

# Sea Lampreys: Flexible Adaptors and Environmental Spoilers

## Summary

In many of the world's waters today, a creature called lamprey has the ability to self-regulate its sex at a young age so that it can better adapt to a dynamic environment. But problems ensued. Most lampreys, as invasive species, have been able to take over the ecological niches of other species by virtue of their ability to survive, leading to a crisis in marine biodiversity and ecosystem stability. In an effort to protect our ecosystems in a fragile balance, this post is a problem-oriented look at the various impacts of the unique sex characteristics of the lampreys.

First, it is important to figure out what the relation between is lampreys' sex ratio and resource availability. After consulting the literature, we obtained a more precise equation. Then, we build up **three models** to get the results of problems.

For **Problem 1:** we construct **Basic Ecosystem Model Based on Differential Equation** step by step. We divided the model into a **Logistic model** and a **Lotka-Volterra model**. Then we combined them with newborn sex ratio equation and obtain a system of quadratic equations to describe a basic relationship among lampreys, their preys and their predators and analyze lampreys' roughly impact on the ecosystem.

For **Problem 2:** we tried **two** approaches to realize **Lampreys Propagation Model** and discuss the pros and cons to the population of lampreys. The first one is similar to the Basic Ecosystem Model, considering the **Fecundity** additionally. For the other one, we use **Agent-Based Model** to simulate every individual of lampreys and predict lamprey population trends. We compared the two ideas above and discussed their similarities and differences, thus setting the stage for the next section on combining the two

For **Problem 3 & 4:** Borrowing from Basic Ecosystem Model's ideas about ecosystem, we improve our Agent-Based Model for lampreys propagation with a **food web** with complex relationships, which is called **Agent-Based Multiple Ecosystem Model**. Based on this model, we conclude how the changes of lamprey sex ratio influence ecosystem and other species more precisely and in detail. In the end, we discuss how **parasites** carried and spread by lampreys benefit from the special sex identity of lampreys.

In the end, based on our conclusions of these problems, we hope that our effort can make people more aware of the characteristics of the seven-gill eel and the damage it can cause to the ecosystem.

**Keywords:** Sex ratio; Resource Availability; Differential Model; Agent-Based Model; Multiple ecosystem

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# 1 Introduction

## 1.1 Problem Background

Lampreys are an ancient lineage of jawless fish of the order Petromyzontiformes. They feed on the blood, fluids, and tissues of fishes and cetaceans as juveniles following migration to marine environments and prior to returning to freshwater systems to spawn. As a kind of parasite and as food for some other species, sea lampreys have a significant influence on the ecosystem. [1]

The sex of some organisms is determined by the environment that an individual lives in, rather than being fixed by genotype at conception. Prior studies have indicated that sex differentiation in sea lampreys is also sensitive to environmental influence, especially during their prolonged period of sexual indeterminacy as larval.[2] Observation on sea lamprey population indicates a negative correlation between the sex ratio and the food availability in the environment. Analysis of how lampreys sex ratio interact with the ecosystem has important meanings beyond biological research area, in helping the development of fishery and aquaculture industry.

Though sea lampreys have existed for long in some regions like the Baltic Ocean[3], they are regarded as invading species in other regions such as the Great Lake[4]. Figure 1 shows the distribution of sea lampreys in these two regions.

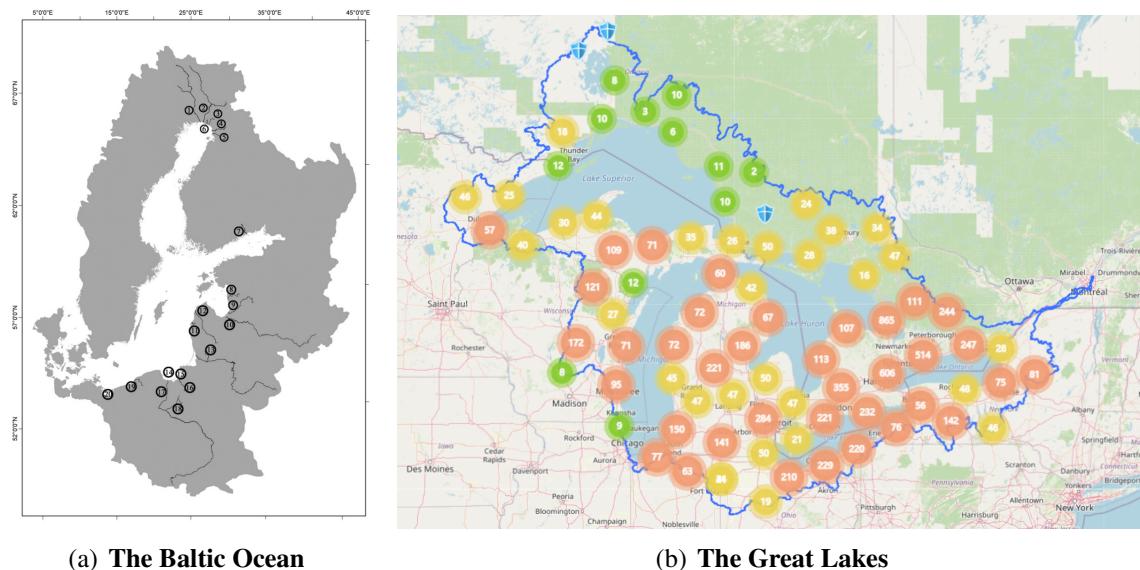


Figure 1: Sea Lampreys Distribution in Great Lakes and Baltic Ocean

## 1.2 Restatement of the Problems

Considering the background information of fungi and limiting conditions identified in the problem statement, we are supposed to address the following problems:

- **Problem 1:** Build a mathematical model to describes the impact of sea lampreys' environment determined sex ratio to the large environment compared to the situation with fixed sex ratio. Notably, we are supposed to consider the sea lampreys' ecological niche in the food chain to construct our model.

- **Problem 2:** Characterize on the dynamics of the sea lamprey population. Compare the result to the situation with fix sex ratio and conclude the impact to the population.
- **Problem 3:** Analyze the stability of the mathematical model you use the study the dynamics of the ecosystem. Give conclusion on the robustness and biodiversity of the ecosystem when the initial sex ratio of the sea lampreys changes.
- **Problem 4:** Use the mathematical model you construct to include dynamics of the population of other significant components of the ecosystem, such as parasites.

### 1.3 Literature Review

Back in 1961 M. W. HARDISTY studied the variable sex ratio in sea lampreys population[5]. Lots of later researches point out and confirm that the sex ratio of sea lampreys population is related to population density and relative food abundance(i.e. resource availability)[1, 6, 4]. L Jones et al. (2009) gives an operating model to predict sea lampreys propagation [7], though they didn't include variable sex ratio to their model. NS Johnson, WD Swink, TO Brenden(2017) found direct relationship between sex determination and years for larval to metamorphosis[8]. These paper uses this result as our foundation of our mathematical model.

The book *Lampreys: Biology, Conservation and Control* by Margaret F. Docker summarized the natural behavior in the ecosystem including detailed information about its predators, its food, the parasitic and non-parasitic sea lampreys[4]. This is equally significant for our work.

## 1.4 Our Work & Model Overview

After literature review, we establish two models for sea lampreys propagation including the differential equation model and the Agent-Based Model.

