (1 - x_t) \cdot \tanh(a_1 t) \cdot a_2 \cdot G_x \\ \frac{\partial y_t}{\partial t} &= F_t y_t (1 - y_t) \cdot \tanh(a_1 t) \cdot a_2 \\ G_x &= 1 - a_3 F_t \\ \text{s.t.} \quad &x_t + y_t = 1.0\end{aligned}\quad (2)$$

In equation (2), $\frac{\partial x_t}{\partial t}$ is the differentiation of the sex ratio of female lampreys with respect to time; $\frac{\partial y_t}{\partial t}$ is the differentiation of the sex ratio of male lampreys with respect to time; and $a_i (i=1,2,3)$ is the parameter obtained from the fit G_x , which is the selfishness modification formula of the female gene relative to the male gene.

3.1.2 Model Fitting and Evaluation

Our model utilized different data on food abundance in the water and lamprey population size from various coastal rivers and lakes' bodies along the shores of the Great Lakes. A map of the distribution of data sources is shown in Fig. 2.

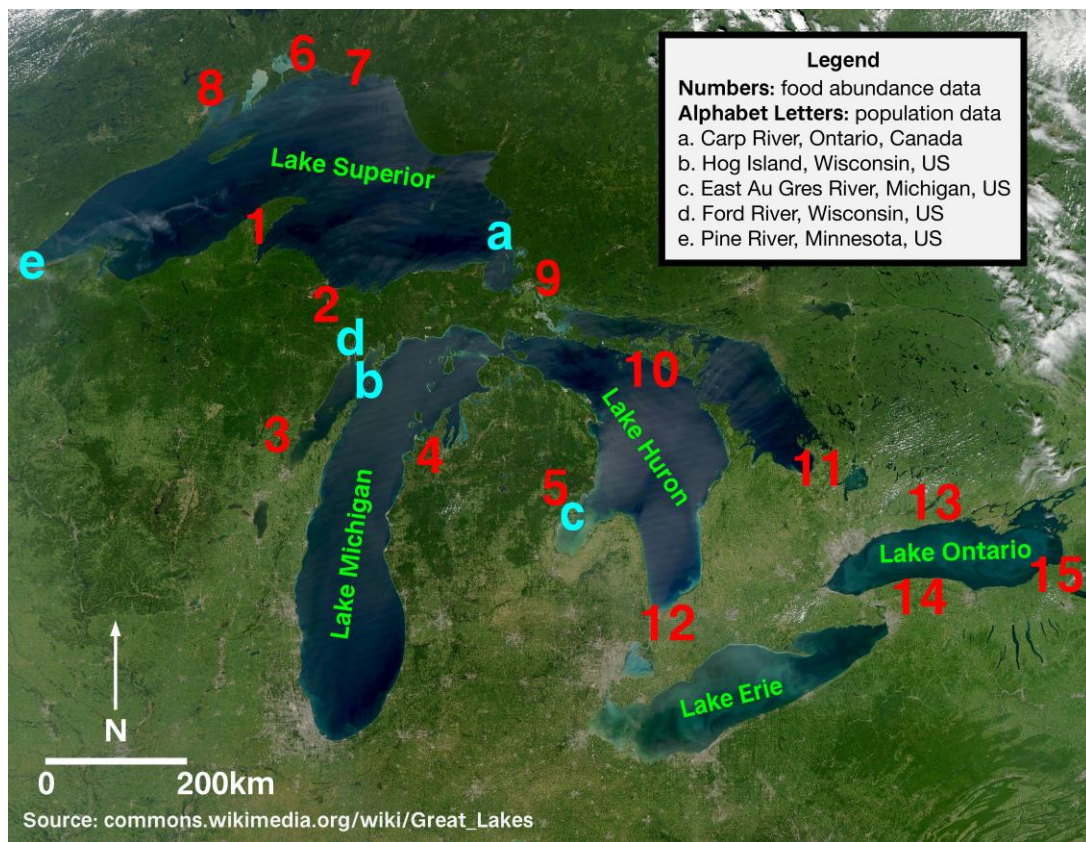


Figure 2 Geographic sources of food abundance and population sex ratio change data used in model fitting (Bowen., 1994) (Johnson, Swink, & Brenden, 2017)

a. Fitting and Evaluation of the Fourier Transform Model

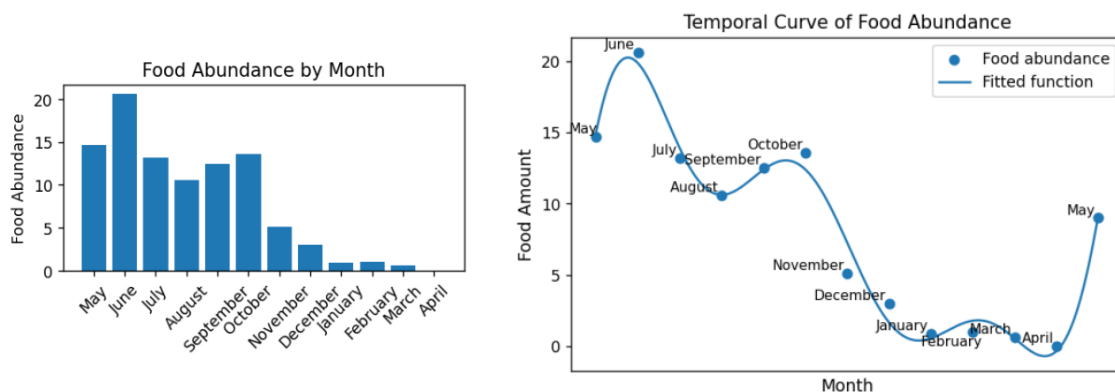


Figure 3 Source of data on water body food abundance in 15 different regions of the Great Lakes (left) (Bowen., 1994); Fitting results with our Fourier model (right)

Unit: $\text{mg ash-free-dry-mass} \times L^{-1}$

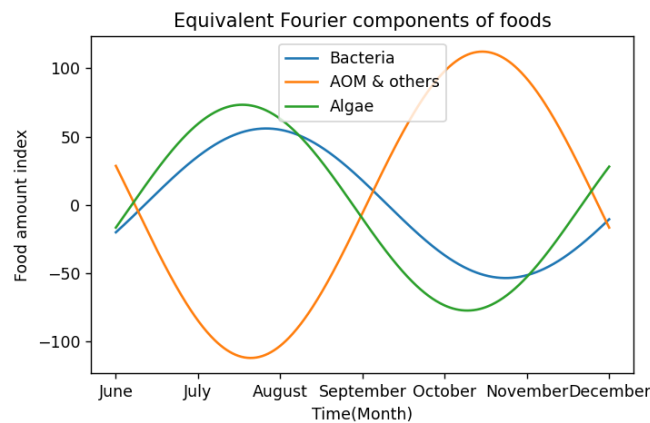


Figure 4 Fitting the Fourier transform model to actual water body food abundance data, the curves of three equivalent component indicators are obtained, where “AOM & others” refer to the comprehensive components of abiotic organic matter and other environmental factors.
(Holmes, 1994)

For the Fourier transform model, we conducted and fitted statistics on the abundance of food available for lampreys in the water of 15 different regions of the Great Lakes for each month of the year (as shown in the left in the Fig. 3) and performed fitting.

