Problem Chosen	2024	Team Control Number
A	MCM/ICM Summary Sheet	2401132

Altering the Sex Ratio: Survival Widsom for Lampreys

Summary

Lampreys are peculiar creatures that have changing sex ratios. In food-rich environments, lamprey populations exhibit approximately 78% males, decreasing in more resource-scarce settings. In this paper, we present *a model describing the migration of lampreys between environments with different food abundance* and *models describing the effects of lampreys on hosts, and predict lamprey survival by varying the sex ratio in the models*. Our model explains well why lampreys have evolved variable sex ratios. We further modelled the relationship between lamprey sex ratios and the larger ecosystem, and analysed the effects of lamprey sex ratios on ecosystem stability and on other species.

In TASK 1, we established the logical chain of sex ratio affecting the ecosystem indirectly, through the growth of its parasitic juvenile density. We developed a model based on the population growth, survival and metamorphosis rate of lamprey, and the number of lamprey attacks and survival rate of the host species, calculating the effect of sex ratio toward the relative mortality of hosts in the ecosystem.

In TASK 2, we built a hypothetical environment consisting a resource-rich lake and a resource-poor lake adjacent to each other. Lampreys can migrate between the two environments with a certain probability. By setting different sex ratios at birth in the two environments, we found that the sex ratio of the most adapted environment corresponded to the actual situation. Models reflected the different impact of sex ratio on the lamprey population under different resource conditions, by the growth rate of the respective males and females in the two environments. We further analysed the model and proposed a hypothesis to explain the evolution of the lamprey's ability to alter sex ratios.

In TASK 3, based on the relationship between sex ratio and the relative mortality of hosts in the ecosystem obtained in Task 1, we built an index of species diversity by combining species richness and species evenness, and reflected the effect of sex on the stability of the ecosystem through the effect of sex on species diversity.

In TASK 4, we utilised normal distribution estimates, and calculated the 95% confidence interval for the probability of parasite infestation. Subsequently, we distinguished between lamprey susceptible and non-susceptible parasite species. Further, we identified parasitic species that can take advantage from variable sex ratios in the lamprey population.

Finally, we performed sensitivity analyses on some key variables in the model to get a deeper understanding of the model and discuss the conclusions. We further provide the strengths and weaknesses of the model for future studies.

Keywords: Ecosystem, Resource Availability, Differential Equation

Contents

1 Introduction

1.1 Background

Lampreys are a type of fish with a complex role. Viewed as parasites that have a notable effect on the ecosystem in certain lake habitats, while in other parts of the world, considered a source of food for people.

The life cycle of lampreys (shown in Fig.1) can be divided into three distinct stages: *larva, parasitic juvenile, and adult*[1]. Each stage occupies a different ecological niche and impacts the environment differently.

- **Larval Stage**: During the larval stage, lampreys are buried in sediment and filter feed on microorganisms and detritus. At this stage, lampreys serve as food sources for fish, birds, and small mammals.
- **Parasitic Juvenile Stage**: At this stage, lampreys serve as parasites, attaching to and feeding on the blood and tissue of fish. After migrating to the open areas of the lake, they perform attacks on their potential hosts and suck on them until their deaths, resulting in dramatic reductions in populations of host species.
- **Adult Stage**: This is when lampreys stop feeding and move up rivers to spawn. Adults play little direct role in predation or as food sources due to their short lifespan.

The sex ratio of sea lampreys can vary based on external circumstances. Shifts toward male-dominated populations in low-resource environments may affect reproductive rates and the species' role in the food web and nutrient cycle. Examining these aspects can shed light on the delicate balance lampreys maintain within their ecosystems and the broader implications of their adaptive capacities.

While the sex ratios of lampreys are not expected to impact ecosystems directly, understanding the effects of sex ratio variations on lamprey populations and their ecological impact remains a vital area of investigation. A mathematical model can provide valuable insights into these interactions and the long-term sustainability of ecosystems featuring such adaptive organisms.

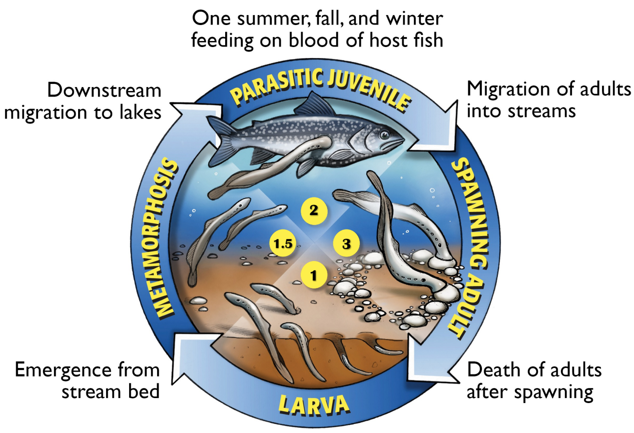

Figure 1: **The lamprey life cycle** [1]
Larval: stage 1, *Juvenile*: stage 2, *Adult*: stage 3

1.2 Our work

1. We established a logical chain linking sex ratio to ecosystem impact via parasitic juvenile density. Our model incorporates lamprey population dynamics, host mortality, and ecosystem stability.

2. Creating a hypothetical environment with resource-rich and resource-poor lakes, we explored sex ratio effects on lamprey populations in varied resource conditions.

3. Building on Task 1's findings on sex ratio and host mortality, we developed a species diversity index, considering richness and evenness, reflecting sex's impact on ecosystem stability.

4. Utilizing normal distribution estimates, we calculated the 95% confidence interval for the probability of parasite infestation. Furthermore, we identified parasitic species significantly influenced by the lamprey.

2 Preparation of the Models

2.1 Assumptions and Justifications

- Since our problem is to analyse the impact of sea lamprey arbitrarily altering its sex ratio, it is unnecessary to consider the feedback given by the environment.
- We ignore the effects of external perturbations to large ecosystems, including pollution, invasive alien species, etc.
- We ignore the effects of species genetic diversity. We assume that there are no significant trait differences between offspring and parents in the same environment.
- Based on the different ecological niches of the lamprey in different life stages, the larval and adult lampreys are a food source for other species, and only during the parasitic juvenile period do they act as parasites.