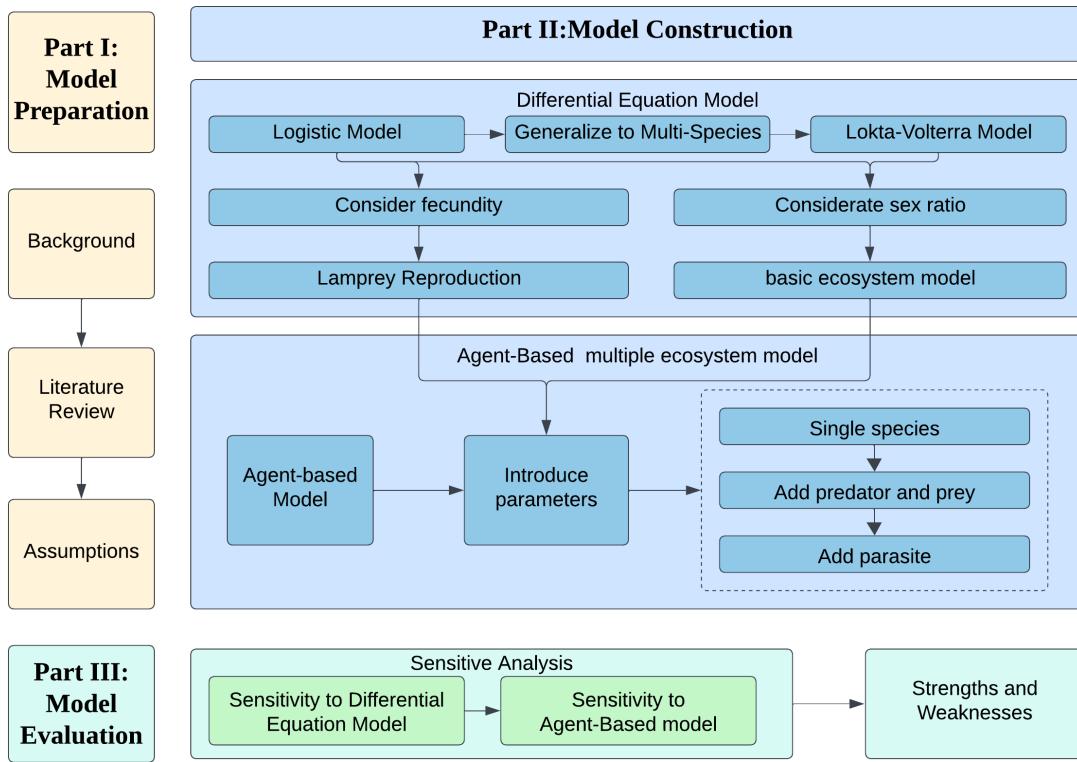


Figure 2: Our Work & Model Overview

## 2 Assumptions and Justifications

To simplify the given problem, we make the following basic assumptions, each of which is properly justified.

- **Assumption 1: Though sea lampreys are divided into parasitic and non-parasitic, we mainly study the parasitic ones in this article.**

**Justification:** Obviously, with reference to the problems, the parasitic class of lamprey has a greater impact on the ecosystem and parasitism is also an important feature that distinguishes them from other animals that can be studied.

- **Assumption 2: As for resource availability, we mainly concern the average amount of food available to each individual.**

**Justification:** Factors such as climate, water environment, and breeding area occupancy are also part of the resource availability. However, compared to food resources, they have little effect on sex ratio of lampreys and are not easy to include in our model.

- **Assumption 3: We primarily consider lampreys in the Great Lakes region..**

**Justification:** This assumption is prepared for our concrete lamprey-centered food web in Section 6. According to many reports, lampreys have done considerable damage to the Great Lakes ecosystem. So analysis on lampreys in the Great Lakes region has great practical significance.

- **Assumption 4: Male lampreys are more likely to survive with fewer resources, more likely to parasitize other fish and less likely to be eaten by predators.**

**Justification:** According to literature[9], it has been proved that male (parasitic) sea lampreys exhibit higher feeding rate and greater swimming activity. This indicates that males have higher predation rate and lower probability to be predated. And considering that females need to lay eggs to reproduce, they definitely require more resource and energy than males.

- **Assumption 5: Parasites are transmitted throughout the ecosystem and, for all organisms except the lampreys, parasites are transmitted only by organisms eating other organisms that contain the parasite. In the case of the lampreys, it can also pass the parasite on to other species while it is parasitizing them.**

**Justification:** In Section 6, we will consider the effects of variable sex ratios of lampreys on parasitism in a multiple ecosystem. For the real-life parasites that are transmitted by lampreys, most of them are also transmitted during the parasitization of other organisms by lampreys. And the role of the lampreys in the ecosystem is more indirectly demonstrated by the parasite that spreads throughout the ecosystem.



Figure 3: Fish Captured in the Great Lakes with Injury Made by Sea Lampreys Parasitism

### 3 Notations

The primary mathematical notations used in this paper are listed in **Table 1**.

Table 1: Notations used in this paper

Symbols	Description
$P$	Population of the sea lamprey
$A$	Population of the predators of lamprey
$B$	Population of the preys of lamprey
$\lambda$	Sex ratio (i.e. proportion of males) of the sea lampreys
$\theta_{BA}$	Predation rate of predator B and prey A
$\theta_{BP}$	Predation rate of predator B and prey P
$\theta_{PA}$	Predation rate of predator P and prey A
$\delta_{BA}$	Digestibility of predator B and prey A
$\delta_{BP}$	Digestibility of predator B and prey P
$\delta_{PA}$	Digestibility of predator P and prey A
$\mu$	Death rate of $A$ after parasitism
$K_P$	Carrying Capacity of the sea lampreys
$K_A$	Carrying Capacity of A
$K_B$	Carrying Capacity of B
$r_A$	Natural growth rate of A
$r_B$	Natural growth(death) rate of B
$r_P$	Natural growth(death) rate of the sea lampreys

where we define the main parameters while specific value of those parameters will be given later.

### 4 Problem 1: Basic Ecosystem Model Based on Differential Equation

#### 4.1 Logistic Model of Single Species Propagation

To build up the Sea lampreys Propagation Model, we first study the dynamics of the population with only a single species into consideration.

As a species continue to reproduce itself, their population size  $n$  increases with time goes by, which can be expressed as:

$$\frac{dn}{d\tau} = r \cdot n \quad (1)$$

where  $r$  represents the natural growth rate of the species here. However, due to limited natural resources and water produced and heat released in the process, the actual growth rate will diminish as population size enlarges, namely  $n$  increases. Therefore, we consider the actual grow rate  $r(n)$  as function with variable  $n$ , and according to observation results we have the following fomular:

$$r(n) = r - s \cdot n \quad (2)$$

Therefore we get the differential equation:

$$\frac{dn}{d\tau} = H(n) \cdot n = n(r - sn) \quad (3)$$

Solving equation (3) we obtain  $R := \lim_{\tau \rightarrow +\infty} n(\tau) = \frac{r}{s}$ . The limit  $R$  is called the Carrying Capacity of the given species, and therefore we can rewrite (3) as follows:

$$\frac{dn}{d\tau} = rn(1 - \frac{n}{R}) \quad (4)$$

We call equation the Logistic Model. It is worth noting that the Carrying Capacity of one species can vary with the environment fluctuations(e.g. the sea lampreys, we will further discuss this later)

## 4.2 Generalized Lotka-Volterra Model for Sea Lamperys without Sex Ratio

In consideration of the predator-prey relationship, prior studies[10, 11] constructed and verified the Lotka-Volterra Model. In the following discussion in this subsection, the symbol  $U$  represents the prey in the food chain, for example a species of plant. And  $V$  represents the predator in the food chain, a herbivorous animal species for instance. By the Lotka-Volterra Model we have:

$$\begin{cases} \frac{dU}{dt} = \alpha U - \gamma UV \\ \frac{dV}{dt} = -\beta V + e\gamma UV \end{cases} \quad (5)$$

Here  $\alpha$  and  $\beta$  represents the natural growth and death rate of  $U$  and  $V$  respectively. Additionally  $\gamma$  is the predation rate and  $e$  is the digestibility of species  $V$ .