By fitting multiple sinusoidal functions superimposed on each other, our model not only effectively captures the seasonal variability but also reflects the characteristics of time delays and multiplicities magnitude in the components of the function (see Fig. 4). This result is consistent with the overall pattern of academic studies on food distribution in the Great Lakes, i.e., namely, the food abundance in the water column is higher in warmer months and relatively lower in colder months (S., Yap, & R., 2018).

Regarding the detailed patterns, we found that the abundance cycle of bacteria generally lagged one month behind the abundance cycle of algae. Specifically, the abundance cycle of bacteria peaked in July and August, which was consistent with the actual observations. This specific pattern reflects both the interactions of different biological components of the ecosystem and the differences in time series.

b. Fitting and Evaluation of the Zero-Sum Game Model

For the zero-sum model, we first conducted a direct test of the zero-sum game model under different static food abundance levels to evaluate its simulation effect. The simulation results in Fig. 5 indicate that the final stabilized sex ratio of the lamprey population will gradually shift from male-dominated to female-dominated as food abundance gradually increases with initial unchanged conditions held constant. In addition, the increase in food abundance also

accelerated the speed of the gaming process, which further verified the significant effect of food abundance on the growth rate of the lamprey population.

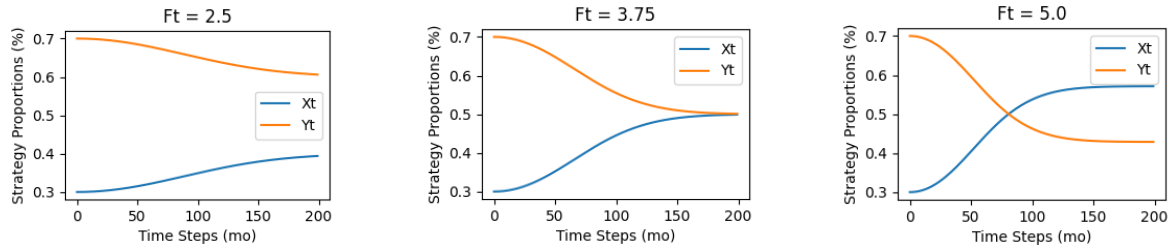


Figure 5 Game model simulation effect under different static food abundance levels, where X_t is the proportion of females in the population, and Y_t is the proportion of males

In order to align our model with actual observational data, we selected population sex ratio data from lampreys' spawning sites in five rivers in the Great Lakes watershed of North America from 2007 to 2011 as a reference (Johnson, Swink, & Brenden, 2017). Combined with our expression analysis of monthly variations in food quantity, we obtained the following fitting results, as shown in Fig. 6:

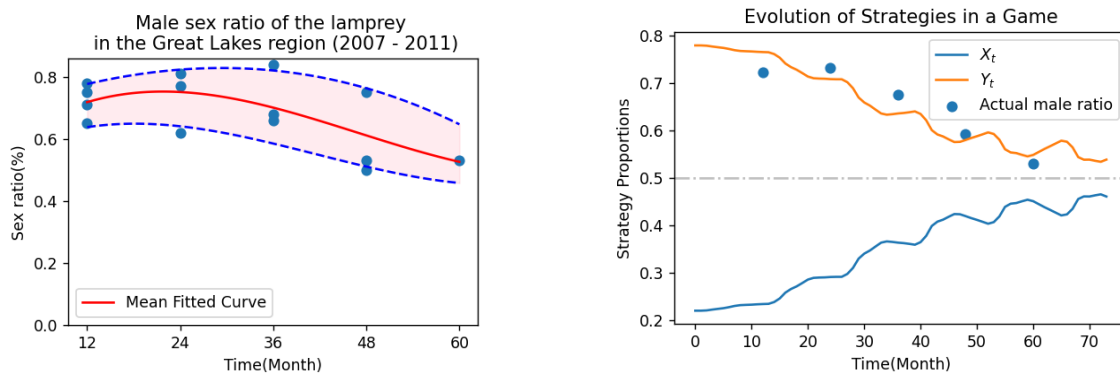


Figure 6 Fitting the zero-sum game model to the population sex ratio data, and obtain the simulated lamprey population sex ratio results in the Great Lakes region of North America for five years under the actual common scenario, where the origin of the time coordinate (time = 0) represents January 2006.

The fitting results showed that our model has high practical application value, especially considering that the population sex ratio is affected by food abundance when applying the Fourier transform model to the zero-sum game model.

In the follow-up study, in order to further refine and improve the model, we plan to introduce the mechanism of the population size impact on the sex ratio of the lamprey population, with a view to obtaining more precise and comprehensive research results.

3.2 Model 2: Model of Predicting Lamprey's Population Based on Optimized Logistic Population Model with Feedback Process

3.2.1 Model Establishment

In the present model, we modified the traditional Logistic population growth model to predict the temporal variations relationship between the population size of the sea lampreys. Relevant studies have indicated that the growth, maturation and survival rates of Lamprey decrease with increasing population density (S., Yap, & R., 2018), which implies that an increase in population density will have a constraining effect on the rate of population growth under other constant conditions. Therefore, the Logistic model has significant reference value in explaining the population dynamics of the lamprey population.

As for the improvement part of the model, we first adjusted the definition of the intrinsic growth rate $j(F_t)$. In the traditional Logistic model, this parameter represents the intrinsic growth rate of the population. Studies have shown that the growth rate of lamprey is directly proportional to food abundance F_t (Yang, 2007). Therefore, we defined $j(F_t)$ as a variable linearly related to food abundance F_t .

Secondly, given the negative correlation between population density and the female proportion (Hardisty, 1961), we corrected x_t as x'_t in the model to incorporate the effects of population size P_t on population sex ratio. As shown in the figure, x'_t represents the rate of change in the revised population sex ratio, which incorporates the effects of population size P_t . Due to the zero-sum game relationship between the male and female ratios of the lamprey population, the current modeling only needs to consider the effect of one of them, and this time we selected the female proportion as a representative.

Finally, $h(x_t)$ in our model represents the normal distribution of the female sex ratio x'_t with the population, multiplied by the environmental carrying capacity K with respect to reflect the influence of the sex ratio under the ideal environmental carrying capacity. In this model, K maintains its role as the maximum environmental carrying capacity, and $h(x_t)$ represents the distribution of sex ratios, where the mean μ of the normal distribution represents the optimal population sex ratio. Deviations from the population sex ratio will increase the constraints on population growth.

It is also important and crucial to note that, for the interpretation and prediction of lamprey population size over time, we have formed and developed a negative feedback

relationship between the population size and the population sex ratio based on the traditional Logistic model, which can help to explain the steady state equilibrium of the lamprey population under the constraint of the population sex ratio in actual situations.

