Resource-Dependent Sex Ratios in Lampreys: Implications for Ecological Stability and Economic Impact

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Abstract: The sex ratio of the lamprey, a fish that is both bottom and active in the middle of the food chain, varies according to the state of environmental resources. Over the long term, due to its population explosion, the lamprey has taken a significant toll on economic fish stocks and has become a species considered a disaster by humans. This study aimed to assess the specific adaptive strategies of the lamprey and its impact on the ecosystem. In this paper, a detailed assessment of the impacts on the ecosystem and its stability was carried out by constructing an accurate model. The results of the study revealed key indicators such as economic losses, resource utilization, and impact factors of the lamprey on other organisms, thus effectively evaluating the resource utilization capacity of the lamprey within its habitat. This paper provides insight into the complexity of sex ratios to accommodate varying resource availability. By analyzing the pros and cons of such adaptations, thereby providing a comprehensive understanding of the subtle ecological interactions in the ecosystems inhabited by the lamprey.

1. Introduction

The Lamprey, an ancient jaw-less fish, is valued as an important food source in many parts of the globe because of its unique feeding pattern and parasitic behavior on other fish. This fish not only has a profound impact on the ecosystem, but also plays a complex role in maintaining ecological balance. Their presence challenges the traditional sex dichotomy, demonstrating the importance of adaptive changes in sex ratio for reproductive strategies. By studying lampreys, we can gain a deeper understanding of how they interact with ecosystems, both as potential stressors and contributors to their environment. In particular, the sex ratio of lampreys is influenced by environmental conditions, similar to the phenomenon of American alligators where incubation temperature affects sex, reflecting the adaptability of organisms to environmental change. The lifecycle and migratory habits of lampreys (as shown in the Figure 1) further reveal their impact on ecosystem dynamics, emphasizing the importance of studying their ecological roles and adaptive mechanisms.

In the first model, we assumed that the proportion of males in the lamprey increases when food is abundant and developed a quantitative model that takes into account the population dynamics of the lamprey, the interaction of sex ratio with environmental resources. By optimizing the model, we show the relationship between the sex ratio of the lamprey and fish in the environment, and its indirect effects on the ecosystem. Given the complexity of the impacts of the lamprey sex ratio on ecosystem stability and other organisms, we selected biodiversity, community structure, and material cycling as scoring metrics in the second model.

2. Population growth model

2.1. Evaluation on the degree of environmental impact of sex ratios

In this section, we model the growth of lampreys before sexes are differentiated. Lamprey's experience 3-4 years from birth to reproduction as shown in the Figure 2, and the duration of the larval stage of the lamprey life cycle has been found to vary between and within species, but generally ranges from 3 to7 years.[2]

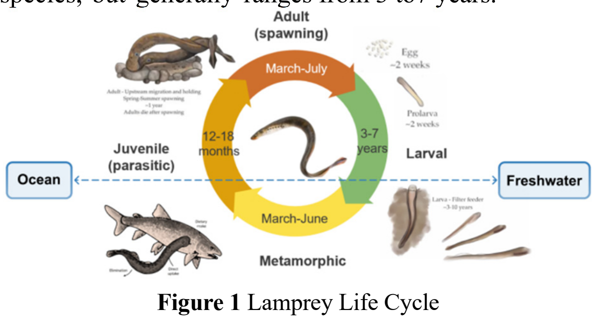

Figure 1 Lamprey Life Cycle

We assumed and modeled 4 years as the intergenerational reproduction cycle of the lamprey in order to better capture the intergenerational relationships of the lamprey. Ideally, lampreys will vary at some constant rate of change. However, in the presence competition, the rate of change is different. We assumed N_{t_former} to be a freshly hatched juvenile of the current generation, and created the model with only the invasive species.