2.2 Notations

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

Table 1: Notations

Symbol	Definition
sex	sex ratio of the lamprey population
$\%M$	male percentage of the lamprey population
N^{larval}	population density of larval lampreys
$N^{juvenile}$	the population density of juvenile lampreys
D^{larval}	the duration of larval period in years
$D^{juvenile}$	the duration of juvenile period in years
P_y	the probability that a larva born y years ago had survived to the present time
B	the number of larvae born each year
R_y	the probability that a larva born y years has metamorphosed,

Table 1 – continued from previous page

Symbol	Definition
	and survived on or before this year
S^{larval}	the survival rate of the juvenile lamprey per year
m_i	the probability of larvae metamorphosing into juvenile in year i
A_i	the number of lamprey attacks to host species i each year
$P_{s,i}$	the possibility of host species i surviving each attack
M_i	host death caused by lamprey per year

3 TASK 1: Impact on the Ecological System

3.1 Model Construction

Without considering the effect of sex ratio on genetic diversity, the effect of arbitrary sex ratio changes in lampreys is mainly reflected in the reproductive capacity of the species. It was shown that the sex ratio of lampreys at spawning and the population density of larval lampreys after spawning were significantly correlated[2]. Thus, lamprey populations can regulate their population density by adjusting their sex ratio.

It is clear that when the lamprey population is able to change its sex ratio, it has an indirect effect on the ecosystem mainly through changes in population density. Based on the information about the ecological niche of lamprey in a large ecosystem, in the following, we mainly study the effect of lamprey on the population density of other fish in the ecosystem when it occupies the ecological niche of a parasite.

The model structure corresponding to Task 1 is shown in **Fig.2**. We refer to the fish parasitized by lampreys as hosts. It is easy to obtain that *the mortality rate of the host due to lamprey parasitism* affects *the population density of the host*, which is the product of *the probability of being attacked by a lamprey* and *the probability of the host dying in this attack*.

- Regrardless of the variability in the effectiveness of different host immune systems against lampreys, *the probability of the host dying in this attack* is related to *the weight ratio of the juvenile lamprey to the host*. (This is easy to understand; after all, for the same species, greater body weight indicates higher nutrient stores and greater resistance to sustained bloodsucking by the lamprey.)
- *The probability of a host being attacked by a lamprey* is related to *the population density ratio of juvenile lampreys to hosts*.
- *Population density of juvenile lampreys* is related to *population density of larval lampreys*, which is related to *the sex ratio of lampreys*.

3.2 Algorithm

3.2.1 Inference from sex to $N^{juvenile}$

- sex **to** N^{larval}

Based on previous studies, the proportion of lamprey males is significantly related to larval density[2]. We fitted the percentage of males in lampreys to the population

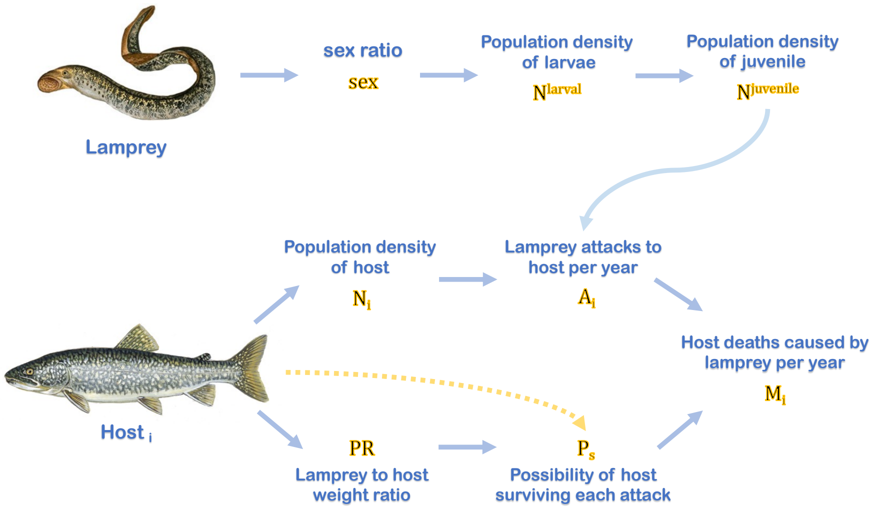

Figure 2: The structure of **Model 1**

density of juvenile lampreys with a quadratic polynomial as follows:

$$N^{larval} = -0.0000965 \times \%M^2 + 0.0154956 \times \%M - 0.3658665 \quad (1)$$

where N^{larval} is the population density of larval lampreys and $\%M$ is the proportion of males.

The relationship between the proportion of males and sex ratio is: $sex = \frac{\%M}{1-\%M}$. Then the functional equation between N^{larval} and sex can be obtained as:

$$N^{larval} = -0.0000965 \left(\frac{sex}{1+sex}\right)^2 + 0.0154956\frac{sex}{1+sex} - 0.3658665 \quad (2)$$

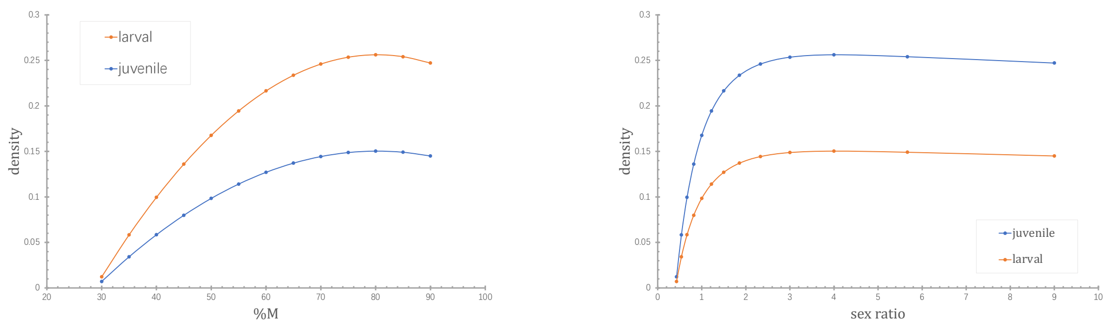

Figure 3: The curves of larval and juvenile density fitting with %M and sex ratio

- N^{larval} **to** $N^{juvenile}$

To find the relationship between the population density of parasitic juveniles ($N^{juvenile}$) and the population density of larvae (N^{larval}), we need to solve for the number of larvae born per unit volume per year of larvae (B).

Our model assumes that the environment is in steady state, the number of larvae born per unit volume per year B is constant, and the survival rate of larvae per year is constant at $S^{larval} = 0.627$.

Based on data from Minnesota DNR on the life cycle of lamprey in the Great Lakes[3], we took the larval stage duration $D^{larval} = 4$ years, during which time the larva undergoes metamorphosis and steps into the juvenile period. Juvenile period duration $D^{juvenile} = 2$ years, and adult period duration is negligible, so that the maximum lifespan of the fish is $D^{juvenile} + D^{larval} = 6$ years.