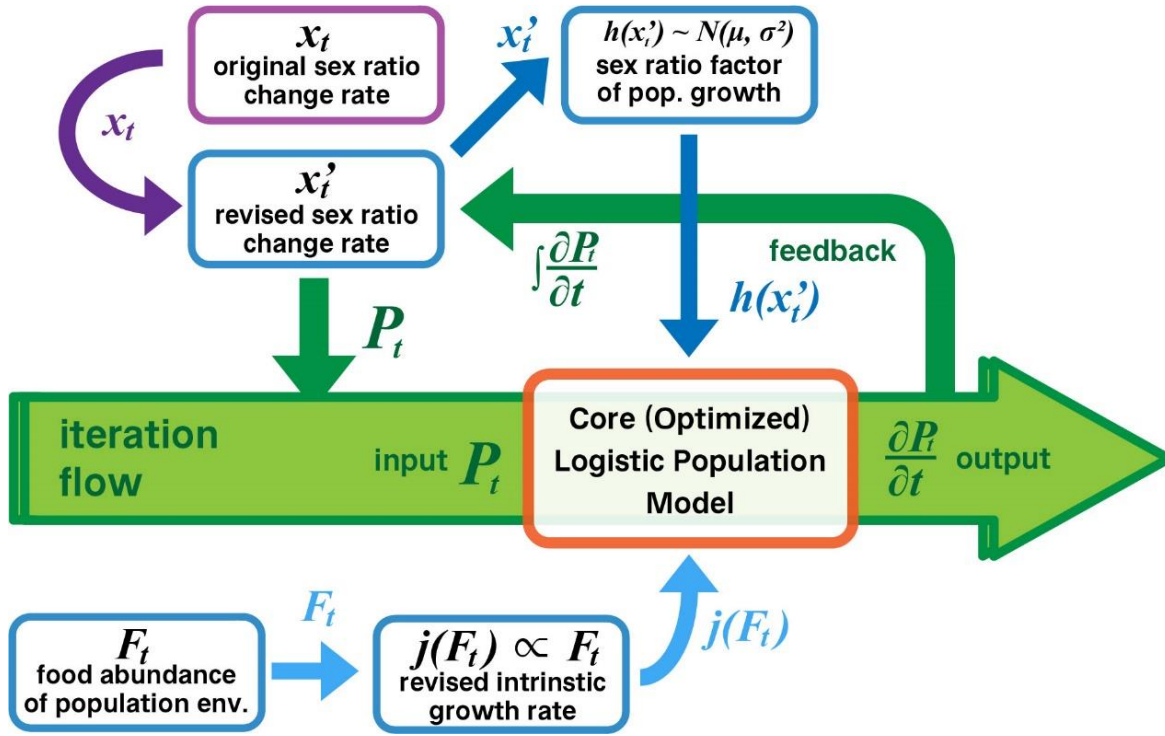


Figure 7 Workflow diagram of the optimized Logistic growth model for estimating the Great Lakes lamprey population

Below is the expression of the optimized Logistic model we obtained based on the above inference:

$$j(F_t) = a_1 F_t + a_2 \quad (3)$$

$$x_t' = \frac{x_t}{b_1 \cdot \ln(b_2(P + b_3))} \quad (4)$$

$$h(x_t') = \frac{1}{\sqrt{2\pi}\sigma} \exp\left(-\frac{(x_t' - \mu)^2}{2\sigma^2}\right) \quad (5)$$

$$\frac{\partial P_t}{\partial t} = j(F_t) \cdot P_t \left(1 - \frac{P_t}{h(x_t') \cdot K}\right) \quad (6)$$

where:

$j(F_t)$ in Eq. (3) represents the corrected intrinsic growth rate, F_t is the food abundance of the environment in which the population is located, a_1 and a_2 are the slope and bias parameters, respectively; x_t' in Eq. (4) represents the modified rate of change in the female sex ratio of the population, x_t is the original rate of change in the female sex ratio of the population before the

modification; b_1 , b_2 and b_3 are the feedback influence parameters; $h(x_t)$ in Eq. (5) represents the impact factor of environmental carrying capacity, where μ and σ are normally distributed impact parameters; P_t in Eq. (6) is the number of individuals in the lamprey population, which varies over time t , and K is the intrinsic environmental carrying capacity constant in the classical Logistic model.

3.2.2 Model Fitting and Evaluation

Prior to conducting this model validation, we have set the following ideal case assumptions to ensure that the environment in which the model operation is run is controllable:

- 1) *We assume that the natural environment to which the model applies is generally stable and that the simulation process is not subject to any large-scale external variability events.*
- 2) *In the current model, we only consider the interactions between the sea lamprey and its food environment in the ecosystem, and do not address the interrelationships between other organisms in the ecosystem, which will be explored in the subsequent Model 3.*
- 3) *The model starts with the assumption that the population size is very close to 0, in order to better simulate the process of population growth from almost zero to natural increase.*

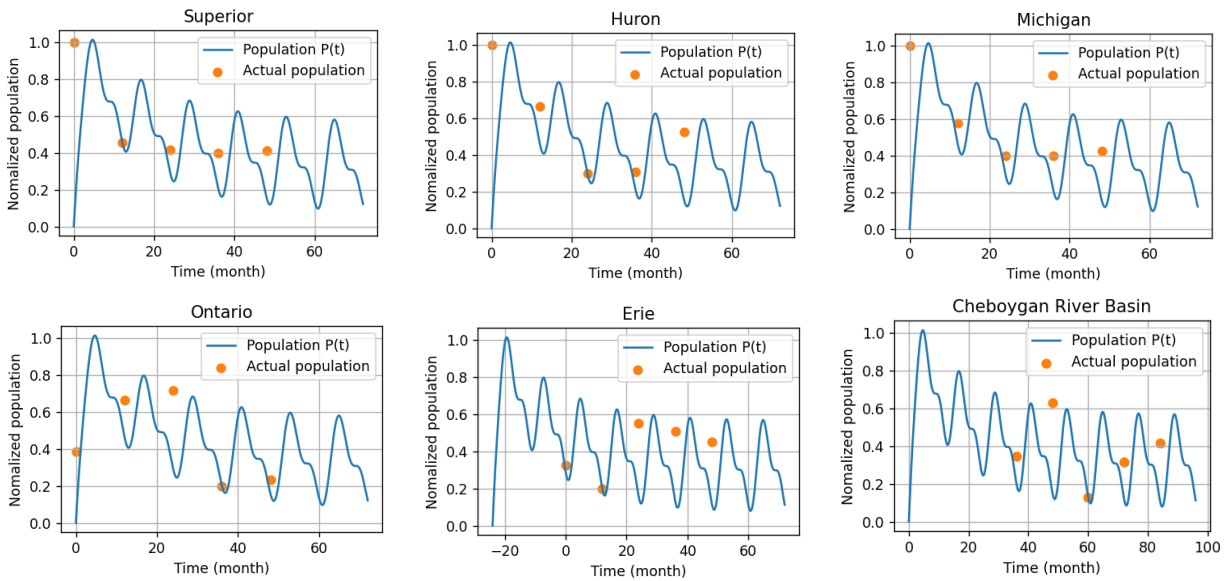


Figure 8 Fitting results of actual lamprey population data and models in the waters of the Great Lakes and Cheboygan River basins in North America, where the origin of the time coordinate (time = 0) represents January 2007.

