Adaptive Sex Ratio Variation in Lampreys: Implications for Ecosystem Dynamics and Species Interactions

Jiuchen Chen [1, *], Ruoqing Hao [2], Jingyi Li [3]

[1] School of Mechatronical Engineering, Beijing Institute of Technology, Beijing, China, 100081

[2] School of Automation, Beijing Institute of Technology, Beijing, 100081

[3] School of Cyberspace Science and Technology, Beijing Institute of Technology, Beijing, 100081

* Corresponding Author Email: castlechen@bit.edu.cn

Abstract. Lampreys can alter the sex ratio of their population in response to resource availability in the environment, which has significant implications for the ecosystem. This paper built a population growth model based on the Malthusian Model to describe the relationship between the natural growth rate of lamprey populations and resource availability. It highlights how variations in the sex ratio contribute to changes in birth rates while also considering the influence of resource availability on mortality rates. This model incorporates a specific coefficient to measure the rate of resource consumption, underlining the adaptability of lampreys in various ecological contexts. Then, to explore the interaction between lamprey and other species, this paper devised a simplified food web reflecting real-world conditions and established an ecological interaction model based on the Lotka-Volterra equations. This model employs a simplified food web that mirrors real-life ecosystems, categorizing related species into predators, competitors, and prey/hosts, thus offering a comprehensive view of lampreys' ecological relationships. Simulation results indicate that lampreys' strategy of sex ratio adaptation significantly bolsters their survival and reproductive success across both resource-depleted and resource-rich environments. This adaptive mechanism underscores their competitive edge in diverse ecological settings, confirming the critical influence of lampreys on ecosystem balance and biodiversity.

Keywords: Resource Availability, Adaptive Sex Ratio, Interspecific Competition, Lotka-Volterra Equations.

1. Introduction

In ecosystems, the sex ratio of a species is a fundamental parameter that has profound implications on population dynamics, species interactions, and ecosystem stability [1]. Typically, a 1:1 sex ratio at birth is the norm for most animal species, a pattern explained by Fisher's principle [2]. However, in response to environmental factors, the sex ratio of certain species deviates from an even split, which is known as adaptive sex ratio variation [3]. One such species that demonstrates this adaptive potential is the lamprey, an anadromous parasitic species that has pivotal roles in aquatic ecosystems [4]. The sex ratio of sea lampreys is not fixed at conception but is instead influenced by the rate of larval growth, which is, in turn, affected by the availability of food resources in their environment [5]. In regions with food scarcity, slower larval growth rates lead to a significantly higher proportion of males compared to females. Conversely, in environments with abundant food resources, faster larval growth rates result in a gradual increase in the proportion of females. Such adaptability in sex determination presents an intriguing aspect of sea lamprey biology that warrants comprehensive investigation.

In the field of ecological and evolutionary biology, the adaptive variation of sex ratios has been the subject of extensive research, revealing intricate mechanisms and profound implications for population dynamics. Gaughwin et al. [6] investigated the sex ratio of pouch young and adult hairy-nosed wombats to determine if sex ratio biases have evolved as an adaptive response to environmental unpredictability. Lockley et al. [7] discuss the effects of global warming on species with temperature-dependent sex determination, highlighting the potential threat to population viability due to biased sex ratios. Valdebenito et al. [8] conducted a meta-analysis on wild birds to investigate seasonal

variation and sex-specific immunity, suggesting that both seasonal variation and sex differences in the immune system are common in birds. Bock et al. [9] examined the impact of incubation temperature and maternal resource provisioning on hatchling phenotypes in species with temperature-dependent sex determination, such as the American alligator. Wang et al. [10] emphasize the importance of understanding the intersection of age and sex to comprehend variation in incidence and survival for primary malignant gliomas.

However, there have been few studies on the sex ratio of lampreys in recent years. Most existing research has focused on the reasons behind the changes in the sex ratio of lamprey populations, without exploring the implications of the lamprey's ability to vary its sex ratio. In this paper, the effect of this adaptive trait is explored from two perspectives: its impact on the sea lamprey's own population development, and the repercussions for other species and the broader ecosystem. Figure 1 is a flowchart depicting the framework of the proposed method.