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$$\frac{dN_{t\_former}}{dt} = r_0 N_{total\_before} \left(1 - \frac{N_{t\_former}}{m}\right) \quad (1)$$

Where r_0 denotes the average mortality rate of lampreys over the four-year period, and m is the average maximum number of lampreys carried in the current environment. Further analysis of r_0 enables us to obtain the following equation for $P_{survial-rate}$.

$$r_0 = 1 - P_{survial-rate} \quad (2)$$

Unlike normal vertebrates, lampreys have a long larval period, during which they are vulnerable and the rate of larval loss is generally relatively high. However, during this period, larvae mostly live in the riverbed, digging holes in the riverbed sediment and feeding on detritus and algae. In addition, larvae are mostly immobile and have a small range of action, effectively reducing the probability of being detected by natural enemies. Based on the fact that lampreys are in a relatively safe environment as juveniles, we assumed that juvenile and adult mortality rates are nearly equal.

As an invasive species, the native environment holds at least one native organism. Therefore, we established a link between the lampreys and other organisms in the Great Lakes region, assuming that there is only one type of predator, in this case with the lamprey to build a Lotka-Volterra model.

$$\frac{dN_{t\_former}}{dt} = r_0 N_{total\_before} \left(1 - \frac{N_{t\_former}}{m} + \frac{\sigma B}{B_{max}}\right) \quad (3)$$

Where σ presents the impact factor of the lamprey on a predator, B is the current number of individuals of the species, and B_{max} denotes the average maximum number of individuals carried by the species in the current environment. For σ,we took is as its value a percentage of the total economic losses caused by the lamprey to population B, giving a quantifiable indicator of the impact of this impact factor on the species.

$$\sigma = \frac{W_{cost}}{W_{total}} \quad (4)$$

Where W_{cost} is the economic loss to the species caused by the lamprey and W_{total} is the economic benefit due to the species. In the Great Lakes ecosystem, there must be more than one type of native organism present. The lamprey invades this ecosystem and engages in predation, competition. So the next step is to add these factors to correct the equation.

$$\frac{dN_{t\_former}}{dt} = r_0 N_{t\_former} \left(1 - \frac{N_{t\_former}}{m} - \sum_{i=1}^{n} \frac{\sigma_{1i} B_i}{B_{imax}}\right) \quad (5)$$

Where σ_{1i} is the impact factor of the ith species on the lamprey, B_i is the current number of individuals of the ith species, and Where B_{imax} is the average maximum carrying capacity of the ith species in the current environment. Then we proceeded to establish equations for the effects of the lamprey and other organisms in the ecosystem on a given species:

$$\frac{dB_i}{dt} = r_i B_i \left(1 - \frac{\sigma_{i1} N_{t\_former}}{m} - \sum_{j=1,\ j\neq i}^{n} \frac{\sigma_{ij} B_i}{B_{imax}}\right) \quad (6)$$

Where σ_{1i} is the impact factor of the lamprey on the i organism, σ_{ij} is the impact factor of the j organism on the i species, and r_i is the average rate of change based on ecological and reproductive efficiency. At this stage, we define a sex ratio r (the proportion of males to the total number of lampreys in this generation) and a N_{female} is representing the number of female lampreys in this generation, which can be obtained:

$$N_{female} = (1 - r)\ N_{t\_former} \quad (7)$$

Next, we introduce a coefficient α_{number} representing the number of larvae that can be produced by each female lamprey, and the next generation of larvae by a coefficient N_{later} :

$$N_{later} = \alpha_{number} N_{female} \quad (8)$$

We can get the range of the number of eggs produced by females in each generation, take the mean value β_{number} as the average number of eggs produced by females in each generation, and combine it with the rate of larval births in the eggs β_{born} to get the following equation:

$$\alpha_{number} = \beta_{born} \beta_{number} \quad (9)$$

We obtained a small and variable surplus of males among upstream migrants and spawning adult lampreys. At the same time,we have to make an update on the number of individuals in this generation[2] . To be updated, and since the number of male surplus is uncertain in each generation it is updated with a random value N_t'

$$N_t' = \delta \quad (10)$$

Since we modeled the lamprey from larvae until reproduction, the number of larvae in that generation can only decline in the number of individuals due to environmental and other biological factors, and $\frac{dN_{t\_former}}{dt}$ also tends to 0 when N_{t_former} tends to $N_{t\_former} > m$, we creatively add tail terms after the logistic model to make the equation more realistic.