Then N^{larval} is related to B by the equation:

$$\begin{aligned} N^{larval} &= \sum_{y=0}^{D^{larval}} P_y B \\ &= \left[\sum_{y=0}^{D^{larval}} P_y \right] B \end{aligned} \tag{3}$$

where N^{larval} is the number of larvae per unit volume at the current moment, $D^{larval} = 4$ years is the duration of the larval period in years, P_y is the probability that a larva born y years ago has survived to the present time and has not metamorphosed, B is the number of larvae born each year (unknown, we have to solve for B)

P_y is obtained from Eq.4. To simplify the model, we assume that a larva born 5 or more years ago ($y \in (N^{larval}, \infty)$) is assumed to be either dead or adult. When y=0, mortality rate, metamorphosis rate are not considered, $P_y = 1$.

$$P_y = \prod_{i=1}^{y} S^{larval}(1 - m_i) \tag{4}$$

where $S^{larval} = 0.627$[4] is the survival rate of juvenile lamprey per year, m_i is the probability of larvae metamorphosing into juveniles in year i.

m_i is calculated using the logistic regression model with the following formula[5]:

$$m_i = \frac{exp[\beta_0 + \beta_1(\bar{l} + \Delta l_i)]}{1.0 + exp[\beta_0 + \beta_1(\bar{l} + \Delta l_i)]} \tag{5}$$

where β_0 and β_1 are parameters characterising the length at which metamorphosis occurs[4], $\bar{l}$ is the midpoint of the length interval of the fish (we use the mean/median length instead, see below for the formula), Δl_i is the expected amount of length change in fish i years ago.

Δl_i is calculated as follows. Based on existing studies in the Great Lakes, our model makes $L_\infty = 159mm$, $d = 0.515years(188days)$, and $\bar{l} = L_\infty/2 = 79.5mm$[4].

$$\Delta l_i = (L_\infty - \bar{l})[1.0 - exp(-i \times d)] \tag{6}$$

B can be calculated by bringing the calculated P_y and the N^{larval} calculated in the previous subsection into the equation at the top:

$$B = \frac{N^{larval}}{\sum_{y=0}^{D^{larval}} P_y} \tag{7}$$

Then the population density of parasitic juveniles this year, $N^{juvenile}$, is equal to the probability of B times these larvae surviving and metamorphosing over the lamprey's lifespan time horizon (6 years), i.e.:

$$N^{juvenile} = \sum_{y=1}^{D^{juvenile}+D^{larval}} R_y B \tag{8}$$

where R_y is the probability that a larva born y years ago has metamorphosed, and survives on or before this year.

- **Calculation of R_y**

If a larva has not metamorphosed after more than 4 years, we consider it dead. Below we calculate the typical value of R_y to demonstrate the computation idea of this variable.

A larva born this year will not metamorphose, so R_0 = 0.

The probability that a larva born 1 year ago became a juvenile this year is equal to the probability that: the larva survives for a year and metamorphoses:

$$R_1 = S^{larval} m_1 \tag{9}$$

The probability that a larva born 2 years ago became a juvenile and is alive this year, is equal to the probability that: the larva was born a juvenile (with probability of 0) + the larva survived for 1 year and then metamorphosed + the larvae survived for 2 years and metamorphoses this year.

$$\begin{aligned} R_2 &= S^{larval} m_1 \\ &+ S^{larval}(1 - m_1) \times S^{larval} m_2 \end{aligned} \tag{10}$$

The probability that a larva born 5 years ago became a juvenile and is alive this year, is equal to the probability that: the larva was born a juvenile (with probability of 0) + the larva survived for 1 year and then metamorphosed (but dies after living 2 years) + the larva survived for 2 year and then metamorphosed (but dies after living 2 years) + the larva survived for 3 year and then metamorphosed + the larvae survived for 4 years and then metamorphosed.

$$\begin{aligned} R_5 &= S^{larval}(1 - m_1) \times S^{larval}(1 - m_2) \times S^{larval} m_3 \\ &+ S^{larval}(1 - m_1) \times S^{larval}(1 - m_2) \times S^{larval}(1 - m_3) \times S^{larval} m_4 \end{aligned} \tag{11}$$

The probability that a larva born 6 years ago became a juvenile and is alive this year, is equal to the probability that: the larva was born a juvenile (with probability of 0) + the larva survived for 1 year and then metamorphosed (but dies after living 2 years) + the larva survived for 2 year and then metamorphosed (but dies after living 2 years) + the larva survived for 3 year and then metamorphosed (but dies after living 2 years) + the larvae survived for 4 years metamorphosed.

$$R_6 = S^{larval}(1 - m_1) \times S^{larval}(1 - m_2) \times S^{larval}(1 - m_3) \times S^{larval} m_4 \tag{12}$$

Then the above equations can be boiled down to:

$$\begin{aligned} & R_y = \sum_{i=max(y-D^{juvenile},0)}^{min(y,D^{larval})} P_{i-1} S^{larval} m_i \\ & where: \\ & \quad P_0 = 1 \\ & \quad y = 1, 2 \ldots (D^{larval} + D^{juvenile}) \end{aligned} \tag{13}$$

- **Summary of the calculation process**

The Inference from sex to $N^{juvenile}$ can break down into the following steps:

- calculate N^{larval} by substituting sex into Eq.2.
- calculate B by substituting N^{larval} into Eq.3.
- calculate $N^{juvenile}$ by substituting B into Eq.8.

The effect of the lamprey population on the ecosystem can then be deduced from $N^{juvenile}$.

3.2.2 Inference from $N^{juvenile}$ to the effects on the ecosystem

The parasitism of species by lampreys as parasitic juveniles causes a dramatic decrease in the population density of some host species and a weaker effect on the population density of other host species.

To measure differences in the extent of impacts of lamprey on population densities of different species in the ecosystem, we calculated host death caused by lamprey per year (M_i) based on the following formula:

$$M_i = (1 - P_{s,i})A_i \tag{14}$$

where $P_{s,i}$ is the possibility of host species i surviving each attack, A_i is number of lamprey attacks to host species i per year.