This model doesn't take the Carrying Capacity of the plant into consideration. If we obtain the Carrying Capacity and expand our model to include more species, we can get the Generalized Lotka-Volterra Model for Sea Lamperys.

According to literature review citethebook, the major predators which prey on the sea lampreys are ducks and herons and some species of fish. It might be unfair to say various species of fish mainly contribute to be the food of sea lampreys, because the parasitic lampreys do not and cannot prey on the fish. Instead, they parasitize the fish, which cause a much lower death rate to the fish(this is why we use a small value  $\mu$  to represent the death rate caused by parasitism).[4]



Arrows here represent the energy flows in the food chain. Figure 10 provides a detailed food network involving the sea lampreys.

$$\begin{cases} \frac{dA}{dt} = \gamma_{AA}(1 - \frac{A}{K_A}) - \theta_{BA}AB - \mu\theta_{PA}AP \\ \frac{dB}{dt} = \delta_{BA}\theta_{BA}AB + \delta_{BP}\theta_{BP}BP - \gamma_B B \\ \frac{dP}{dt} = \delta_{PA}\theta_{PA}AP - \theta_{PB}BP - \gamma_P P \end{cases} \quad (7)$$

Meanings of notations in equation (7) are available in section 3.

### 4.3 Relationship between Sex ratio and Resource Availability

Prior research[8] found a statistical relation between the probability a lamprey larval becoming male or female and the larval growth rate. Whether a lamprey larval become male or female after metamorphosis can be modelled as a Bernoulli random variable with the probability of being male equal to

$$\text{logit}(p_{\text{male}}) = k_0 \cdot y + b_0 \quad (8)$$

where  $b_0$  and  $k_0$  is the intercept and slope of linear relation respectively with  $y$  being the years to metamorphosis. The logit function here is the anti-function of the logistic function, namely

$$\text{logistic}(x) = \frac{1}{1 + e^{-x}}. \quad (9)$$

By assumptions in section 2, we assume that years to metamorphosis is negatively related to resource availability(i.e. food abundance), and we use linear function to fit this relationship. With food abundance being represented by the ratio  $\frac{A}{P}$ , we can obtain the formula as follows:

$$p_{\text{male}} = \text{logistic}(k \cdot \frac{A}{P} + b) \quad (10)$$

With proper parameter taken, formula (10) can describes the sex ratio of newborn lampreys in statistic significance.

According to **Assumption 4**, it is easy to conduct a linear function to describe the linear relationship between predation rate and sex ratio as follows:

$$\begin{cases} \theta_{PA} = \alpha_1 \cdot \lambda + \beta_1 \\ \theta_{BP} = \alpha_2 \cdot \lambda + \beta_2 \end{cases} \quad (11)$$

where  $\alpha_1, \beta_1, \beta_2 > 0$  and  $\alpha_2 < 0$  are slops and intercepts of the linear relationships. This explains how sex ratio has impacts on the environment, and we will further discuss this in subsection 5.4.

Using equation (10) , we can take sex ratio  $\lambda$  as a variable in the Generalized Lotka-Volterra Model (7). And by calculation we can obtain the differentiation of the sex ratio  $\lambda$  as follows:

$$\begin{aligned}\lambda|_{t=t_0+\Delta t} &= \frac{\lambda|_{t=t_0} \cdot P + p_{\text{male}} \cdot \Delta P}{P + \Delta P} \\ \frac{d\lambda}{dt} &= \frac{(p_{\text{male}} - \lambda)}{P + \Delta P} \cdot \frac{dP'}{dt}\end{aligned}\quad (12)$$

Notably, the symbol  $\Delta P'$  above represents the new metamorphosed sea lampreys, namely the growth of lamprey population which is  $\delta_{PA}\theta_{PA}AP$ .

Combining equation (7), (12) and (11), we obtain the following model describing the population dynamics in the ecosystem with variable sex ratio taken into consideration:

$$\begin{cases} \frac{dA}{dt} = \gamma_A A \left(1 - \frac{A}{K_A}\right) - \theta_{BA} AB - \mu \theta_{PA} AP \\ \frac{dB}{dt} = \delta_{BA} \theta_{BA} AB + \delta_{BP} \theta_{BP} BP - \gamma_B B \\ \frac{dP}{dt} = \delta_{PA} \theta_{PA} AP - \theta_{PB} BP - \gamma_P P \\ \frac{d\lambda}{dt} = \left(\text{logistic}\left(k \cdot \frac{A}{P} + b\right) - \lambda\right) \cdot \delta_{PA} \theta_{PA} A \end{cases}\quad (13)$$

#### 4.4 Impact on Ecosystem: Model Simulation Results

In this subsection, we will discuss how environment determined sex ratio has impacts on environment by considering the dynamics of specific species in the ecosystem.

First, let's consider the influence of variable sex ratio on hypothetical species  $A$ . We assume that only the prey  $A$  and the sea lamprey  $P$  are involved and predator species  $B$  doesn't exist. Now we run the comparative trials using python.

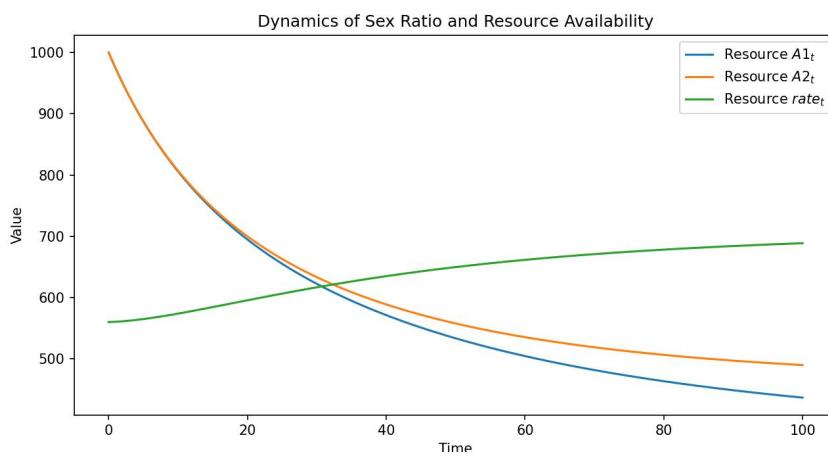
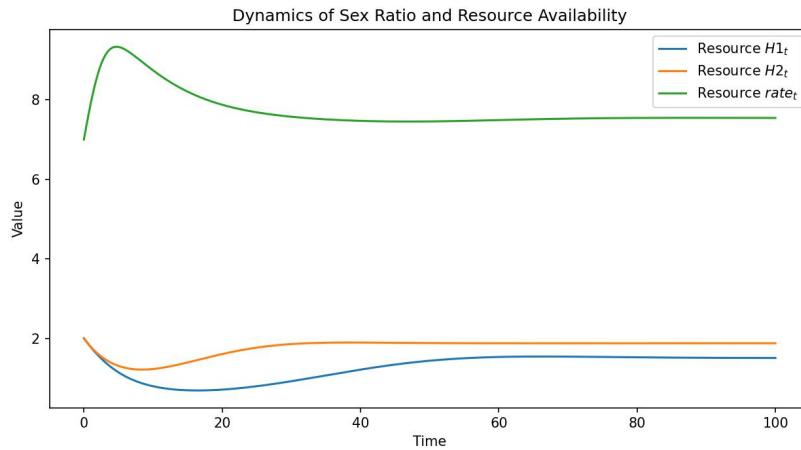


Figure 4: The Population dynamics of  $A$  with or without variable sex ratio

In Figure 4,  $A_1$  is the population of  $A$  without the consideration of variable sex ratio, and  $A_2$  is the population with variable sex ratio considered. Both two curves decrease at the beginning and