$$\frac{dN_{t\_former}}{dt} = r_0 N_{t\_former} \left(1 - \frac{N_{t\_former}}{m}\right) \frac{-N_{t\_former}}{m} \quad (11)$$

Then, we can then proceed to correct equation (12) as follows:

$$\frac{dN_{t\_former}}{dt} = r_0 N_{t\_former} \left(1 - \frac{N_{t\_former}}{m} \sum_{i=1}^{n} \frac{\sigma_{1i} B_i}{B_{imax}}\right) \frac{-N_{t\_former}}{m} \quad (12)$$

Under Assumption 3, based on the characterization of a small and variable excess of males and the average lifespan of lampreys as seven years, we used the MA(3) time-series prediction model for N_{t_former}:

$$N_{t\_former} = N_{t\_former\_1} + \gamma_1 N_{one\_year\_before} + \gamma_2 N_{two\_year\_before} + \gamma_3 N_{three\_year\_before} \quad (13)$$

Where Y_1, Y_2, Y_3 are the scale factors for three years, and $N_{one\_year\_before}$, $N_{two\_year\_before}$ and $N_{three\_year\_before}$ are the number of lampreys that still have not completed reproduction in three years, respectively. Juveniles tend to slow down in size change (rate) in the year before they approach reproduction and do not change significantly. The body size is similar to the lampreys that have already failed to reproduce[1].

Since their body size is about the same, we assume that all lampreys that need to migrate again will have the same survival rate as well as the same reproduction rate during the cycle. We are able to obtain the following equation:

$$\begin{cases} N_{one\_year\_before} = \frac{N_{t\_former}}{KN_{t\_former\_1}} N_t' \\ N_{two\_year\_before} = \frac{N_{t\_former} - N_t'}{KN_{total\_former\_1}} N_{one\_year\_before} \\ N_{three\_year\_before} = \frac{N_{totle\_before} - N_{total}'}{KN_{total\_before\_1}} N_{two\_year\_before} \end{cases} \tag{14}$$

Also, at this stage, for the Lotka-Volterra competition model, we get:

$$\begin{cases} \frac{dN_{t\_former}}{dt} = r_0 N_{t\_former} \left(1 - \frac{N_{t\_former}}{m} - \sum_{i=1}^{n} \frac{\sigma_{1i} B_i}{B_{imax}}\right) \\ \frac{N_{t\_former}}{m} \\ \frac{dB_i}{dt} = r_i B_i \left(1 - \frac{\sigma_{i1} N_{t\_former}}{m} - \sum_{j=1,\ j \neq i}^{n} \frac{\sigma_{ij} B_i}{B_{imax}}\right) \\ (15) \end{cases} \tag{15}$$

$$\begin{cases} \frac{dN_{t\_former}}{dt} = r_0 N_{t\_former} \ (1 - \frac{N_{t\_former}}{m} + \frac{\sigma B}{B_{max}}) \frac{N_{t\_former}}{m} \\ \sigma = \frac{W_{cost}}{W_{total}} \end{cases} \tag{16}$$

$$\sigma_{1i} = \frac{W_{1icost}}{W_{1itotal}} \tag{17}$$

Where W_{1icost} is the economic loss caused by the lamprey to the species i , and W_{1icost} is the economic benefit due to the ith species. Adding up the losses to all the organisms in the ecosystem from the lamprey, we get $N_{t-former}$ of the total economic losses to fish stocks from the lamprey:

$$W_{lamprey\_total} = \sum_{i=1}^{n} W_{icost} \tag{18}$$

Through the above equation, we can get the relationship between the number of lamprey s and economic loss:

$$\frac{N_{lamprey}}{N_{t\_former}} = \frac{W_{lamprey}}{W_{lamprey\_total}} \tag{19}$$