For the validation of the model, we selected water bodies in the Great Lakes of North America and the Cheboygan River Basin watershed of the Michigan Peninsula in the United

States, spanning the period from 2007 to 2011, for which we had accurate and specific data on the number of sea lamprey populations (Jean V. Adams, 2021) (Johnson N. &, 2020). Given the differences in areas and other environmental factors between waterbodies, all population data collected were normalized to facilitate subsequent comparisons and analyses.

The six subplots presented in Fig. 8 clearly reflect the relationship between the status of the sea lamprey populations in the six selected waterbodies and the results of the model fits.

The simulation results reveal that, under idealized conditions, the growth of the sea lamprey population is relatively faster in the initial stage, and then undergoes a gradual fluctuating decline after reaching the peak and eventually reaches a fluctuating steady state. The initial rapid growth rate at the beginning of the population was due to the small population size at the outset, and the population growth rate was much far smaller than the carrying capacity of the environment; the subsequent overshooting and slow decline reflected the regulatory effect of the population growth rate by $h(x_t)$, i.e., after reaching the limit of the carrying capacity of the environment, the food supply was rapidly reduced, and the $h(x_t)$ facilitated the increase of the proportion of males in the population, and the superimposed action of the two mechanisms resulted in overshooting phenomenon, which drove the transition of the population state to a steady state, while the later slow fluctuation decline was due to seasonal variations in food supply simulated in the model.

By analyzing data from the six water bodies between 2007 and 2011, we found that Lake Superior, Huron, Michigan, and Ontario were in the early and middle stages of the entire change process, i.e., experiencing overshooting and rapid declines, while Lake Erie and the Cheboygan River Basin were in the late stages of the change process and had already reached stable fluctuations. This indicates that our model can reveal the ideal process of population growth in different stages, and has high robustness and applicability

3.3 Model 3: Model of Multispecies Ecosystem Simulation Based on Game Theory with Symbiotic and Competitive Relationships

3.3.1 Model Establishment

a. Model settings

In related academic studies, the sea lamprey has been recognized as a destructive species in the Great Lakes ecosystem of North America (Renaud, 2011). As an exotic invasive species since the early 20th century, the invasion of lampreys into dominant local fish populations has had disastrous and catastrophic effects on the entire ecosystem (Jean V. Adams, 2021). Therefore, our model was designed to explore the impacts of the sea lamprey on the abundance

of different biological populations in the Great Lakes ecosystem of North America. Consistent with the previously mentioned Model 1 and Model 2, here we also set the time t to be in months.

The model is set in a localized water ecosystem along the Great Lakes of North America. In order to elucidate the effects of the sea lamprey on the abundance of different biological organisms and to emphasize the different parasitic and symbiotic relationships between the sea lamprey and the organisms affected by them, we assume that the whole ecosystem consists of three independent but inter-competitive populations.

- a. **Sea lampreys:** Given the lack of natural predators for the sea lamprey in the Great Lakes, its population is growing rapidly. However, from the establishment of Model 1 and Model 2, it is clearly known that the population size of sea lampreys is significantly affected by the sex ratio, which in turn is directly or indirectly affected by the food abundance in the ecosystem.
 - a) Considering that there is a metamorphosis from larvae to adults in the life cycle of sea lampreys, and based on the consideration of its developmentally metamorphic stage and lifespan (Wikipedia, 2024), we hypothesized that the population size of the sea lampreys was divided into the larval stage P_{1a} according to its life cycle stage($t - 48$ to t , totaling 4 years), metamorphosis stage P_{1b} ($t - 48$ to $t - 60$, totaling 1 year), and adult stage P_{1c} ($t - 60$ to $t - 84$, totaling 2 years); the overall lifespan of the sea lampreys is set to be a fixed 7 years.
 - b) We set the sea lamprey larvae to live by filter-feeding, the adults mainly to live parasitically, and the metamorphosis period to be non-feeding. Therefore, there are differences in the symbiotic and competitive relationships among juveniles, adults and metamorphosis stages of sea lampreys' population towards native fish and parasites.
- b. **Native fish:** Such as trout, lake perch, etc., are regarded as unified objects discussed in this model. Compared to sea lampreys, native fishes grow at a slower rate, but they are less dependent on ecosystem food abundance. Since native fish do not undergo metamorphic growth process of the sea lampreys, native fish population size P_2 is not further subdivided in the model. Additionally native fish can prey on parasites in the modeled setup, whereas sea lamprey's crabs cannot prey on parasites.
- c. **Parasites:** In the model, parasites can infect both native fish and sea lampreys and are considered to be discussed in a unified manner. It is important to note that the parasites discussed here do not refer to the parasitic relationship of adult sea lampreys, but rather to a distinct and separate type of organism that can survive in both sea lampreys and native

fish. In the model setup, the parasite population grows at a fast rate and its population P_3 is significantly influenced by the population size of sea lampreys P_1 and the population size of the native fish P_2 . Although parasite infections may primarily affect the nutritional status and reproductive success of fish and rarely lead to mortality in the absence of other stressors, the model assumes that parasite population size P_3 has a relatively small effect on P_1 and P_2 . At the same time, the effect of food abundance from environmental sources was not considered in the modeling of the population growth of the parasite, since the parasite itself survives parasitically and does not obtain food sources from the environment.

In addition, given that the details and causality of the interactions between sea lamprey hosts and pathogens are not fully understood in the academic community (Shavaliar, Faisal, Moser, & Loch, 2021), the construction of this model also provides a theoretical reference framework for related studies.

b. Description of symbiotic and competitive relationships in Model 3

In our model, the effects of symbiotic and competitive relationships among all species are described by the parameter α in the model expression. Here, we define α_{ij} as the influence factor of the population size P_i of species i on the differential $\partial P_j / \partial t$ of the population size of species j against time during the game process. Possible symbiotic and competitive relationships between all species in the model are listed below.

1. Relationships between lampreys and native fishes (4 in total):

- a) α_{1c2} : Adult lampreys P_{1c} parasitize on native fish for nutrients, leading to a decrease in the reproductive capacity of native fish, thereby weakening the growth of native fish population size P_2 ;
- b) α_{1a2} : Juvenile sea lampreys P_{1a} increase the overall food abundance in the environment through feces produced by filter feeding, indirectly contributing to the growth of native fish population size P_2 , albeit with a relatively small effect;
- c) α_{21c} : Native fish P_2 are parasitized by adult lampreys P_{1c} , which enhances the reproductive capacity of adult lampreys, promoting to the growth of lamprey's population size P_1 ;
- d) α_{21a} : feces excreted by native fish P_2 similarly increased the food abundance in the environment, similar to α_{1a2} , contributing to the growth of the lamprey's population size P_1 .