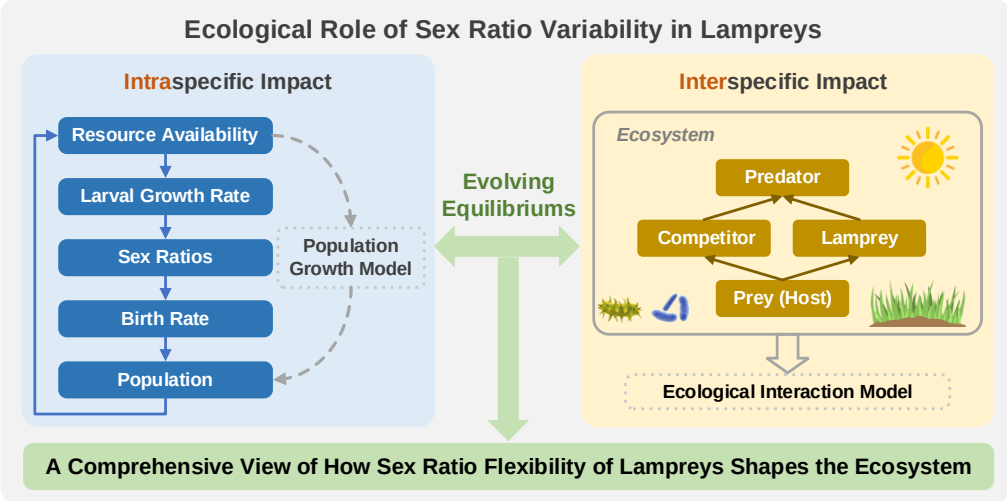


Figure 1. The framework of the proposed method

2. Proposed method

2.1. Model 1: population growth model

The Population Growth Model is an essential tool for predicting the future dynamics of the sea lamprey population. According to the principles of the Malthusian Model [11], in the absence of predators, the population of the sea lamprey is related to its natural growth rate, which in turn is closely associated with two factors: birth rate and natural mortality rate. The relationship between these variables can be expressed as follows:

$$\begin{cases} \frac{dN}{dt} = \lambda \cdot N \cdot \left(\frac{k - N}{k} \right) \\ \lambda = R_b - R_{nm} \end{cases} \tag{1}$$

where N is total number of individuals in the population of lamprey, λ is the natural growth rate of the sea lamprey population, k denotes the maximum car-rying capacity of sea lampreys in the ecosystem, R_b is the birth rate, and R_{nm} is the natural mortality rate.

The birth rate of the sea lamprey population is fundamentally influenced by the mating behavior of the species. According to the literature review by Docker [12], a single male can mate with multiple females, suggesting that the presence of males enables a proportional increase in the population's birth rate with the increase in the number of females. Therefore, R_b can be directly linked to the proportion of female individuals in the population, leading to the formulation:

$$R_b = \begin{cases} \alpha m, & 0 \le m < 1 \\ 0, & m = 1 \end{cases} \tag{2}$$

where α is a coefficient representing the fecundity rate per female and m is the proportion of female individuals in the population of lampreys

According to the research conducted by Johnon et al. [5], within a short period of time (more precisely, within 6 years), the proportion of females approximately follows a direct proportional relationship with resource availability. To simplify subsequent calculations, it is advisable to set the rate of change in m equal to resource availability, that is:

$$\frac{dm}{dt} = S \tag{3}$$

where S represents resource availability in the environment.

Considering the initial proportion of females, the relationship between m and S can be represented as follows:

$$m = S \cdot t + m_0 \tag{4}$$

where m_0 is the initial proportion of females.

It is noteworthy that when the population of lampreys is in a small ecosystem, the resilience of the ecosystem is weak, and the resource availability in the environment may gradually decrease over time. Conversely, when the population is in a larger ecosystem, the resource availability remains almost constant. Thus, S can be represented as follows:

$$S(t) = \begin{cases} S_0, & \textit{large ecosystem} \\ S_0 \cdot q^t, & \textit{small ecosystem} \end{cases} \tag{5}$$

where S_0 denotes the initial resource availability, and q is a coefficient representing the rate of resource consumption.