Economic loss is an indicator to quantify ecological loss, which includes not only fish loss, but also associated abiotic losses due to abnormalities in the homeostasis ofthe biological chain. Finally, we obtained information about the relationship between sex ratio rand ecological indicators:

$$\begin{cases} N_{female} = (1-r) N_{t\_former} \\ N_{latter} = \alpha_{number} N_{female} \\ \alpha_{number} = \beta_{born} \beta_{number} \\ \frac{N_{lamprey}}{N_{t\_former}} = \frac{W_{lamprey}}{W_{lamprey\_total}} \end{cases} \tag{20}$$

For r_0, we get it by looking up the literature, and from the sampling results we get that $P_{survial\_rate}$ is 85%[3], thus, we can find the value by equation (2). We get that β_{number} averages 60000, while $\beta_{born}$is roughly 90 %[4].

Considering the high accuracy and efficiency of the fourth-order Runge-Kutta algorithm in solving the system of differential equations, we apply this algorithm to solve the differential equations in Eq. (11) and derive the relationship graph between sex ratio and ecological indexes based on the constraints by the association of Eq. (20).

Based on Figure 3, we can get the relationship between sex ratio and ecological impact at a certain abundance. As the sex ratio increases, its impact on the ecological environment first gradually increases and then begins to gradually decrease after reaching a certain sex ratio.

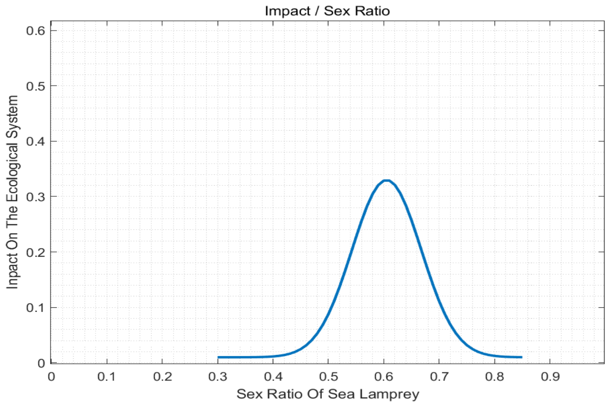

Figure 2 The degree of environmental impact of sex ratios at a maximum

2.2. Evaluation model of ecosystem stability

We took data from the Great Lakes Fishery Commission's Lake Erie Commission Cold Water Working Group published from 2007-2022 on sex ratios corresponding to fish at different population densities and eliminated unreasonable samples through an outlier test based on the Marginal Distance Cull.

The protection of fish populations within a certain reasonable range is important to maintain the stability of the ecosystem. As a parasitic fish, the lamprey invaded the Great Lakes at an alarming rate in the early days, surviving and reproducing in the lake area, resulting in a large-scale decline in the fish population, which led to the destabilization of the ecosystem within a certain range. This develops effective ecological indicators and reliable assessment models for the effects of the sex ratio attribute of the lamprey on organisms in the ecosystem and can be of great help in analyzing ecosystem stability. In the initial stages of modeling, among the complex set of indicators for evaluating ecosystem stability[5], we have selected three typical indicators (relationship with ecosystem stability is shown in Figure 2.): Biodiversity (BD), Community Structure (CS), Material Cycle (MC).