2. Relationships between native fish and parasites (2 in total):

- α_{23} : Native fish P_2 reduces the number of parasites P_3 and their eggs through predation, thus having a weakening effect on the growth of parasite population size P_3 ;
- α_{32} : This relationship contains two layers of meaning at the same time: firstly, the parasite P_3 parasites inside the native fish P_2 , which has a slight weakening effect on the growth of the native fish population number P_2 ; secondly, the parasites and their eggs are preyed upon by the native fish, which indirectly promotes the growth of the native fish population number P_2 . In fact, whether this relationship is a weakening or promoting effect in general depends on which of the above two effects dominates.

3. Relationships between parasites and lampreys (2 in total):

- α_{13} : Lamprey P_1 is parasitized by parasite P_3 , which contributes to the growth of parasite population size P_3 ;
- α_{31} : Similar to α_{13} , but in this case referring to a slight weakening effect of the parasite on the population growth of lamprey P_1 .

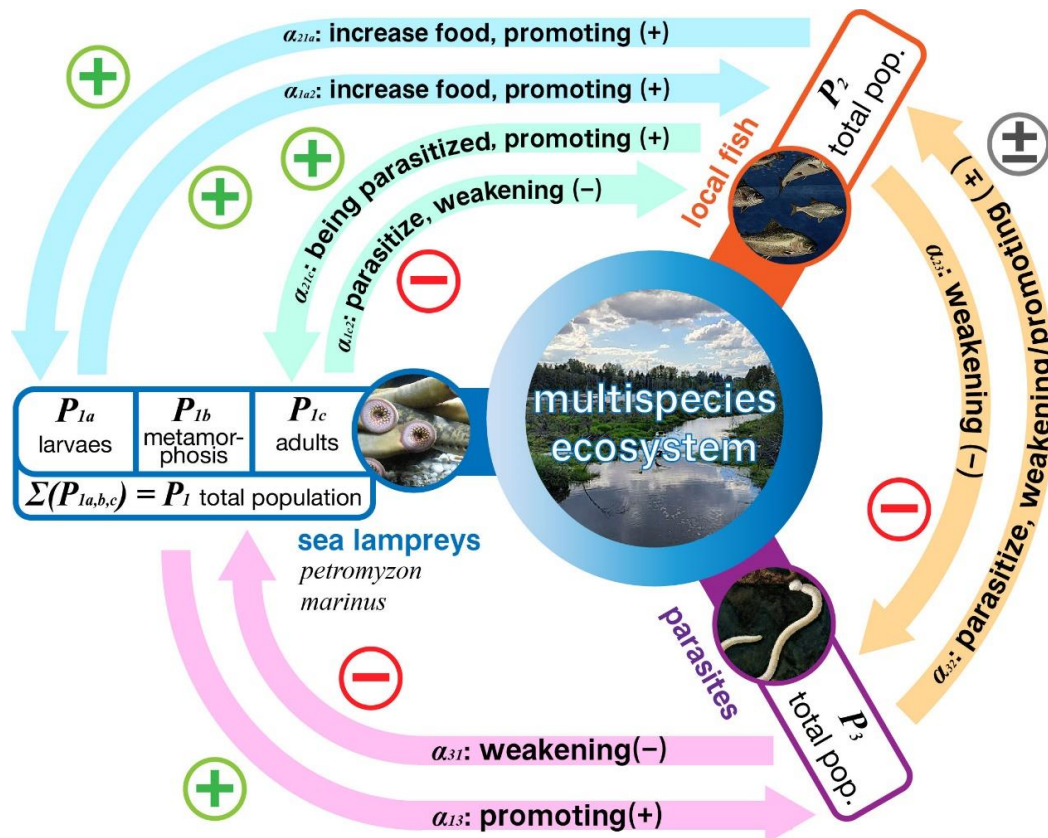


Figure 9 Schematic diagram of the symbiotic and competitive relationships of all species in Model 3

c. Formula explanation

The mathematical expressions of the three-species game model proposed in this model is described below:

$$P_{1a} = \int_{t-48}^t \frac{\partial P_1}{\partial t} dt \quad (7)$$

$$P_{1b} = \int_{t-60}^{t-48} \frac{\partial P_1}{\partial t} dt \quad (8)$$

$$P_{1c} = \int_{t-84}^{t-60} \frac{\partial P_1}{\partial t} dt \quad (9)$$

$$P_1(t) = \int \left(\frac{\partial P_1}{\partial t} dt \right) + P_1(t - \Delta t) \quad (10)$$

$$\frac{\partial P_1}{\partial t} = j_1(F_t) \cdot P_1 \left(1 - \frac{P_1}{h(x'_t) \cdot K_1} \right) + (\alpha_{21a} P_2 P_{1a} + \alpha_{21c} P_2 P_{1c} + \alpha_{31} P_3 P_1) \quad (11)$$

$$\frac{\partial P_2}{\partial t} = j_2(F_t) \cdot P_2 \left(1 - \frac{P_2}{K_2} \right) + (\alpha_{1c2} P_{1c} P_2 + \alpha_{1a2} P_{1a} P_2 + \alpha_{32} P_3 P_2) \quad (12)$$

$$\frac{\partial P_3}{\partial t} = P_3 \left(1 - \frac{P_3}{j_3 P_1 P_2} \right) + \alpha_{13} P_1 P_2 + \alpha_{23} P_3 P_2 \quad (13)$$

where:

Expression (7) to expression (10) describes the division of lamprey population into different life cycle stages. According to our description of the lamprey population setup, P_{1a} in expression (7) represents the population size of lamprey in the larval stage, P_{1b} in expression (8) represents the population size in the metamorphosis stage, and P_{1c} in expression (9) refers to the population size in the adult stage.

Expressions (11) through (13) illustrate the dynamic game relationship among the three species, lampreys, native fishes, and parasites. As discussed earlier in the previous section on the symbiotic and competitive relationships among these three species, these game relationships are not the zero-sum game relationships for the sex chromosomes of lampreys as mentioned in Model 1, but are more complex, involving multi-faceted relationships that mutually reinforce and constrain each other.

Expression (11) is improved on the basis of Model 2, which adds the influence factors of local fish and parasites on the growth rate of lamprey population on the basis of the original relationship between the population size of lampreys over time. Expression (12) and expression (13) represent the relationship between the population size of native fish and parasites over time, respectively. In order to facilitate the comparison with the population size of lampreys and to take into account more practical situations, expressions (12) and (13) are also improved based on the Logistic population growth model. These two expressions, like expression (11), add the influence of other populations on the growth rate of their respective populations.

However, expression (12) takes into account the fact that the population growth rate of native fish is also influenced by environmental food abundance, but does not take into account the interference of sex ratio, whereas expression (13) does not consider the influence of environmental food abundance and sex ratio on the population growth rate of parasitic populations based on their characteristics. In Addition, expression (13) moves the inherent growth rate to the negative constraint term based on the traditional logistic model, and also moves the lamprey and local fish populations to the negative constraint term, which reflects the parasite Population size and tracking of lamprey and native fish populations.