The natural mortality rate of the sea lamprey population is associated with the availability of resources in the environment. According to the review by Docker [12], adult sea lampreys exhibit an annual natural mortality rate between 4% and 48%. Thus, the average of this range, approximately 26%, is taken as the baseline natural mortality rate. Based on a Sigmoid function, a relationship between natural mortality rate and resource availability can be constructed. The specific formula for R_{nm} is as follows:

$$R_{nm} = \frac{\gamma}{1 + e^{-\beta S}} + R_{nm0} \tag{6}$$

where R_{nm0} represents the baseline natural mortality rate, taken as 0.26; γ denotes the range of R_{nm}, that is 0.44; and β serves as a coefficient to regulate the rate of change of R_{nm}.

Based on equation (1)-(6), the Population Growth Model can be represented as follows:

$$\begin{cases} \dfrac{dN}{dt} = \lambda \cdot N \cdot \left(\dfrac{k-N}{k} \right) \\ \lambda = R_b - R_{nm} \\ R_b = \begin{cases} \alpha m, & 0 \le m < 1 \\ 0, & m = 1 \end{cases} \\ m = S \cdot t + m_0 \\ S(t) = \begin{cases} S_0, & \textit{large ecosystem} \\ S_0 \cdot q^t, & \textit{small ecosystem} \end{cases} \\ R_{nm} = \dfrac{\gamma}{1+e^{-\beta S}} + R_{nm0} \end{cases} \tag{7}$$

where k represents the maximum capacity of lamprey in the ecosystem.

2.2. Model 2: ecological interaction model

In a large-scale ecosystem, the population dynamics of the sea lamprey are not only influenced by abiotic environmental factors but also by interactions with other species within the food web. Sea lampreys are preyed upon by species such as rays, sharks, and seals; it competes with species like cymothoa exigua, pearlfish, and cestodes; and its primary hosts include species such as cod, trout, and salmon.

The inter-species relationships can be described by the Logistic-Volterra model [13], the equation of which is presented as follows:

$$\begin{cases} \dfrac{dX}{dt} = \left(r_1 - \mu_1 C - \mu_2 N \right) \cdot X \\ \dfrac{dC}{dt} = \left(r_2 + \mu_3 X - \delta_1 N - \sigma_1 Z \right) \cdot C \\ \dfrac{dN}{dt} = \left(r_3 + \mu_4 X - \delta_2 C - \sigma_2 Z \right) \cdot N \\ \dfrac{dZ}{dt} = \left(-r_4 + \mu_5 C + \mu_6 N \right) \cdot Z \end{cases} \tag{8}$$

Where $X(t)$ is the population size of all prey/host species; $C(t)$ is the population size of all competitors; $Z(t)$ is the population size of all predators; r_1, r_2, and r_3 are the natural growth rates of X, C, and N, respectively; r_4 is the mortality rate of Z; μ_1 and μ_2 are the predation pressure of C and N on X, respectively; μ_3 and μ_4: the efficiency of energy transfer from X to C and Z, respectively; μ_5 and μ_6 are the efficiency of energy transfer from C and N to Z, respectively; δ_1 and δ_2 are the competitive abilities of N and C, respectively; σ_1 and σ_2 are the predation pressure of Z on C and N, respectively.

In section 2.1, the expression for the natural growth rate of the sea lamprey population was introduced when discussing Model 1. Therefore, it is possible to substitute r_3 in Equation (8) with λ, yielding the following equations:

$$\begin{cases} \dfrac{dX}{dt} = \left(r_1 - \mu_1 C - \mu_2 N\right) \cdot X \\ \dfrac{dC}{dt} = \left(r_2 + \mu_3 X - \delta_1 N - \sigma_1 Z\right) \cdot C \\ \dfrac{dN}{dt} = \left(\lambda + \mu_4 X - \delta_2 C - \sigma_2 Z\right) \cdot N \\ \dfrac{dZ}{dt} = \left(-r_4 + \mu_5 C + \mu_6 N\right) \cdot Z \\ \lambda = R_b - R_{nm} \\ R_b = \begin{cases} \alpha m, & 0 \le m < 1 \\ 0, & m = 1 \end{cases} \\ m = S_0 \cdot t + m_0 \\ R_{nm} = \dfrac{\gamma}{1 + e^{-\beta S}} + R_{nm0} \end{cases} \tag{9}$$