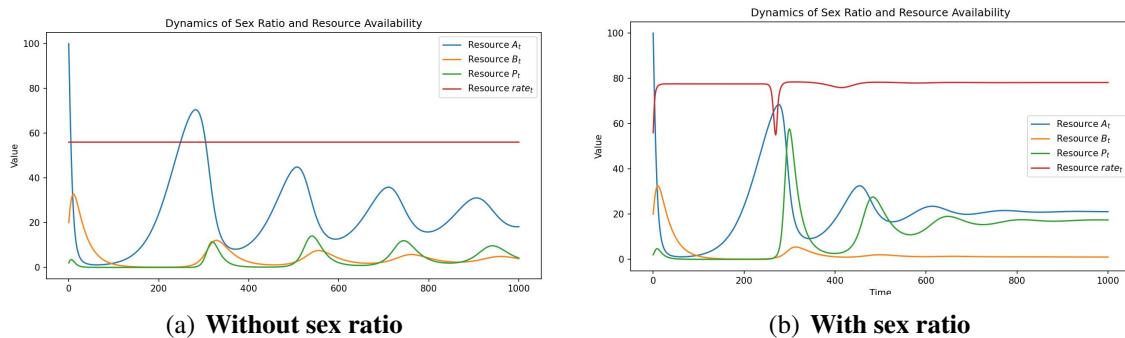
become stable in population afterwards. It can be observed that population of species  $A$  decrease much faster as the sex ratio of sea lamprey increase. From that we can conclude that variable sex ratio generally harm the growth of the prey  $A$ .

Now, we study the influence of variable sex ratio of hypothetical species  $B$  which is the predator of sea lamprey. Similarly, here we assume that population of  $A$  doesn't change overtime and do the comparative trials.



**Figure 5: The Population dynamics of  $B$  with or without variable sex ratio**

In Figure 5, the curve  $H_1$  represents the population change of species  $B$  in consideration of the sex ratio, and curve  $H_2$  is under the assumption of fixed sex ratio. It can be observed that the sex ratio of sea lampreys rockets up rapidly in 0s-5s and recovers to a stable region afterwards. The variable sex ratio made that population of  $B$  to decline at a larger scale, and the stationary point of the population is lowered.



**Figure 6: The Population dynamics of the propagation model**

Now we can take all three species  $A$ ,  $B$  and  $P$  into consideration, which means running a numerical experiment of the complete model given in equation (13).

Both Figure 6(a) and Figure 6(b) are set to the same parameters and the same initial values, but the dynamics are different. In Figure 6(a), the dynamics exhibits a special case of the Generalized

Lotka-Volterra Model, in which the population of all three species behave as vibration in the start and flatten out in the end of time. In Figure 6(b) with consideration of the variable sex ratio, the population of three species come to a stationary point same to the case in Figure 6(a).

The behavior and trend seems similar at first, but the difference in values at the equilibrium shows how exactly sex ratio influence on the ecosystem. With variable sex ratio, the population of predator  $B$  almost come to 0, which means it extincted. Compared to this, the population of  $P$  is much higher than the situation without variable sex ratio. We will further develop this discussion on Figure 6 in subsection 5.1.3 where we answer Problem 2 about the impacts of variable sex ratio on sea lampreys propagation.

In conclusion, this phenomenon shown in Figure 4, 5 and 6 indicates that variable sex ratio shapes the balance of the ecosystem in ways that benefits lampreys.

All detailed codes for these numerical experiments are available in Appendix A.

## 5 Problem 2: Two Approaches to Lampreys Propagation Model

In Section 4, we used the Generalized Lotka-Volterra Model to study the population dynamics in the food chain. In this Section, we will study how variable sex ratio has impact on the sea lampreys propagation.

### 5.1 First Approach: Differential Equation Model

#### 5.1.1 Sex Ratio's Influence on Fecundity

Now we are going to study how variable sex ratio has impacts to lampreys fecundity. To better accomplish this discussion, we will simplify the model to the Logistic Model 4.1 in Section 4.1 . Here we divide natural growth rate into two parts: natural birth rate and natural death rate. The former one is apparently positive proportional to the fecundity rate, since all lamprey eggs have the same possibility to hatch successfully.

$$\frac{dP}{dt} = r_P \cdot P \left(1 - \frac{P}{R_P}\right) - \mu \cdot P \quad (14)$$

Here we are going to discuss the relation between sex ratio and the natural birth rate  $r_P$ . Prior research has found valid relations between fecundity and sex ratio as a convex function in other species with Environment Determined Sex such as bradysia difformis and redband trout[12, 13], even species without Environment Determined Sex such as moose[14]. So we are confident enough to suppose that the same relationship exists for the sea lampreys.

To better model the effect of variable sex ratio on the propagation, we assume that the Carrying Capacity of sea lampreys is linearly related to its sex ratio. Also, the natural growth rate  $r$  should also be a convex function of sex ratio, since research has found that lamprey fecundity is maximum when the sex ratio is 0.5 . In order to fit this hypothetical convex function, a quadratic function will do.

$$R_P = k_1 \cdot \lambda + b_1 \quad (15)$$

$$r_P = -k_2 \cdot (\lambda - \lambda_0)^2 + b_2 \quad (16)$$

Where  $\lambda_0 = 0.5$ .

### 5.1.2 Simulation of Lampreys Propagation in Setting Environment

Now we are finally ready to study effects of resource availability on lampreys propagation. In Figure 7, we set the resource availability  $A_1, A_2$  to 500 and 20 respectively. Both  $P_1$  and  $P_2$  and the sex ratios rocket up in the start at first and flatten out in the end. It is worth noting that the red curve (i.e. the population  $P_2$ ) increase first but soon decrease to an rather low level. This behavior is common and it even happen without variable sex ratio, but the variable sex ratio help lampreys to come to a rather higher stationary point to avoid worse population loss. This can be varified in Subsection 5.1.3 when we take the whole ecosystem into consideration.

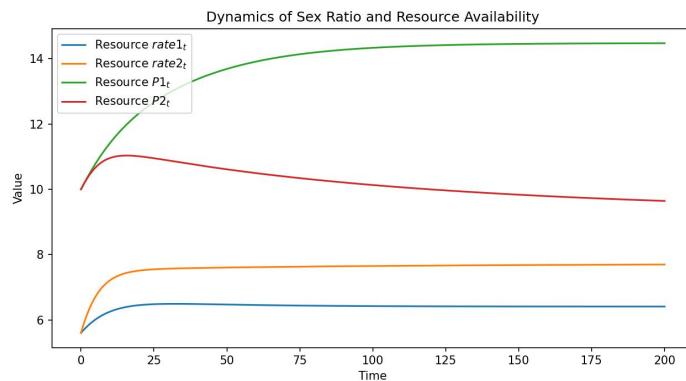


Figure 7: Fecundity and Resource Availability

And Figure 8 shows the behavior of sea lampreys when the Resource Availability varies in time. It can be observed that the sea lampreys population respond to environmental changes by changing their sex ratio. To be specific, when resource availability  $A$  in the Figure increase, the sex ratio of lampreys decrease (i.e. the proportion of male decline) as a react, and then the population leaps.