3.3.2 Model Simulation and Evaluation

a. Modeling Background Description

In this study, the population size data of lamprey species from the open waters of the Lake Michigan estuary in 2014 were selected as the starting point for the simulation in order to evaluate the proposed model (Jean V. Adams, 2021). Given that the lack of data relative to Model 1 and Model 2, and taking into account the diversity and abundance of native fish populations, it was assumed that the number of native fish populations in this body of water is approximately ten times the number of lampreys populations. At the same time, based on the fact that the larvae of lampreys are exposed to more freshwater sediments and microorganisms than other fish species, and have the potential to be exposed to a wider range of pathogens (Shavaliar, Faisal, Moser, & Loch, 2021), the potential impacts of the number of parasites carried by lampreys on the ecosystem have been taken into account in the present simulation. In conjunction with the rate of parasite infection in lampreys mentioned in the relevant literature (Bence, et al., 2003), it was assumed that the number of initial parasite populations at the beginning of the simulation was equal to the number of lamprey populations. On this basis, a long-term simulation was conducted for 25 years (300 months in total) from January 2014 onwards.

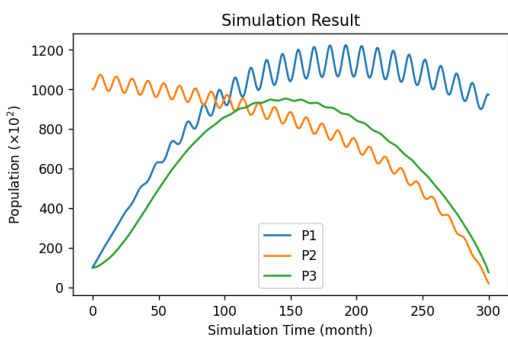


Figure 10 Based on the original data, reasonable inferences and assumptions, the simulation results of an estuary water along Lake Michigan for 25 years since January 2014

<i>Param.</i>	<i>Value</i>	<i>Param.</i>	<i>Value</i>
α_{1c2}	-5.0×10^{-1}	α_{23}	$+1.0 \times 10^{-8}$
α_{1a2}	$+1.0 \times 10^{-11}$	α_{32}	-9.0×10^{-6}
α_{21c}	$+1.0 \times 10^{-2}$	α_{13}	$+1.0 \times 10^{-8}$
α_{21a}	$+8.0 \times 10^{-4}$	α_{31}	-1.0×10^{-7}

Table 1 Model parameter table derived from the simulation described in Figure 10

b. Analysis of the Results

As shown in Figure 10, the fluctuating increase of lamprey population P_1 in the first 15 years led to the fluctuating decrease of native fish population P_2 , and the fluctuation phase of P_2 has a 180-degree phase difference with that of P_1 . Compared with the theoretical setting of Model 2, this phenomenon demonstrates the significant influence and sensitivity of lampreys on the native fish population. As P_2 decreases significantly from the 15th year to the 25th year, P_1 also begins to show a fluctuating downward trend. This change characterizes and signifies the destabilization and disruption of the ecosystem when the native fish population decreases to a certain critical value, which leads to a delayed decline in the population size of lampreys, even though the lampreys exhibit population inertia after invading into the ecosystem. Parasite population size P_3 increased along with P_1 during the first 10 years of the simulation, suggesting that the parasite reproduces and spreads rapidly in response to the growth of the lamprey population; However, P_3 decreased with P_2 in the following 15 years, which may reflect the inability of the model to fully capture the reality of the change in parasitic worm population with the population size of all the hosts in the model.

As shown in Table 1, we performed a twofold analysis of the model parameters:

- 1) The first focus was on the sign of the four parameters. The sign of α_{1c2} , α_{32} and α_{31} are negative, which is consistent with the model settings, while α_{23} should be negative theoretically negative, but the simulation results are positive, which is related to the simulation flaws in the aforementioned trend of P_3 decreasing with P_2 .
- 2) The second focus is on the order of magnitude of the five parameters. Parameters α_{1a2} , α_{13} , and α_{21a} are relatively small in order of magnitude, indicating that the interaction between these three species exists but has little effect, whereas parameters α_{21c} and α_{31} are large in order of magnitude, demonstrating that the growth of lamprey population has a significant negative effect on other species.

Overall, although Model 3 has some errors in the simulation of parasite populations, the simulation results of lampreys and other organisms in the context of the whole ecosystem show its practical application value and fully validate the effectiveness of the model.

3.4 Summary and Further Discussion

3.4.1 Summary

In this paper, we summarize the conclusions drawn from the three models constructed.

Firstly, for the exploration of the population dynamics of lampreys, it is conclusively indicated in the academic literature that the sex ratio of lamprey populations is directly affected by environmental food abundance (Yang, 2007), which in turn significantly affects their population size. Therefore, this key relationship was fully demonstrated in the development and data validation of Model 1 and Model 2. The patterns derived from Models 1 and Model 2 show that there is a clear cyclical relationship between the sex ratio and consequently the population size of the lamprey population and the seasonal variation in food abundance.

At the same time, the population size of lampreys was constrained by two aspects of environmental food abundance: One is the total environmental carrying capacity reflected by food abundance, and the other is the feedback regulation mechanism of sex ratio on the population size. These two constraints provide assurance for the stability of the lamprey population size under ideal conditions, but also imply a sensitive response of its population size and sex ratio to food abundance. The coexistence of these advantages and disadvantages reveals the peculiar and unique pattern of changes in the population size of lampreys over time, reflecting the dialectical unity of its population dynamics.

When the perspective is extended to a broader ecosystem level, the construction of Model 3 allows us to further explore the ecological effects of the lamprey population. In Model 3, we simulated an ecosystem of a localized water area in the Great Lakes of North America for a 25 years' simulation experiment (300 months).

The simulation results show that the changes in the lamprey population size are significantly different from the steady state after overshooting in Model 2, which is characterized by and manifested as an explosive population growth, taking into account the game between the native fish populations and the biological populations such as parasites. In contrast, Under the influence of lampreys, the overall quantities of native fish population showed an accelerated decline, which highlights the destabilizing and disruptive effect of the lamprey, an invasive and non-native alien species with no natural enemies, on the stability of the original ecosystem.

However, in the analysis of parasite population dynamics, although Model 3 simulations indicated that parasite populations could increase with the growth of the lamprey and showed its potential negative impact on ecosystem stability in parameter analyses, the post-simulation did not accurately capture the relationship between parasite population size and the quantity changes in the size of other host populations in the ecosystem.

In addition, the volatile changes in the population size of lampreys show an inverse phase to the phase of the fluctuations in the native fish population and parasites, further reflecting the fact that the population size of lampreys is strongly influenced by the sex ratio and the underlying food abundance. This also suggests the possibility of exploiting the volatility-

sensitive nature of the sex ratio of the sevendill eel by modulating its pattern of change over time, ultimately achieving a balance of species populations throughout the entire ecosystem. This strategy is explored in the next subsection as a topic for Further Discussion.

3.4.2 Further Discussion: Exploration of Stabilizing the Ecosystem with Proportional-Integral-Derivative Control Method

In this subsection, we simulated and analyzed the trend of the sevendill eel population size P_1 over time based on the Model 3 model (refer to Fig. 10). By applying the equivalent analysis method in engineering control principles, we aim to investigate how to adjust the sex ratio of the lamprey population to achieve stable coexistence with other biological populations in the ecosystem set in Model 3 and effectively reduce the lamprey population size to a lower level. For ease of analysis, this section assumes that the female ratio x'_i of the sevendill eel population in Model 3 can be controlled to a fixed mean value and simplifies the model to an equivalent zero-free second-order system for steady-state control analysis.