To calculate $P_{s,i}$, the weight ratio of lamprey to host (PR) is the key component of the formulae, for the more nutrient is stored by host species i, the likelier they are to host species i, and the more nutrients they are to host species i. The weight ratio of lamprey to host (PR) is the key component of the formulae, for the more nutrient is stored by host species i , the likelier they are to survive an attack.

$$P_{s,i} = 1 - \frac{PR_i^2}{1 + PR_i^2} \tag{15}$$

As for A_i, it can be calculated by the following formula:

$$A_i = \frac{a_i L}{N_i} \tag{16}$$

where a_i: number of attacks by parasitic organisms on host species i, $L = N^{juvenile}$: density of parasi lamprey, N_i: density of the ith host. a_i can be calculated by the following equation:

$$a_i = \frac{F\lambda_i N_i}{1 + \sum_j \lambda_j N_j h_j} \tag{17}$$

where $F = 0.41$: length of the feeding season[6], N_i: density of host species i, λ_i: effective search rate for host species i, h_i: time of attachment of host species i. Since the value of h_i does not have an extreme effect on the results, we take $h = 0.0548$ for all species[6].

λ_i is mainly determined by the distance swung by host in the attack season (S_i)[6], we let:

$$\lambda_i = S_i = 7.884L_i \tag{18}$$

where L_i is the body length of host.

Adding various assumptions, the formula for a_i simplifies to:

$$a_i = \frac{FS_iN_i}{1 + \sum_j S_jN_jh} \tag{19}$$

- **Summary of the calculation process**

The Inference from $N^{juvenile}$ to M_i can break down into the following steps:

- Calculate a_i through Eq.17.
- Calculate A_i by substituting a_i and $L = N^{juvenile}$ into Eq.16.
- Calculate $P_{s,i}$ through Eq.15.
- Calculate M_i by substituting A_i and P_s into Eq.14.

Combined with the $N^{juvenile}$ process derived from sex in the previous subsection, it is possible to clarify the effect of sex on the population densities of other species in the ecosystem through the link between $N^{juvenile}$ and host mortality.

3.3 Results

We rank the vulnerability of each species to lamprey attack into three levels:

- "vulnerable": *species likely to experience dramatic declines due to sea lamprey*. These species large-bodied fish that are typical hosts for lampreys, which have historically been heavily impacted by lampreys.
- "likely to be attacked": *species that may experience some impact from sea lamprey*. While these species can be affected by lampreys, they may not be as heavily targeted as the larger-bodied fish, or they have more resilience or alternative survival strategies.
- "strong": *species least affected by sea lamprey.* Due to their smaller size or different ecological niches, these species might not be preferred by Sea Lamprey or might not be as critically affected by their presence.

Based on the relative mortality rates of different species obtained by the model algorithm, we obtained predictions of the vulnerability of each species to lamprey attack. (Since the mortality rates of the different species at a proportion of male lampreys of 0.7 significantly characterise the vulnerability of each species to attack by lampreys, we validated the model by taking $\%M = 0.7$).

We compared *the model predictions of species' vulnerability to attacks* with the searched result of *the actual vulnerability of the species* on a two-by-two basis. Based on the percentage of correctly predicted results, we obtained that **our model correctly predicted the mortality of all host fish by 78.66%**, proving that our model is reliable.

4 TASK 2: Impact on the Population of Lampreys

4.1 Environmental assumptions

In order to study the effect of sex ratio on the populations of lampreys, we classified the environments in which lampreys live into two types: *resource-rich(Production)* and *resource-poor(Unproductive)*. We believe that the same sex ratio in these two different environments will have different effects on the natural growth rate of lamprey populations.

To prove our idea, we built an environmental model such as Fig.4, which consists of two relatively independent lakes, and the river that connects them. The lake on the left is a *resource-rich environment* (P), and the lake on the right is a *resource-poor environment* (U). We make the following assumptions about the model:

- The environment as a whole is relatively stable and the model calculations only consider short-term changes, with no population mortality.
- There will be a $\beta\%$ exchange of lamprey between the two environments due to current movement.

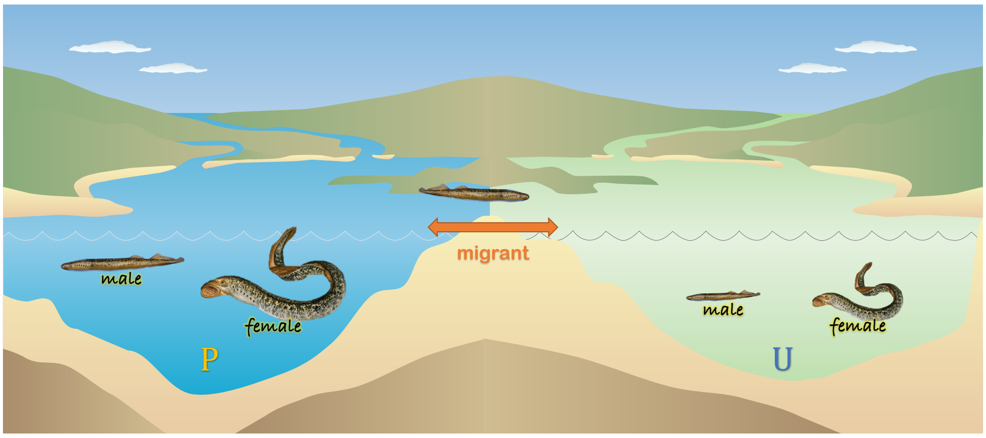

Figure 4: The Task 2 Environment scenario

4.2 Model construction

The core assumption of the model is that: *the growth rate of the male population in this environment = natural growth rate × total number of lampreys × proportion of males amongst births of lampreys + migration rate × total number of lampreys in the other environment × proportion of males in the other environment - number of removals.* The same thing for female can be obtained by replacing 'male' with 'female' in the theorem.

The system of differential equations for environment P, for example, is as follows:

$$\frac{\mathrm{d}N_{PM}}{\mathrm{d}t} = R_P M_{BP} N_P + \beta M_U N_U - \beta M_P N_P \tag{20}$$

$$\frac{\mathrm{d}N_{PF}}{\mathrm{d}t} = R_P(1 - M_{BP})N_P + \beta(1 - M_U)N_U - \beta(1 - M_P)N_P \tag{21}$$

where N_{PM} is the number of males in the P environment, N_{PF} is the number of females in the P environment, $N_P = N_{PF} + N_{PM}$ is the total number of lampreys in the P environment, R_P is the natural growth rate of lampreys in the P environment, M_{BP} is the proportion of males among the born lampreys in the P environment (a constant), M_P is the proportion of male reproductive capacity, α_P is the coefficient of the relationship between the natural growth rate and the proportion of sexes (constant), and β is the rate of immigration and emigration (constant).