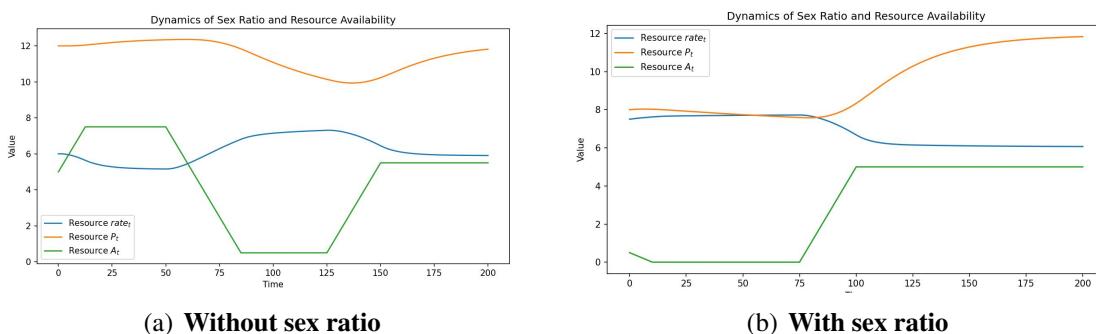


Figure 8: The Propagation Dynamics with Resource Availability Fluctuations

Detailed code is available in Appendix A.

### 5.1.3 Lampreys Propagation in the Ecosystem

In this subsection we continue the discussion about Figure 6 in Subsection 4.4 about the dynamics of population in the ecosystem involving the sea lampreys  $P$ , its prey  $A$  and its predator  $B$ .

Similar to the discussion about population of  $A$  and  $B$ , the dynamics of sea lampreys population in Figure 6 shows essential difference. At the point  $t = 200$ s, both the sea lampreys and the predators nearly extincted due to decrease of food  $A$ . But when the population recovers at  $t = 300$ s, in Figure 6(a) both  $B$  and  $P$  recovers to nearly the same value while in Figure 6(b) the population of the sea lampreys  $P$  rockets up at once and the predators  $B$  stay low in population. This is completely contributed by the variable sex ratio as discussed in Subsection 5.1.1 : Every time when the food abundance (i.e. relative value of  $A$ ) increase, the lampreys decrease their sex ratio to make better use of the food resources to reproduce. On the contrary, when food abundance decrease (mainly cause by the expansion of sea lampreys population) the sex ratio return to a higher value to lower demands in food.

As a result in the stationary point, the sea lampreys take a much better position in the ecosystem (i.e. a much larger quantity) while the number of the predators  $B$  converges to 0 in the end. From Figure 6, we can conclude that variable sex ratio change the ecosystem significantly, and sea lampreys consolidate its position and advantage in the ecosystem.

## 5.2 Introduction to Agent-Based Model and Lampreys Propagation

In previous part of the paper we use differential equation and its numerical solution to analyze the problem. By as the differential equation is continuous while lampreys propagation is a discrete process based on , and the strict assumptions made the model over-simplified to model to real situation. Moreover, adding more species to simulate the food network into the differential equation model will make the equation (13) which is already complicated a complete mess. That's why we are about to introduce the **Agent-Based Model**.

Agent-Based Modeling (ABM) is a computational model for simulating the behavior and interactions of autonomous agents (individuals or collective entities such as organizations or groups) in order to understand the behavior of a system as well as the factors that control its outcomes. It combines elements of emergence, game theory, evolutionary programming, multi-intelligent body systems, computational sociology and complex systems.[15].

Most agent-based models consist of : (1) a large number of agents specified at different scales (often referred to as agent granularity); (2) decision heuristics; (3) learning rules or adaptation processes; (4) interaction topologies; and (5) environments. Agent-based modeling has been used in a wide range of biological applications, including population dynamics, analysis of the spread of epidemics, and threats of biological warfare, to name a few.

In this study involving sea lampreys propagation, Agent-Based Model provides a powerful tool for modeling the behavior of individual organisms. Particularly, we use the *mesa* package for python to accomplish the simulation tasks.

### 5.3 Second Approach: Agent-Based Model

#### 5.3.1 Preparation: Comparison between ABM and Differential Equation Model

**similarities:**

- I. *Equations:* Two models both calculate the Male ratio of newborn individuals by equation (10). So our values for  $k$  and  $b$  in ABM are consistent with the model in Problem 1, and we need the value of A and P as well. For Fecundity, equation (16) remains feasible and we keep the values of  $k_2$  and  $b_2$  still.
- II. *Parameters:* Let's go back to equation (13), which used logistic model to simulate the population dynamics in the ecosystem. When we consider a individual of lampreys or their preys (A),  $\gamma_A$ ,  $K_A$  and  $\delta_{PA}$  remain the same.

**distinctions:**

- I. *Data Type:* Differential equation modelling of time is a continuous variable whereas in ABM time is a discrete variable, which means we can't get a smooth curve through ABM.
- II. *Stochasticity:* In ABM, There are a lot of calculations related to probability. So the result we get when we run the ABM model every time will be different, but the general trend of the data is the same.
- III. *Dominance:* Actually, compared to the differential equation model, we reduce a lot of parameters and instead simulate it with the behaviour in ABM. So adding more species to the analysis becomes workable. What's more, we don't need to calculate the differential equation of sex ratio because we can apply equation (10) directly to newborns.

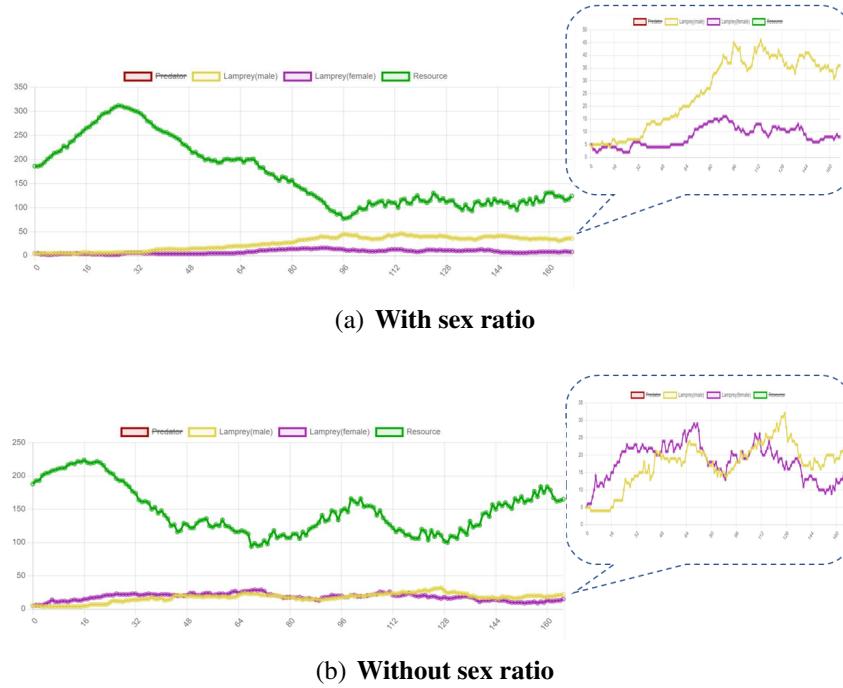
#### 5.3.2 Construction of Lamprey Reproduction Model and Simulation Results

Now we are prepared to build the model for sea lampreys propagation with the Agent-Based Model. This improved lamprey propagation model use two agents: lampreys and resources. Inspired by the Wolf-Sheep-Grass trisomy problem[15, 16, 17], we assume that resources are static as "Grass" and lampreys are dynamic as "Sheep" ("Wolf" will be discussed in Section 6). The model consists of grids, each representing an ecological niche.

**Resource:** On each grid, resources are fixed and categorized into sufficient and depleted states. A depleted resource has a certain natural recovery rate to become sufficient again. This probability corresponds to the natural growth rate of the resource in the previous differential equation.