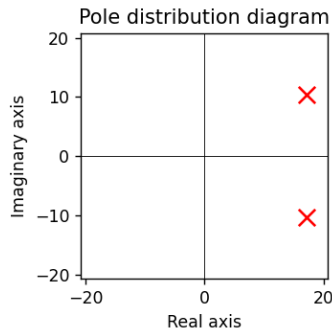


Figure 11 System pole distribution diagram described in Expression 14

$$P_1(s) = \frac{19.98^2}{s^2 - 34.16s + 4.00 \times 10^2} \quad (14)$$

s.t. $\overline{x_i} = 0.65$

Equation (14) is the mathematical expression of the sevendill eel population size P_1 over time in the Model 3, and after Laplace transformation and dimensionality reduction, we obtained the system expression in the frequency domain. According to the analytical results in Figure 11, both poles of the system are located to the right of the real axis in the complex plane. According to the system analysis theory, this indicates that the system is an unstable divergent system, which predicts that the unstable growth of the lamprey population size in the ecosystem simulated by Model 3 may lead to the collapse of the entire ecosystem, in this model, the female proportion x'_i of the lamprey population fluctuates with time and food resources, with an average value of approximately 0.65.

a. Scenario analysis of stable coexistence of biological populations

In the Model 3 simulated scenario, when the female ratio x'_t of the lamprey population decreased to 0.1, the time domain analysis showed that all the populations of organisms in the ecosystem were in a roughly stable state (see the left panel of Fig. 12). After analysis, we found that compared to equation (14), the new system introduced one proportional compensation link with two differential compensation loops in equation (15). Although the poles of the new system are still distributed on the right side of the real axis in the complex plane. Since the real parts of all the newly added poles are closer to the left side of the real axis, which suggests that the system represented by equation (15) has a superior stability compared to the system of equation (14).

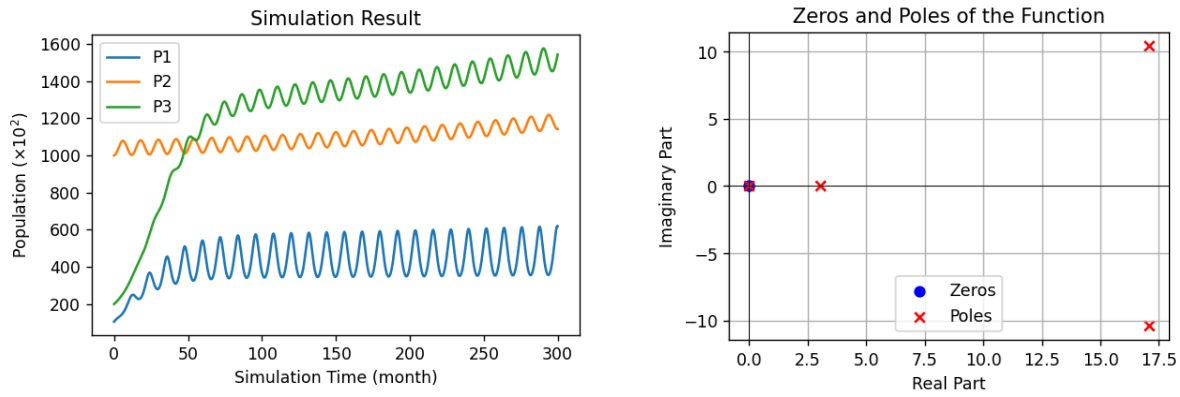


Figure 12 Model 3 simulation results and zero-pole distribution of equivalent compensation system under the condition of stable coexistence of biological populations

$$P_a(s) = \frac{19.98^2}{s^2 - 34.16s + 4.00 \times 10^2} \times 6.19 \times 10^{-3} \cdot \frac{6.44 \times 10^3 s + 1}{-0.33s + 1} \cdot \frac{6.44 \times 10^3 s + 1}{-2.33 \times 10^2 s + 1} \quad (15)$$

s.t. $\overline{x_t} = 0.10$

b. Significant reduction in the population size of sevengill eels

When the average value of the female ratio x'_t of the lamprey population in the Model 3 simulation dropped to 1×10^{-3} , the time domain analysis showed that the lamprey population was able to maintain a low level, while the other populations remained stable and at a high level (see the right panel of Figure 13). Compared with equation (14), the new system described in equation (16) introduced one proportional compensation link with two integral compensation loops. The Bode plot of the new system shows that the amplitude-frequency characteristic curve does not drop down to the unit gain point when the frequency increases, while the phase-frequency characteristic curve stabilizes at around -160 degrees. According to the system analysis theory, such a compensation link makes the system finally reach a steady state.

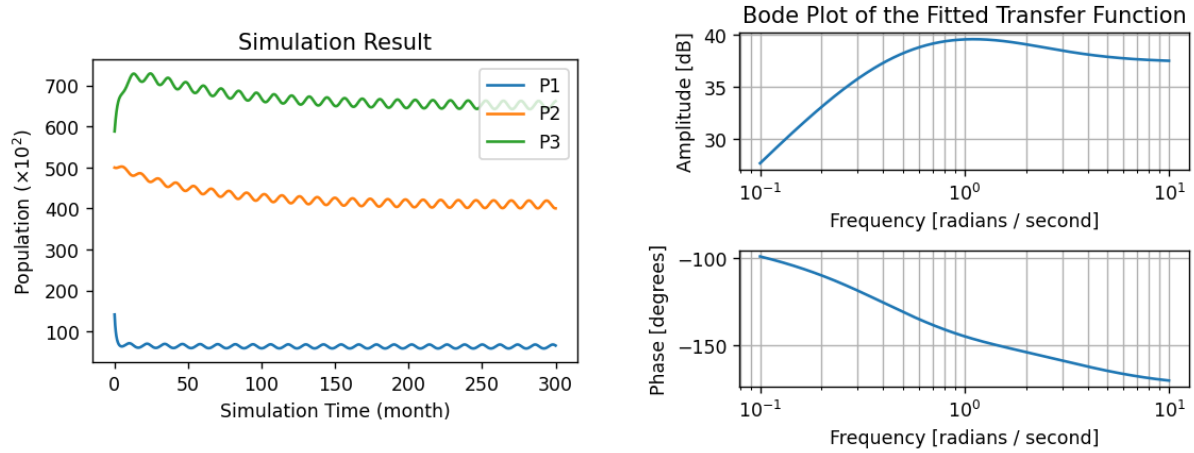


Figure 13 Model 3 simulation results and the Bode plot of the equivalent compensation system when the lamprey population is significantly reduced

$$P_{\beta}(s) = \frac{19.98^2}{s^2 - 34.16s + 4.00 \times 10^2} \times 1.72 \times 10^{-4} \cdot \frac{-0.39s + 1}{3.59 \times 10^4 s + 1} \cdot \frac{-2.82 \times 10^2 s + 1}{0.61s + 1} \quad (16)$$

s.t. $\bar{x}_t = 1.0 \times 10^{-3}$

In summary, this section explores how to control the overgrowth of lampreys in the Model 3 simulation scenario by directly controlling the sex ratio of the population to achieve ecosystem stability. Although the Model 1 and Model 2 suggest that the adjustment of the population sex ratio can be achieved by controlling the food abundance in the aquatic ecosystem, the mean value of the lamprey population ratio derived from the Model 3 simulation may not be consistent with the actual situation. Nonetheless, this study provides important insights into real-world scenarios for preventing and controlling negative impacts of sevendill eel populations in the Great Lakes region of North America, reflecting the value of the discussion in this section.