R_p is the rate of natural increase of lamprey in the environment, which is mainly determined by the smaller proportion of females or males ($min(1-\%M, \%M)$). And the two environments have different rates of natural increase due to different resources[4] [5]. They are calculated by the following formulae respectively:

$$R_P = \alpha_P[min(1 - M_P, M_P)] \tag{22}$$

$$R_U = \alpha_U[min(1 - M_U, M_U)] \tag{23}$$

4.2.1 Modification considering environmental consistency

Due to the difference in nutrient abundance between the two environments, there is a difference in the reproductive capacity of lampreys growing in the two environments. In order to ensure the balance of the environment during the immigration and emigration process, we analysed the female and male lampreys growing in P and U environments as follows:

Females growing in P environment are well nourished and will have higher spawning and offspring survival rates, so *their reproductive capacity should be significantly higher than that of females growing in U environment*. In contrast, *there is no significant difference in reproductive capacity between P and U males.*

Therefore, we hypothesise that P environment lampreys entering the U environment are γ times more likely to reproduce than females in the U. Females in the U environment entering the P environment are $\frac{1}{\gamma}$ times more likely to reproduce than females in the P environment.

Moreover, in the formula for calculating the overall growth rate of males and females, *the total number of lampreys* in the "natural increase" part of the formula should be replaced by *the total reproduction capacity of lampreys*, which takes into account the difference in *the reproduction capacity of lampreys growing in the two environments.*

4.2.2 Final equation

The growth rates of the number of males N_{PM} and the number of females N_{PF} in environment P are:

$$\frac{\mathrm{d}N_{PM}}{\mathrm{d}t} = R_P M_{BP} N'_P + \beta M_U N_U - \beta M_P N_P \tag{24}$$

$$\frac{\mathrm{d}N'_{PF}}{\mathrm{d}t} = R_P(1 - M_{BP})N'_P + \beta\frac{1}{\gamma}(1 - M_U)N_U - \beta(1 - M_P)N_P \tag{25}$$

$$R_P = \alpha_P[min(1 - M_P, M_P)] \tag{26}$$

$$M_P = \frac{N_{PM}}{N_{PM} + N_{PF}} \tag{27}$$

where N_{PM} is the number of males in the P environment, N_{PF} is the number of females in the P environment, N'_{PF} is the reproductive capacity of females in the P environment, $N_P = N_{PF} + N_{PM}$ is the total number of lampreys in the P environment, $N'_P = N'_{PF}+N_{PM}$ is the total reproduction capacity of lamprey, R_P is the natural growth rate of lamprey in P environment, M_{BP} is the proportion of males among the seven-gill lampreys born in P environment (constant), M_P is the proportion of male reproduction capacity, α_P is the coefficient of the relationship between the natural growth rate and the proportion of the sexes (constant), β is the rate of migration in and out (constant), and γ is the multiplicity of female lampreys that are more reproductively capable in the P environment than in the U environment.

Same in U environment. Just replace P with U in the explanation of the above parameters.

$$\frac{\mathrm{d}N_{UM}}{\mathrm{d}t} = R_U M_{BU} N'_U + \beta M_P N_P - \beta M_U N_U \tag{28}$$

$$\frac{\mathrm{d}N'_{UF}}{\mathrm{d}t} = R_U(1 - M_{BU})N'_U + \beta\gamma(1 - M_P)N_P - \beta(1 - M_U)N_U \tag{29}$$

$$R_U = \alpha_U[min(1 - M_U, M_U)] \tag{30}$$

$$M_U = \frac{N_{UM}}{N_{UM} + N_{UF}} \tag{31}$$

4.3 Results

For environments with balanced resource allocation, we set $\alpha_P = 0.7, \alpha_U = 0.7, \gamma = 1$, and for environments with unbalanced resource allocation, we set $\alpha_P = 1, \alpha_U = 0.4, \gamma = 4$. The sex ratio balance is set to $M_{BP} = 0.5, M_{BU} = 0.5$ and the sex ratio balance is set to $M_{BP} = 0.8, M_{BU} = 0.4$. All of these settings are better to reflect the real situation in nature.

Fig.5 show that the population size of lamprey grows over time for all four settings in the ideal environment of our model. It is worth noting that in the setting with unbalanced resources, the population of lamprey with unbalanced birth sex ratios achieved a numerical advantage. In contrast, in environments with balanced resource classification, populations of lamprey with balanced birth sex ratios achieved a numerical advantage.

In real environments, lamprey birth sex ratios are unbalanced. In the productive environment, the sex ratio of lampreys is roughly 1. In the unproductive environment, male lampreys outnumber female lampreys.

We suggest that the variable sex ratio of lampreys is an adaptation to differences in the amount of resources in different environments. Allocating the majority of resources to females to increase the overall fecundity of the population is an advantage of a variable lamprey sex ratio for the lamprey population. However, an unbalanced lamprey sex ratio would be a disadvantage to its survival in an environment with an even distribution of resources.

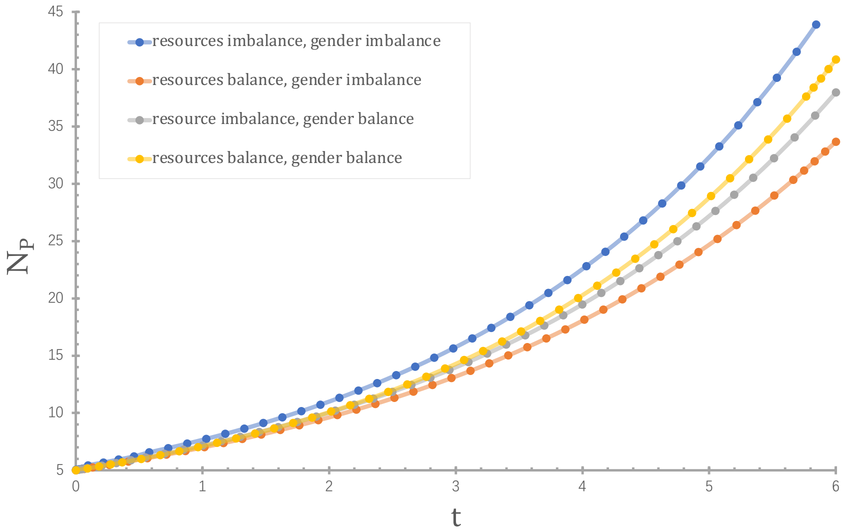

Figure 5: The curve of the total number of lamprey over time, under different levels of resource and gender balances

5 Task 3: Impact on the Stability of the Ecosystem

5.1 Identification of Indicator

The stability of an ecosystem consists of its resistance, resilience, persistence, and stability domains, which are influenced by a variety of factors including species diversity, genetic diversity, environmental carrying capacity, frequency and magnitude of perturbations, and community interactions within the ecosystem.