**lamprey:** Lamprey carries a certain amount of energy and consumes it at a fixed rate each cycle. our behavioral patterns exist for the lamprey: 1. *Random wandering:* the lamprey moves randomly around the grid each cycle; 2. *Reproduction:* the lamprey "splits" with a certain probability each cycle. This probability is affected by the reproduction equation in the previous section. The sex of a newborn lamprey is governed by the sex formula in the previous section; 3. *Natural death:* when a lamprey runs out of energy, it dies; 4. *Feeding:* when a lamprey wanders onto a well-resourced

grid, it consumes the resources on that grid to increase the energy in its body. The resources then shift to a depleted state.



**Figure 9: The Population dynamics by ABM**

In Figure 9(a), we can see that the resource availability increase for a short time before it start to decline at time  $t = 30$ . And after time  $t = 96$  the resource availability generally remain stable. The explanation for this behavior is quite the same as in Subsection 4.4. On the contrary in Figure 9(b) where sex ratio is fixed, the resource availability go through fluctuation all the time, and the total population is relatively lower then the situation in Figure 9(a).

In conclusion, the results that Figure 9 give confirm the discussion in 5.1.1. This verifies that the two models we give are equally valid in simulating the sea lampreys propagation.

## 6 Problem 3 & 4: Agent-Based Multiple Ecosystem Model

### 6.1 Construction of Lamprey-Centered Food Web

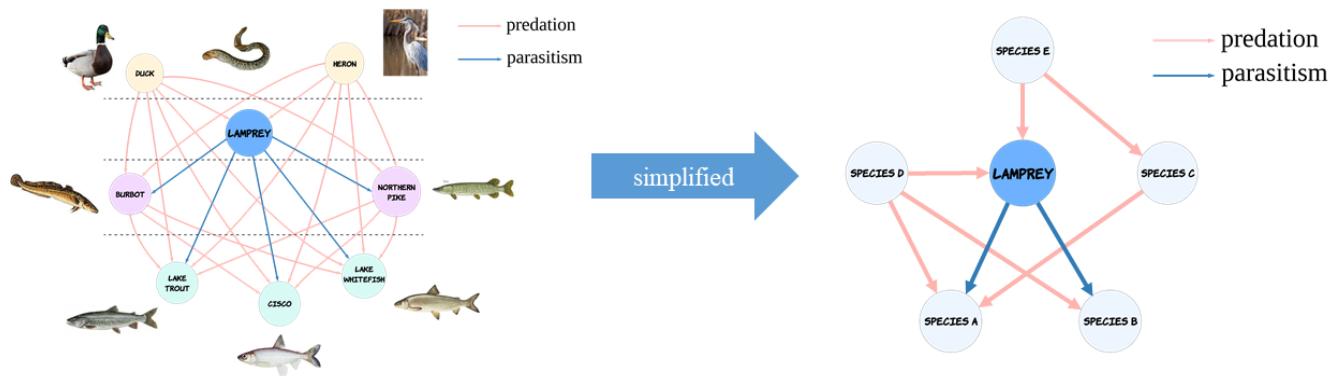


Figure 10: The Food Network in the Great Lakes

To study the ecological niche of the lamprey in the Great Lakes basin, we selected several representative organisms to form the food web shown in Figure. Lake whitefish, lake trout and ciscoes are important species in commercial inland fisheries in the Great Lakes basin. Lampreys are one of the major threats to their survival. Lampreys also parasitize burbot and northern pike, which feed on lake whitefish, lake trout and ciscoes. However, the lampreys have its natural enemies: herons and ducks. While preying on lampreys, both of them also prey on all of the fish mentioned above. These species are widely distributed in the Great Lakes Basin and play an important role in the survival of the lampreys.

### 6.2 Problem 3: Impacts of Sex Ratio Changes on Ecosystem Stability and Biodiversity

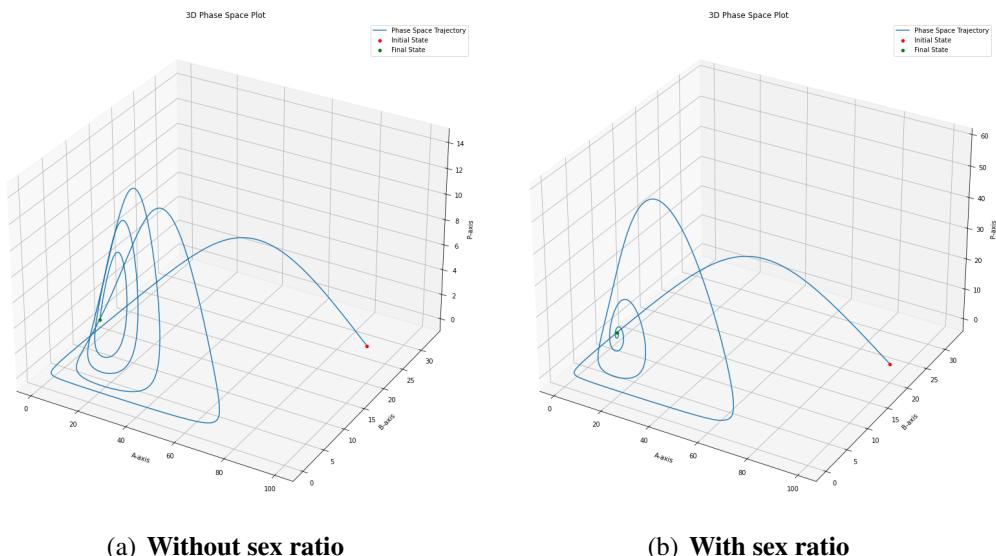


Figure 11: Phase graph of equation (7) and (13)

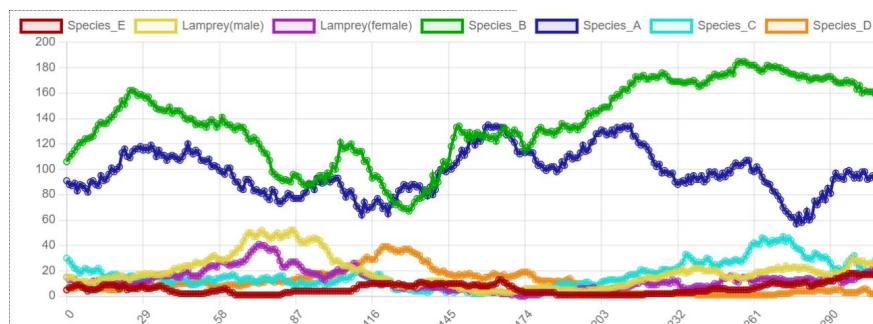
Figure 11 is a phase graph to demonstrate the dynamics in the perspective of fluctuations and stationary points. A phase graph is a visual representation used in dynamical systems theory to depict the behavior and relationships between variables over time. It typically displays the system's state variables on orthogonal axes, illustrating how their values change and evolve, aiding in analyzing system dynamics and stability.

We can observe that there are much less rotations in Figure 11(b) compared to Figure 11(a). This is because the variable sex ratio enables sea lamprey to better adapt the environment, which show as less fluctuations and therefore less rotations in the Figure.

By using the phase graph, we no longer focus too much in the stationary point of the system. Instead we are interested in how the system evolves to the stationary point. With the variable sex ratio, sea lampreys change not only the equilibrium of the ecosystem but also the speed it evolves. In conclusion, as an answer to the Problem, sea lampreys with variable sex ratio make the ecosystem more *stable*.

When considering multiple species in the ecosystem, we first add predators to the model. Predators that feed on lampreys correspond to "wolves". Its behavioral pattern of random wandering and natural death is not dissimilar to that of a lamprey. In its reproductive behavior, its newborns have a fixed sex ratio of 1:1. and its feeding behavior will kill lampreys on the grid where it is located to replenish energy.