4 Review and Evaluation of Our Work

In this study, we constructed and delved into three interrelated mathematical models. First, Model 1 focuses on analyzing the changes of food abundance in the environment over time, as well as comparing it with real data from the Great Lakes, and explains the potential effects of food abundance on the sex ratio of the sevendill eel population through game theory. Next, Model 2 uses an optimized Logistic population growth model to simulate the nonlinear effects of food abundance, sex ratio, and other factors on the population size of the lamprey, revealing the feedback regulation mechanism of the population size under ideal conditions. Finally, Model 3 analyzes the symbiotic and competitive relationships among the local ecosystems of the Great Lakes, Benthic fish populations, and parasites in a broader context, using game theory to investigate the impacts of the sevendill eel population on other species in the ecosystem. The interconnections and coupling of these models provide a solid foundation for the conclusions drawn in the Summary session: the sex ratio of the lamprey population and its

impact on the population size of other species in the ecosystem, and in the Further Discussion section, the prevention and control of the lamprey species from the perspective of engineering control is proposed.

The significant strength of this study lies in the effective combination of conceptual rigor, data authenticity and depth of analysis. In order to gain a deeper understanding of the sevendill eel, we extensively read and cited numerous academic journal papers, which not only supported the establishment of our model, but also ensured that the model could effectively fit the real-world data. In terms of depth of analysis, we not only examined the population characteristics of sevendill eel species, but also attempted to apply our model to a broader, more complex system. In addition, we have addressed the hot topic of invasive sevendill eel species in the Great Lakes of North America and proposed strategies to control sevendill eels in the Great Lakes from an engineering point of view, and explored the balance of species in the ecosystems and the methods to control sevendill eel populations.

Given the limitations of the study conditions, there are still some shortcomings in our work. In Model 1, our model was validated only on annual data over a five-year period from 2007, and has not yet been validated over a broader time scale. At the same time, the increased model complexity and over-parameterization of Model 2 and Mode 3 led to some difficulties in linear processing, which also affected the accuracy of Model 3's simulation of parasite population size. In addition, in the Further Discussion section, we failed to respond directly to the question of how to control population size by controlling environmental factors such as food abundance, and the results were biased when simulating sex ratios of sevendill eel populations in a population equilibrium scenario.

5 Reference

- Bence, J. R., Bergstedt, R. A., Christie, G. C., Cochran, P. A., Ebener, M. P., Koonce, J. F., . . . Swink, W. D. (2003). Sea Lamprey (*Petromyzon marinus*) Parasite-host Interactions in the Great Lakes. *Journal of Great Lakes Research*, Volume 29, Supplement 1, Pages 253-282, ISSN 0380-1330, [https://doi.org/10.1016/S0380-1330\(03\)70493-6](https://doi.org/10.1016/S0380-1330(03)70493-6).
- Bowen., T. M. (1994). Significance of Organic Detritus in the Diet of Larval Lampreys in the Great Lakes Basin. *Canadian Journal of Fisheries and Aquatic Sciences*, 2380-2387.
- Evans, T. M. (2012). Assessing Food and Nutritional Resources of Native and Invasive Lamprey Larvae Using Natural Abundance Isotopes. *Master's thesis, Ohio State University*.
- Hardisty, M. W. (1961). Sex Composition of Lamprey Populations. *Nature*, 191, 1116–1117. <https://doi.org/10.1038/1911116a0>.
- Holmes, J. A. (1994). Long-term Influence of Water Temperature, Photoperiod, and Food Deprivation on Metamorphosis of Sea Lamprey, *Petromyzon marinus*. *Canadian Journal of Fisheries and Aquatic Sciences*. 51(9), 2045-2051. <https://doi.org/10.1139/f94-207>.
- IUCN. (2020, 1). Retrieved from The IUCN Red List of Threatened Species: <https://www.iucnredlist.org>

- Jean V. Adams, J. M. (2021). Quantifying Great Lakes sea lamprey populations using an index of adults. *Journal of Great Lakes Research*, Volume 47, Supplement 1, S335-S34.
- Johnson, N. &. (2020). A case study of sea lamprey (*Petromyzon marinus*) control and ecology in a microcosm of the Great Lakes. *Journal of Great Lakes Research*, 47. 10.1016/j.jglr.2020.09.006. .
- Johnson, N. S., Swink, W. D., & Brenden, T. O. (2017). Field study suggests that sex determination in sea lamprey is directly influenced by larval growth rate. *Proc Biol Sci*, 284(1851), 20170262. <https://doi.org/10.1098/rspb.2017.0262>.
- Renaud, C. (2011). Lampreys of the world. An annotated and illustrated catalogue. *FAO Species Catalogue for Fishery Purposes*.
- S., B., Yap, & R., M. (2018). Crowding reduces feeding rate, effectiveness of diet selection, and efficiency of digestion by Northern Brook Lamprey ammocetes (*Ichthyomyzon fossor*). *Environ Biol Fish* 101, 1385–1394 (2018). <https://doi.org/10.1007/s10641-018-0785-4>.
- Shavalier, M. A., Faisal, M., Moser, M. L., & Loch, T. P. (2021). Parasites and microbial infections of lamprey (order Petromyzontiformes Berg 1940): A review of existing knowledge and recent studies. *Journal of Great Lakes Research*, Volume 47, Supplement 1, Pages S90-S111, ISSN 0380-1330, <https://doi.org/10.1016/j.jglr.2021.09.004>.
- Wikipedia. (2024, 2 5). Retrieved from Lamprey: <https://en.wikipedia.org/wiki/Lamprey>
- Wikipedia. (2024). *Great Lakes*. Retrieved from Wikimedia Commons: https://commons.wikimedia.org/wiki/Great_Lakes
- Yang, J. W. (2007). Progress in the study of mechanisms determining fish gender. *Journal of Fisheries Economics Research*, 14-19.

6 Appendix: Notations of Main Equations

Symbol	Definition	Unit	Symbol	Definition	Unit
t	time	month	F_t	fluctuation of food abundance	mg ash-free-dry-mass $\times L^{-1}$
x_t, x'_t	female sex ratio	%	y_t, y'_t	male sex ratio	%
j	corrected intrinsic growth rate	-	P_t	population	-
h	impact factor of environment carrying capacity (variable)	-	K	impact factor of environment carrying capacity (constant)	-