For an ideal model of an ecosystem that is free from external disturbances, the influence of species diversity is crucial, and systems with high species diversity will generally have higher resistance and resilience.

Therefore, we want to reflect the stability of an ecosystem through its species diversity. To this end, we introduced the *Species Diversity Index* as a performance indicator of ecosystem stability.

5.2 Calculation of Indicator

The Species Diversity Index combines *species richness*, which is the number of species, and *species evenness*, which is the difference in the number of individuals of different species. The formula for calculating *the Species Diversity Index* is as follows. The larger

D is, the greater the species diversity of the system.

$$D = \frac{H + (1 - tanh(\bar{R}))}{2} \tag{32}$$

where H is *the Shannon information entropy* of the proportion of each species in the system, which represents the species evenness, and is calculated as follows:

$$H = -\sum_{i=1}^{N} P_i log_2 P_i \tag{33}$$

$\bar{R}$, on the other hand, represents the number of species in the system and the variation in population density of each species. It is calculated as follows:

$$\bar{R} = \frac{\sum_{i=1}^{N} R_i}{N} \tag{34}$$

- **Summary of the calculation process**
- Calculate H by substituting the percentage of each species (P_i) into Eq.33.
- Calculate $\bar{R}$ by substituting the relative number of deaths of each species (R_i) and the total number of species (N) into Eq.34.
- Calculate D by substituting H, R into Eq.32.

5.3 Results

By investigating and setting reasonable parameters, with the help of MATLAB simulation, we obtained the trend of ecosystem stability with the sex ratio of lamprey. Their values are shown in the above graphs.

Observation of the graph shows that the ecosystem stability decreases abruptly as the sex ratio increases from small to large. It then reaches its lowest point at a sex ratio of roughly 4 (80% males). Finally the ecosystem stability levelled off and slowly increased.

By analysing the data during the experiment, we found that lamprey, as a parasitic organism, tends to have a negative impact on environmental stability. It does little to kill the dominant species in the environment in order to achieve a balance between the species. On the contrary, the results of the simulation experiments showed that environmental stability decreased when the population density of lamprey increased as the sex ratio of lamprey changed.

Our model suggests that the density of lamprey is the main factor affecting environmental stability, and that the authorities should control the number of lamprey or use some means to keep the sex ratio of lamprey away from the extreme value of "4" in order to increase environmental stability.

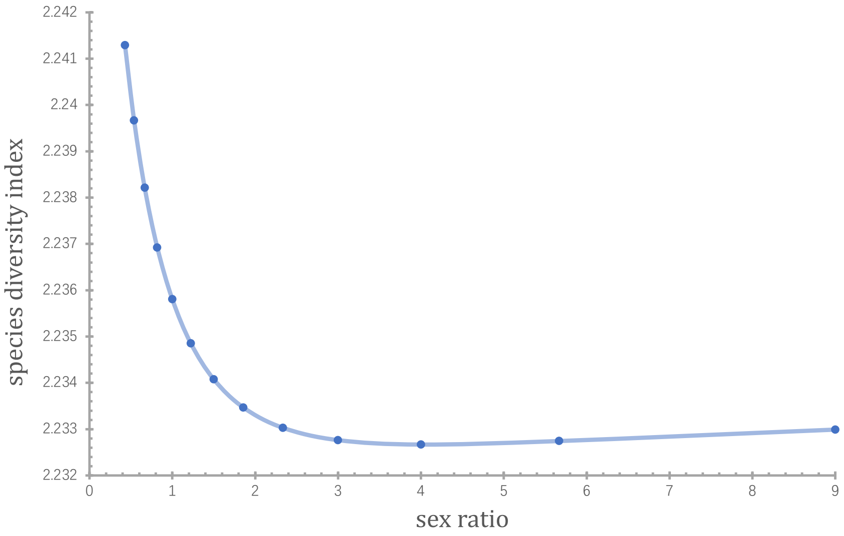

Figure 6: The curve of species diversity index with lamprey's sex ratio

6 TASK 4: Advantages to the Other Parasites

6.1 Problem Analysis

Lampreys are not only parasites on large fish, but also hosts to be parasitized by other parasites. In the Model Construction of Task 1, we analysed that the sex ratio of lamprey mainly affects the population density of lamprey. And the higher the population density of lamprey, the higher the number of parasitized lampreys per unit volume. Therefore, we can also infer that in an ecosystem with variable sex ratios in the lamprey population, the sex ratio of lampreys will give an advantage to parasites that are prone to parasitize lampreys.

The population size advantage gained by parasite species i by lampreys can be measured by the number of lampreys parasitized by parasite species i per unit volume. The formula for the number of lampreys parasitized by parasite species i per unit volume is:

$$K_i = p_i * L \tag{35}$$

where K_i is the number of lampreys parasitized by parasite species i per unit volume, p_i is the probability of parasitism of lamprey by parasite species i, and L is the population density of lampreys.

For p_i, we make the following analysis: *not all parasites capable of parasitizing lampreys are specialised in parasitizing lampreys*, and different parasites have different levels of preference for lampreys. We use a *normal distribution estimate* to measure whether this degree of preference is sufficient for its parasitic behaviour towards lampreys to occur. The formula is as follows:

$$SE_i = \sqrt{\frac{pp_i(1 - pp_i)}{n_i}} \tag{36}$$

where SE_i is the standard error of the sample of parasite species i, pp_i the frequency of parasitism on lamprey by parasite species i, and n_i is the sample size of parasitism behaviour by parasite species i.

Then the 95% significant interval for the probability of lamprey being parasitized by parasite species i is: $[pp_i - 1.96 \cdot SE_i, pp_i + 1.96 \cdot SE_i]$.

- **Summary of the calculation process**
- Substitute the sample data of all the parasite species that may parasitize the lamprey into Eq.36 and calculate their respective normal distributions.
- If 0 falls in the confidence interval, the parasite is considered difficult to parasitize the lamprey and its probability of parasitizing the lamprey is negligible.
- If 0 does not fall in the confidence interval, the parasite is considered to have a non-negligible probability of parasitizing the lamprey.

6.2 Results

In this chapter, we analysed whether adjusting sex ratios in lampreys has the potential to provide advantages to other ecosystems. We focused our attention on both fish ecosystems and parasite ecosystems.

Based on the analyses in Task 3, we found that the effects of lampreys on fish are almost always negative, regardless of sex ratio. Therefore, in this chapter we focused on examining the effects of lamprey sex ratio on parasites and came to the following conclusions.