We have made some optimizations to the agents of our team lampreys. In the previous model, we considered the lamprey as a consumer. Now we consider its properties as a parasitic organism. Lampreys are categorized into two states: **unparasitized** and **parasitized**. 1. Unparasitized: unparasitized lampreys perform random wandering. If there are sufficient resources on the arriving grid, there are two cases: A. The resource is not parasitized, at this point the lamprey will parasitize this resource and enter the already parasitized state. b. The resource is parasitized, at this point the resource will be consumed due to an overabundance of lampreys. Here the resource goes to the depleted state and the lampreys all go to the unparasitized state. Unparasitized lampreys will keep consuming energy and die when they run out of energy. 2. Parasitized: Parasitized lampreys will be fixed on the resources in the current grid, and will not move around. It gains energy steadily and does not consume resources. Parasitized or not, it does not affect the predation and reproduction behavior of the lamprey. Now we use our Agent-Based Model to further develop this point.



(a) **Without sex ratio**

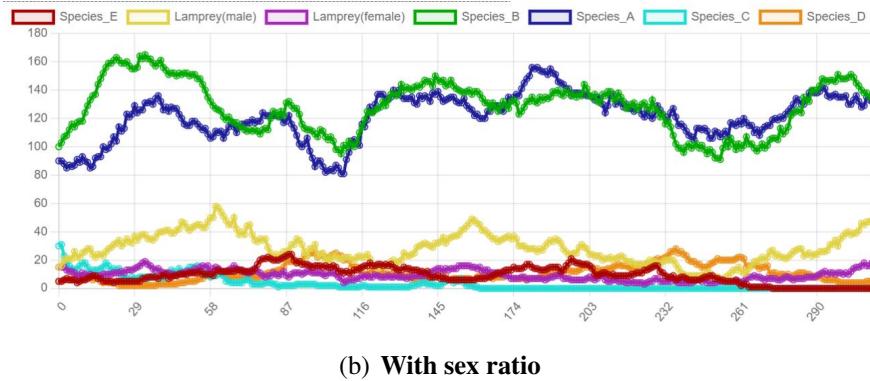
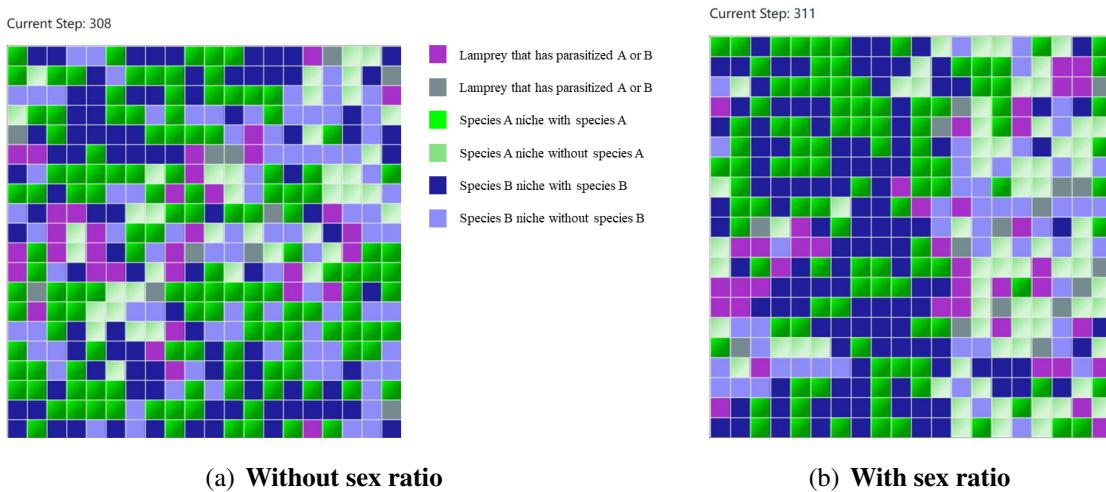


Figure 12: Dynamics simulation by Agent-Based Model



**Figure 13: Grid of Agent-Based Model**

Figure 12 shows the population dynamics simulated by the Agent-Based Model. And Figure 13 is a demonstration of the girds of operating ABM where you can directly see the species who take advantages and disadvantages respectively.

In Figure 12(b) and 13(b), it's obvious that species *C* and species *E* went extinct. The logic behind this is simple: species *C*, species *D* and the sea lampreys are in competition relationship. Due to sea lampreys' strong ability to adapt the environment and consolidate advantages in ecosystem, species *C* finally died out from competition. Species *E* and species *C* are in competition relationship, but after *C* died out, *E* had lampreys as the only food while *D* had plenty other food to eat. Finally species *E* also died out.

This discussion reveals the important fact that sea lampreys can damage the Biodiversity severely, and therefore is a so-called Environment Spoiler.

### 6.3 Problem 4: Species Benefiting from the Sexual Identity of Lampreys

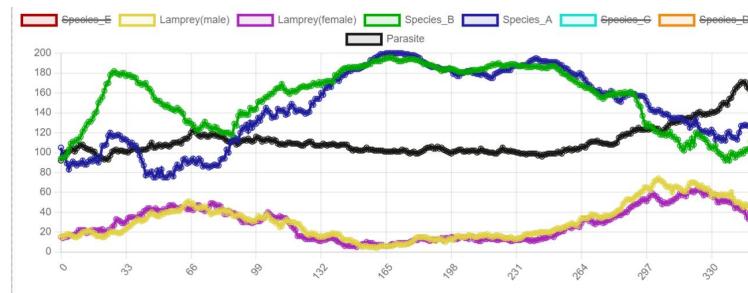
#### 6.3.1 Species in Multiple Ecosystem

Follows by the discussion in 6.2, we can find that the one who can benefits from the sea lampreys in species *A*, and this is obviously according to Figure 12. Because species *C* who prey on species *A* dies out, species *A* get much advantages in the system.

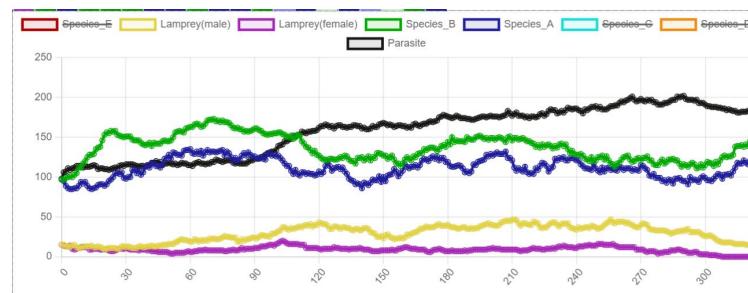
Nevertheless, species *D* is also benefiting from the sea lampreys invasion. Though the Figure didn't show that, the extinction of species *C* and *E* made *D* the top in the food network and therefore it can survive on lampreys and species *A*, *B* for long period afterwards.

#### 6.3.2 Parasite Spreading in the Ecosystem

But the predators and preys are not the only members in the ecosystem that take advantage of the sea lampreys invasion, parasite is another species that take great advantage of the sea lampreys invasion. According to hypothesis 5, we set the parasite to be initially present only in species *A*, species *B*, and lampreys. Here we use a Agent-Based Model to simulate it.



(a) Without sex ratio



(b) With sex ratio

Figure 14: The Propagation Dynamics with Resource Availability Fluctuations

We observe that parasite population in Figure 14(a) is much more then that in Figure 14(b). This is also an effect through interaction between multiple species: variable sex ratio enable lampreys to continue to survive rather than going through a large fluctuation in population as in 14(b). And the surviving lampreys help the parasites to infect other species through parasitism. While sea lampreys can stablize the ecosystem as we have proved it in Section 6.2, it make the parasites continues to spread among the food network.

## 7 Sensitivity Analysis

In this subsection we are going to discuss the sensitivity and robustness of the differential equation model by using numerical simulation.