3. Results

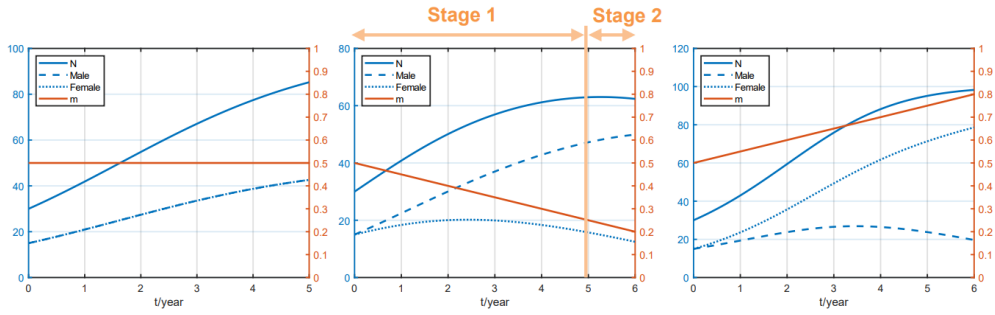
3.1. The implementation of Model 1

Prior to the implementation of Model 1, it is imperative to assign values to the undeter-mined coefficients within the model framework. According to the data presented in [5] and [12], the values for all the coefficients utilized in Model 1 are enumerated in Table 1.

Table 1. Coefficients in Model 1

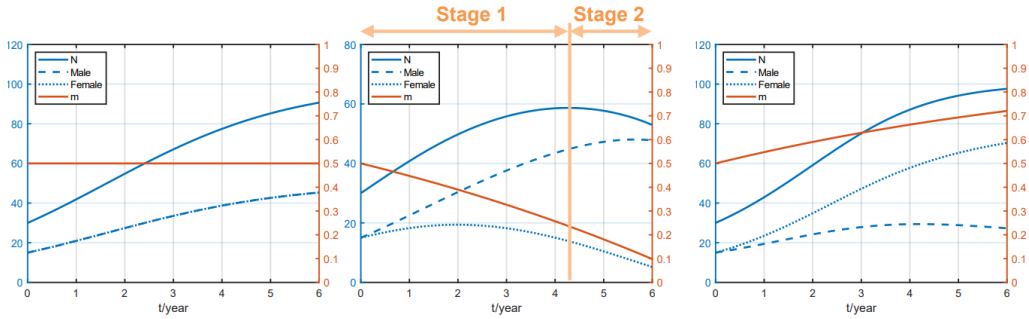
Symbol	Definition	Value
S_0	Initial resource availability	0.05
m_0	Initial proportion of females	0.5
q	Rate of resource consumption	0.95 (if $S \ge 0$), 1.05(if $S < 0$)
N_0	Initial number of individuals in the population	30
R_{nm0}	Baseline natural mortality rate	0.26
γ	Range of R_{nm}	0.44
β	Rate of change of R_{nm}	1
α	Fecundity rate per female	2
k	Maximum capacity of lamprey in the ecosystem	100

When considering the sea lamprey population within a large-scale ecosystem, where S is held constant, the model's outcomes are depicted in Figure 2. Conversely, within a small-scale eco-system where S decreases over time, the model's results are illustrated in Figure 3.



(a) $S_0 = 0$ (b) $S_0 = -0.05$ (c) $S_0 = 0.05$

Figure 2. The results of Model 1 when S is constant.



(a) $S_0 = 0$ (b) $S_0 = -0.05$ (c) $S_0 = 0.05$

Figure 3. The results of Model 1 when S decreases over time

3.2. Results analysis of Model 1

In the analysis of Model 1, three distinct scenarios were examined. In the Control Group (Scenario 1), the sea lamprey population demonstrates an oscillation around the environment's maximum capacity with a constant sex ratio, as depicted in Figures 2(a) and 3(a), indicating synchronized growth between female and male individuals. In contrast, under Low Resource Availability (Scenario 2), as illustrated in Figures 2(b) and 3(b), the population initially expands then enters a decline phase due to resource scarcity, showcasing an adaptive response with male numbers initially increasing then stabilizing, and female numbers eventually decreasing, leading to a population decrease. Conversely, Excessive Resource Availability (Scenario 3), reflected in Figures 2(c) and 3(c), triggers a rapid female population increase with stable male numbers, pushing the growth rate beyond that of the control group and nearing the maximum carrying capacity, with the female-to-male ratio stabilizing at a high level.