Although there have been many studies investigating parasite data in lampreys, they have not been further statistically analysed. After analysing the confidence intervals for the frequency of occurrence of individual parasites, we found that some parasites, such as Neoechinorhynchus cylindratus, Ergasilus megaceros, Diplostomum sp. etc., their probability of parasitism was not statistically significant. Therefore, we concluded that the sex ratio of lampreys had no effect on these parasites. While some other parasites such as Proteocephalus longicollis and Diplostomum huronense, which have a higher probability of parasitising lampreys, we believe that as the sex ratio of lampreys approaches the optimum (about 4), the number of lampreys will increase and this group of parasites will benefit, with their population growth being positively correlated with the number of lampreys.

7 Analysis on Model's Sensitivity

7.1 Sensitivity Analysis of Task 1

Table 2: The four fish species with the highest proportions (proportions>0.1)

host species	gradient	proportions
Freshwater Drum	2.25×10^{-6}	0.143706908
Walleye	2.52×10^{-5}	0.13602812
White Perch	2.13×10^{-4}	0.167284034
Yellow Perch	5.11×10^{-4}	0.18696769

Table 3: The two fish species most sensitive to lamprey density (gradient > 0.5)

host species	gradient	proportions
Mimic Shiner	1.50	0.000189266
Brook Silverside	0.654	0.000351494

By analysing in depth the graphs of fish mortality counts against the gradient of lamprey sex ratio, we found that the number of deaths of fish with a larger share of the watershed was relatively insensitive to changes in the lamprey sex ratio. In contrast, the number of deaths of fish with a smaller occupancy showed a higher sensitivity to changes in lamprey sex ratio. This observation can be attributed to the high population density of the more occupied fish, which is resistant to lamprey parasitism and therefore less sensitive. Fish with small occupancy ratios are themselves less populous, more vulnerable and show more drastic changes in mortality numbers once they are affected by parasitism.

Given the above observations, we can conclude: when protecting fish in waters and consolidating the stability of the ecosystem, we should focus on relatively sparsely populated fish, which will help to improve the stability of the ecosystem. This targeted conservation measure will help maintain the ecological balance of the waters and promote the healthy development of fish populations.

7.2 Sensitivity Analysis of Task 2

For the model that most closely approximates the reality of an unbalanced amount of environmental resources versus an unbalanced lamprey sex ratio, we conducted sensitivity analyses of the two variables, sex ratio and amount of environmental resources (natural growth rate), to the total lamprey population over time.

The lamprey population peaked when the male sex ratio varied around 0.75-0.80 in the unproductive environment, and any further increase or decrease in the sex ratio resulted in a decrease in the total population. This suggests that lampreys changing their sex ratio to around 0.8 is the best option when faced with an environment of uneven resources.

When the resource abundance in the productive environment changes, it is equivalent to the natural growth rate changing around 1. We can observe that when natural resources increase, the total lamprey population increases. When natural resources decrease, the total population increases and then decreases. This suggests that the strategy of changing the sex ratio is effective when the resources are unbalanced, and that if the resources are balanced, the use of a non-1:1 sex ratio will have a bad effect. The coefficient of fecundity of female lampreys, gamma, also reflects this phenomenon well. We assume that females in a productive environment are gamma times more fertile than in an unproductive environment. Observation of the graph shows that when gamma rises, the total number of lampreys first rises steeply and then flattens out. This also suggests that when there is an imbalance in resources (large differences in reproductive capacity), lampreys have more to gain by changing their sex ratio.

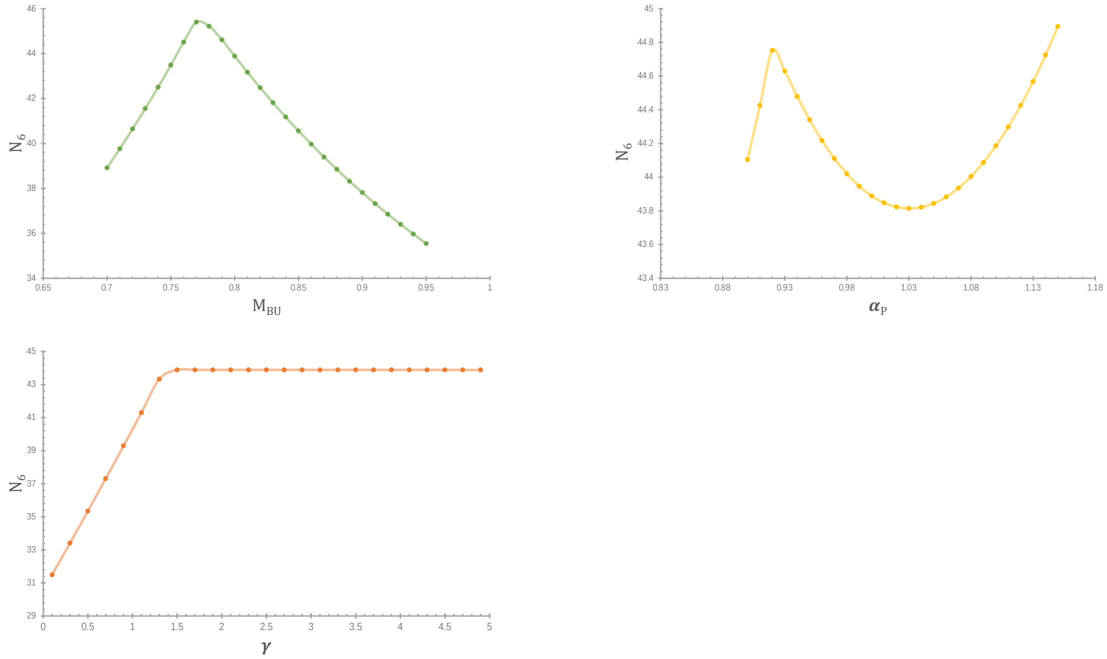

Figure 7: The curves of N_6 with M_{BU}, α_P, γ, where N_6 is the sum of all lamprey populations in the t=6 state, M_{BU} is proportion of males born in unproductive environments, α_P is the coefficient of the relationship between the natural growth rate and the proportion of sexes, γ is the number of times a female lamprey is more fertile in a productive environment than in an unproductive environment

8 Strengths and Weaknesses

8.1 Strengths

- Our findings are in line with those of many previous studies.
- A better fit to realistic data in a limited data interval. A good fit to the trend of realistic data over a larger data range.
- Based on the actual biological mechanism modelling, the reproduction process of lamprey, the parasitism process, and how the host is affected by lamprey are well explained, based on which the advantages and disadvantages of changing the sex ratio are successfully analysed.