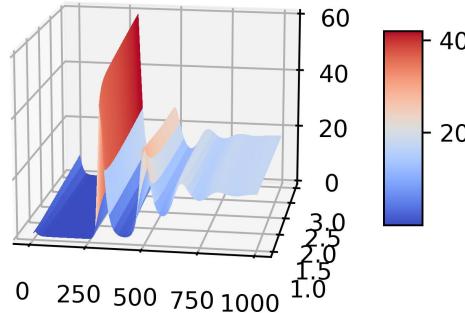


Figure 15: **Responds of Sea Lampreys Population to small initial value disturbance**

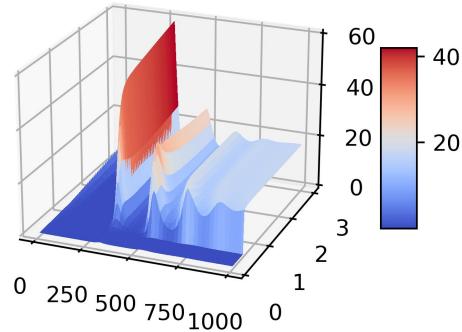


Figure 16: **Responds of Sea Lampreys Population to larger initial value disturbance**

Both Figure 15 and Figure 16 are obtained by model (13) and has the same parameters and initial values as Figure 6. Now we are going to change the initial values to see the influence on the curve.

In Figure 15 where we change  $P|_{t=0}$  in  $[1, 3]$ , it can be observed that the dynamics of sea lampreys population are very similar. But in Figure 16 where we change  $P|_{t=0}$  in  $[0, 3]$ , it can be observed that there is a sharp drop of population around the point  $p|_{t=0} = 0.5$ , and the population of sea lampreys converges to zero in the region  $p|_{t=0} < 0.5$ .

So in conclusion, this model is stable to small disturbance in initial value in certain , but may face remarkable changes when the disturbance is relatively large. This is mainly because the population in the system converges to different stationary point in different regions of initial value.

## 8 Model Evaluation and Possible Improvements

### 8.1 Strengths

- I. *Our model is rigorous and thorough in its consideration of the correlation between sex ratio and environmental resource feasibility:* 1. Our model is rigorous and thorough in its consid-

- eration of the correlation between sex ratio and environmental resource feasibility.
2. We distributed the amount of growth influenced by the environment equally to all individuals in our model. This is a reasonable and well-considered approach.
- II. *We consider rigor in the constructing process of our Differential Equation Model:* 1. Our calculations on sex ratio are based on the sex ratio of newborns. These differential equations are the result of our rigorous derivation and reflect well the changes in the sex ratio due to various factors.  
2. We are thoughtful about the parameters in the differential equation. For example, we consider the effects of human predation on lampreys, which are independent of the food web composed of animals. In addition, we considered the effect of parasites on the mortality of their hosts.
- III. *Our ABM model is rigorously thoughtful:* 1. The idea of energy transfer is added to our model as a way to realize the flow of energy between lampreys, hosts and predators.  
2. Differential equations are usually more complex when analyzing competitive relationships between species because it involves many covariates. But ABM model can be competent in this aspect.  
3. Our method of considering the proportion of newborns fits well into the ABM model, and the previous differential equations are useful here.  
4. In Section 6 we consider very complex biological food webs and obtain good fitting results accordingly, which shows that our model is reliable and can be applied to complex situations.

## 8.2 Weaknesses

- I. The underlying differential equations are over-parameterized, which makes it easy to over-fit them in the process of adjusting the parameters, and the simulation results may not be completely realistic. Meanwhile, adding species will bring huge workload.
- II. Our research on biodiversity is less than ideal. We did not analyze what happens to the model when more species are introduced. Therefore, it is difficult for us to calculate the covariates such as SW or ICV about biodiversity and analyze it.
- III. We did not consider the effect of accelerated host death by the parasite. We did not collect enough data or literature to support an analysis on this issue.

## 8.3 Possible Improvements

- I. More impacts on the availability of environmental resources can be introduced into the model, e.g. lampreys have migratory breeding habits and they have fixed breeding areas. Breeding areas can be delineated in the ABM grid to influence the breeding behavior of lampreys.

II. Our model can take into account the effects of weather, water quality and other factors on lampreys. This requires reviewing more literature and learning more about the relevant studies.

III. We can add more species to the model to form more complex food webs, while better distributing the covariates to obtain more realistic results.

## 9 Conclusion

Our paper provides a detailed analysis of how the variable sex ratio cast influence to the entire ecosystem through interactions among multiple species using three models: **Basic Environmental Model based on Differential Equatio**, **Lampreys Propagation Model** and finally the **Agent-Based Multiple Ecosystem Model**. We utilize numerical experiments for both two models to simulate various situation on single species, multiple species, including consideration of environmental fluctuations and the parasites. Our results agree with prior researches and common sense very well.

By both theoretical and experimental approaches using all three models, we conclude that variable sex ratio enables sea lampreys with strong ability to adapt and survive the environment. As for analysis to the ecosystem, our research found that the sea lampreys increase the stability of the environment and severely damage the biodiversity of the ecosystem. Our study found that several species including parasites and some other species in the ecosystem benefits from the sea lampreys invasion through complex relation between multiple species of different niche.

In conclusion, the sea lampreys are flexible adaptor and environmental spoilers.

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# Appendices

## Appendix A Simulation Codes

The Agent-Based Model codes and all other detailed codes are available here:

<https://github.com/jkxyw/ABM-model-codes-for-MSM-team-2403084>.

## **Report on Use of AI**

### **1. Bing AI**

Query1: I am writing a paer about the population dynamics of the sea lampreys in consideration of sex ratio. To simulate individual behavior, wo use the Cellular Autometa. Please Write an introduction of Cellular Autometa, on what is it, how can it be used in this problem and usual approach to realize it.

Output: Introduction to Cellular Automata:

Cellular Automata (CA) is a computational model used to simulate complex systems composed of simple, interacting components. It operates on a grid of cells, where each cell can exist in a finite number of states. The state of each cell evolves over discrete time steps based on a set of rules that define how cells interact with their neighbors.

In the context of studying population dynamics, CA provides a powerful tool for modeling the behavior of individual organisms within a population and understanding emergent phenomena at the population level. This approach is particularly valuable when studying species like sea lampreys, where individual behavior and interactions play a significant role in shaping population dynamics.

In our study of sea lamprey population dynamics considering sex ratio, CA allows us to model the behavior of individual lampreys within a spatially explicit environment. By assigning different states to cells based on the sex and reproductive status of lampreys, we can simulate various scenarios and observe how changes in sex ratio affect population dynamics over time.

The usual approach to realizing a CA involves defining the following components:

**Grid:** A regular grid of cells representing the spatial environment where the population resides. Each cell can be in one of several discrete states.

**Neighborhood:** A neighborhood defines the set of neighboring cells considered when updating the state of a given cell. Common neighborhood configurations include Moore and von Neumann neighborhoods, where cells are arranged in a square or a cross-shaped pattern, respectively.

**Rules:** Rules determine how the state of each cell evolves over time based on the states of its neighboring cells. These rules typically involve conditional statements that specify transitions between states based on predefined criteria.

**Initialization:** The initial state of the grid is defined based on the specific scenario being modeled. This may involve randomly assigning states to cells or setting up specific initial conditions to represent realistic starting conditions.

**Iteration:** The CA evolves over discrete time steps, with the state of each cell being updated simultaneously based on the defined rules and the states of neighboring cells.

By iteratively applying these components, we can simulate the spatiotemporal dynamics of sea lamprey populations and analyze the effects of varying sex ratios on population growth, distribution, and other relevant metrics. This approach enables us to gain insights into the underlying mechanisms driving population dynamics and inform management strategies for conservation and control efforts.