3.3. The implementation of Model 2

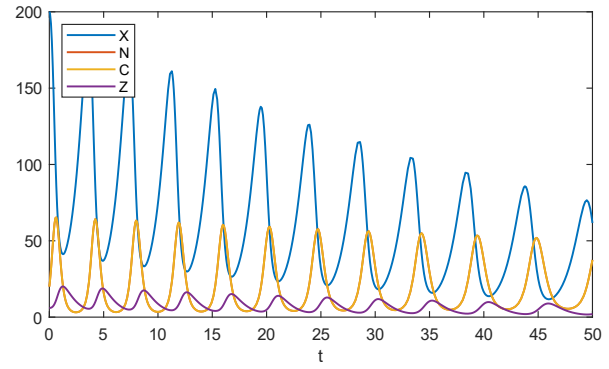
To verify whether the ability of adaptive sex ratio variation of sea lamprey has an impact on the ecosystem, a control group and an experimental group were established. In both experimental setups, the sea lamprey populations were assigned different natural growth rates, while all other coefficients remained identical. Table 2 presents the coefficients corresponding to each of the two experimental groups. It is imperative to note that these coefficients are merely relative magnitudes and do not reflect the actual values present in nature.

In Table 2, **Set 1** represents a scenario with high resource availability, where the natural growth rates of all species are expected to increase. For the sea lamprey population in the experimental group, S_0 should be greater than 0. Conversely, **set 2** simulates a scenario with low resource availability, where the natural growth rates of all species are expected to decrease, and for the sea lamprey population in the experimental group, S_0 should be less than 0.

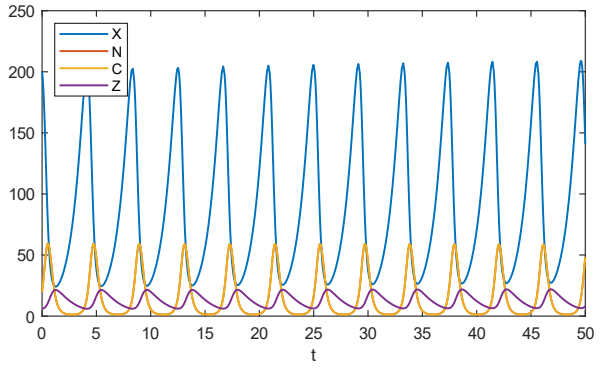
Table 2. Coefficients in Model 2

Symbol	Control Group	Experimental Group
r_1, r_2, r_3	1, 0.5, 0.5 (Set 1) 0.9, 0.1, 0.1 (Set 2)	1, 0.5, λ (Set 1) 0.9, 0.1, λ (Set 2)
S_0	/	0.009 (Set 1) -0.009 (Set 2)
r_4	0.6	0.6
μ_1, μ_2	0.0332, 0.0332	0.0332, 0.0332
μ_3, μ_4	0.02, 0.02	0.02, 0.02
μ_5, μ_6	0.02, 0.02	0.02, 0.02
δ_1, δ_2	0.0002, 0.0002	0.0002, 0.0002
σ_1, σ_2	0.18, 0.18	0.18, 0.18

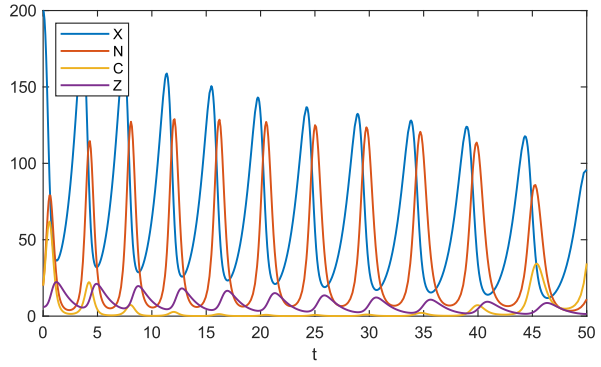
The results of the model are shown in Figure 4, which illustrates the changes in population size of different species over time.