8.2 Weaknesses

- Given the serendipitous nature of this study, some aspects of the design were not ideal, but do not necessarily discount our observation of skewed sex ratios and our working hypothesis.
- Larvae stocked in stream and lentic environments were collected from different source streams and during different years. Therefore, the observed differences in sex ratios could simply be an artefact of the streams from which the larvae were sourced.
- We are unable to exclude the possibility that the observed sex ratios were the result of differential rates of mortality or metamorphosis between the sexes.

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Appendix: Code

TASK 1 - **main.m**

```
% Main function for task1, outputs the death situations of various hosts
clear;close;clc
i = 0;
for Malerate = 30:1:90
    i = i + 1;
    N_larval(i) = -0.0000965 * Malerate ^ 2 + 0.0154956 * Malerate - 0.3658665;
    N_juvenile(i) = juvenile_density(N_larval(i));
end

matrix = deathnum(N_juvenile);

x_values = 0.3:0.01:0.9;


figure;
hold on;

for i = 1:size(matrix, 1)
    plot(x_values ./ (1 - x_values), matrix(i, :));
end

xlabel('X');
ylabel('Y');
hold off;

figure;
average_curve = mean(matrix, 1);
xxx = x_values ./ (1 - x_values);
plot(xxx, average_curve, 'LineWidth', 2);

xlabel('X');
ylabel('Y');
```

TASK 1 - **juveniledensity.m**

```
function N_juvenile = juvenile_density(N_larval)
    D_larval = 4;      % Duration of larval stage in years
    D_juvenile = 2;    % Duration of juvenile stage in years
    S_larval = 0.627;    % Annual survival rate of larvae
    beta_0 = -23.886;    %
    beta_1 = 0.186;      %
    l_inf = 159;         % mm
    l_bar = l_inf/2;     % Midpoint of the length interval
    d = 0.515;           % Duration of the growth season for a specific stream,
                         % in years

    % Calculate the value of B
    sum = 0;
    for y = 0:D_larval
       sum = sum + P_y(y,S_larval, beta_0, beta_1, l_bar, l_inf, d);
    end
    B = N_larval / sum;

    % Calculate the density of adult fish
    sum = 0;
    for y = 1:(D_larval + D_juvenile)
```

```
        sum = sum + R_y(y, D_larval, D_juvenile, S_larval,
                         beta_0, beta_1, l_bar, l_inf, d) * B;
    end
    N_juvenile = sum;
end
```

TASK 1 - deathnum.m

```
function M = deathnum(den)
    [num, txt, raw] = xlsread('statisticalresultsnew.xlsx');
    Lmm = num(:, 2);     % Host length column
    Lg = num(:, 3);      % Host mass column
    N = num(:,1);        % Host density column
    F = 0.41;            % Feeding season length
    S = 7.884 * Lmm;     % Effective search rate for the i-th host, column
    h = 0.0548;          % Attachment time
    m_lamprey = 200.9;   % Lamprey mass
    PR = m_lamprey ./ Lg;
    P_s = 1 - PR .^ 2 / (1 + PR .^ 2);      % Survival rate of hosts per attack

    tempsum = sum(S .* N * h);
    a = (F * S .* N) / (1 + tempsum);
    A = a * den ./ N;
    M = (1 - P_s) * A;
end
```

TASK 1 - extra.m

```
clear;close;clc

[num, txt, raw] = xlsread('task1ex.xlsx');
name = txt(2:end, 1);
death = num(:, 1);
rank = num(:, 2);

up = 0;
down = 0;

n = size(rank, 1);
for i = 1:n - 1
    for j = i + 1:n
        if (death(i) > death(j) && rank(i) > rank(j))
            || (death(i) < death(j) && rank(i) < rank(j))
            up = up + 1;
            down = down + 1;
        elseif (death(i) > death(j) && rank(i) < rank(j))
                || (death(i) < death(j) && rank(i) > rank(j))
            down = down + 1;
        end
    end
end

rate = up / down
```

TASK 2 - ode.m

```
% Main function for task2, solving a system of ordinary differential equations
clear;close;

ap = 1;
au = 0.4;
```

```
mp = 0.4;
mu = 0.8;
b = 0.4;
r = 4;

% ap = 0.7;
% au = 0.7;
% mp = 0.4;
% mu = 0.8;
% b = 0.4;
% r = 1;

ode_system = @(t, y) [
    ap * mp * min(y(1), y(2)) + b * (y(3) - y(1)); %Npm
    ap * (1 - mp) * min(y(1), y(2)) + b * (y(4) / r - y(2));
    au * mu * min(y(3), y(4)) + b * (y(1) - y(3)); %Num
    au * (1 - mu) * min(y(3), y(4)) + b * (y(2) * r - y(4));
    ap * (1 - mp) * min(y(1), y(2)) + b * (y(6) - y(5)); %Npf
    au * (1 - mu) * min(y(3), y(4)) + b * (y(5) - y(6)); %Nuf
];


tspan = [0 6]; % 0-6years

y0 = [1.5; 1.5; 1; 1; 1.5; 1]; % ordinary

% ode45
[t, y] = ode45(ode_system, tspan, y0);

y_pic = [y(:,1), y(:,3), y(:,5), y(:,6)];
figure;
plot(t, y_pic);
xlabel('Time');
ylabel('Num');
legend('Npm', 'Num', 'Npf', 'Nuf');
title('env and sex rate');

disp(sum(y_pic(end, :)))
```

TASK 3 - **envtask3.m**

```
clear;close;clc
i = 0;
for Malerate = 40:2:100
    i = i + 1;
    N_larval(i) = -0.0000965 * Malerate ^ 2 + 0.0154956 * Malerate - 0.3658665;
    N_juvenile(i) = juvenile_density(N_larval(i));
end

death = deathnum(N_juvenile);

x_values = 0.4:0.02:1;
xxx = x_values ./ (1 - x_values);

% matrix = env_stability(death);

% %%%%%%%%%%
R = death;
[num, txt, raw] = xlsread('statisticalresultnew.xlsx');
    P = num(:, 1);
    P1 = P * 36985 - R;
```

```
    P2 = P1 ./ sum(P1);
    H = - sum(P2 .* log2(P2));
    R_ave = mean(R);
    D = 0.5 * (H + 1 - tanh(R_ave));
    matrix = D;
% %%%%%%%%%%

figure;
hold on;
% plot(xxx, H);
plot(xxx, matrix);
```