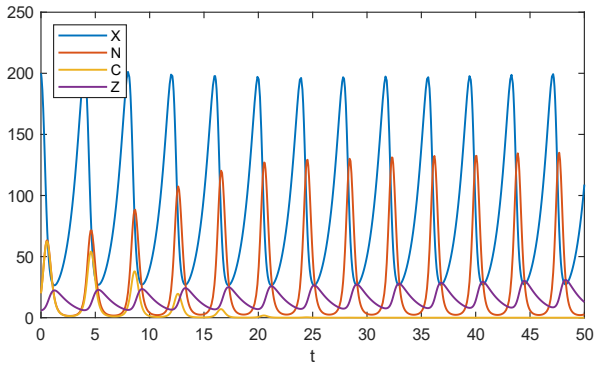
(a) Control group, Set 1



(b) Control group, Set 2



(c) Experimental group, Set 1



(d) Experimental group, Set 2

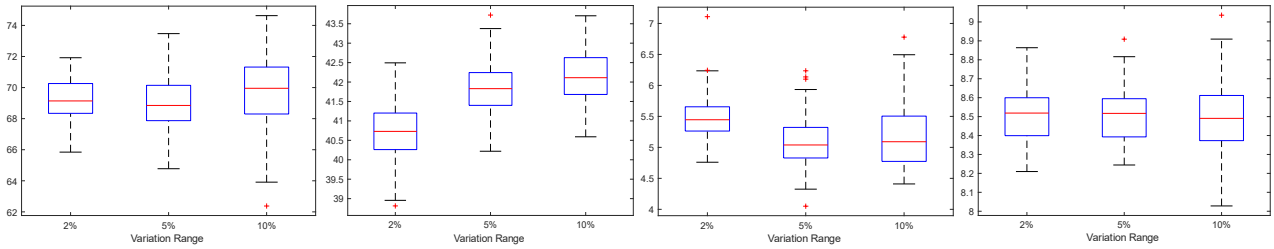
Figure 4. Changes in the population size of different species over time

3.4. Results analysis of Model 2

Under conditions of low resource availability, a comparison of Figure 4(a) and Figure 4(c) reveals that, within the control group, the population size of the sea lamprey is entirely consistent with that of its competitors. In contrast, within the experimental group, the average population size of the sea lamprey significantly surpasses that of its competitors. Similarly, under conditions of high resource availability, the same pattern is observed when comparing Figure 4(b) and Figure 4(d). This indicates that the adaptive sex ratio capabilities of the sea lampreys confer a competitive advantage upon this species, enabling it to dominate both in environments with scarce resources and those with abundant resources.

3.5. Stability Analysis

In Table 2, a series of coefficient values were assigned within the model framework. It is acknowledged that in nature these coefficients are not static; they are subject to random fluctuations within certain bounds. To ascertain the stability of the proposed model, a stability test was conducted in which each coefficient was randomly perturbed by 2%, 5%, and 10%, and this process was iterated 100 times to observe the fluctuations in the mean values of X, C, N, and Z. The results of these experiments are presented in Figure 5. Figure 5 suggests that the fluctuations in mean values for X, C, N, and Z remain within reasonable bounds, indicating that the proposed model exhibits a high degree of stability. This insensitivity to moderate stochastic disturbances confirms the model's validity and reliability for predicting population dynamics over time.



(a) X (Predator) (b) N (Lamprey) (c) C (Competitor) (d) Z (Prey/Host)

Figure 5. Stability Analysis of X, C, N and Z

4. Conclusions

This paper provides a detailed analysis of the impact of the variable sex ratio ability of lampreys on themselves and the ecosystem, utilizing population growth models and ecological interaction models. Results demonstrate that lampreys can adaptively modify their sex ratio to optimize survival and reproduction under varying resource conditions, significantly influencing ecosystem balance. In particular, these adjustments can affect predator-prey relationships, potentially leading to species decline, and reduced biodiversity. Furthermore, in environments where lampreys are considered invasive, such as North America's Great Lakes, their adaptability may intensify negative impacts on native species and fisheries, with potential long-term ecological damage.

Due to the lack of long-term data on lamprey sex ratios and resource availability, it is chal-lenging to predict with precision what may happen in the more distant future. However, it is clear that the ability of lampreys to alter their population sex ratio in response to environmental resource availability warrants further in-depth investigation by researchers. This adaptability highlights a significant area of study that could yield insights into not only lamprey population management but also broader ecological conservation strategies.

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