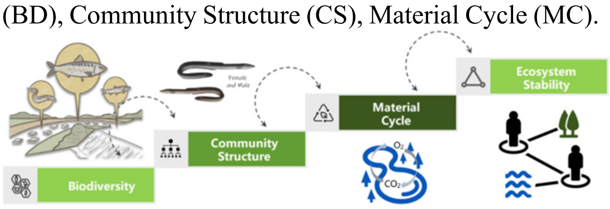

Figure 3 Sequential analysis of three typical indicators on ecosystem stability

Since the biodiversity of the Great Lakes is directly affected by the abundance of fish resource, and in the Lotka-Volterra model of Module 4.3, Eq. (7) and Eq. (8) show the sex ratio r as a function of the number of progeny larvae. In addition, in the ecological environment, lampreys as predators prey on fish resources in the Great Lakes, and the change in their population affects biodiversity to a certain extent. Based on the above correlation analysis, we can clearly get that the change of the sex ratio of lamprey s will directly change the biodiversity of the Great Lakes. We know that there are communities of many organisms in a given range of ecosystems. The diversity of inter-species relationships, such as predation, cooperation, and competition, is reflected in the lamprey 's relationships with other organisms in the Great Lakes. The team returned to examine Model 1 and discovered that different sex ratios of lampreys have different effects on organisms in different food chains in the ecosystem. As in equation (6), it is easy to see that the ecosystem community structure is directly affected by the sex ratio of the lamprey.

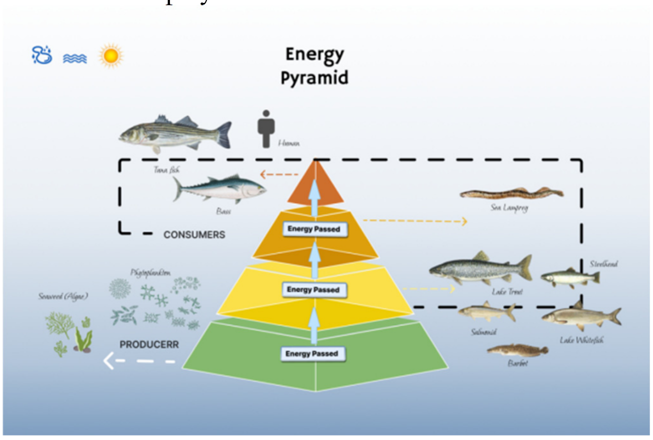

Figure 4 Energy Pyramid Model around Lampreys

Intriguingly, fish organisms are important in maintaining the ecological balance of water bodies as a key link in the food chain of water bodies (Figure 4), helping to manage important water quality regulators such as eutrophic substances in water bodies. Through model 1 we were able to obtain that sex ratio directly affects the number of offspring of the lamprey. The number of offspring of lamprey s has different impacts on fish stocks. Therefore, for the three major indicators of biodiversity (BD), community structure (CS), and material cycling (MC), the first two indicators have resistance stability in ecosystems (application), while all the behaviors of the lamprey in ecosystems are related to material cycling, so it is more sensitive in the same situation, so we assigned the greatest weight to material cycling. Therefore, we assigned them a weight of 0.2, 0.3, and 0.5 respectively

From this, we get a judgment matrix in Table 1:

Table 1 Judgment matrix based on entropy weight method TOPSIS

	BD	CS	MC
BD	1	2/3	2/5
CS	3/2	1	3/5
MC	5/2	5/3	1

Next, we used 56%, 62%, and 78% as the three sex ratios of the lamprey as an example to obtain the agreement matrix IR about the three indicators under different sex ratios, respectively (in Table 2).

Table 2 Consistency Matrix

BD	56%	62%	78%
78%	1	4/5	1/2
62%	5/4	1	3/4
56%	2	4/3	1
CS	56%	62%	78%
78%	1	5/6	1/3
62%	6/5	1	4/5
56%	3	5/4	1
MC	56%	62%	78%
78%	1	5/4	5/7
62%	4/5	1	2/3
56%	7/5	3/2	1

Next, a consistency test is performed for the data, and the relevant formula is as follows:

$$CR = \frac{CI}{RI} \tag{21}$$

Where CI is the consistency indicator, calculated as follows:

$$CI = \frac{\lambda_{max} - \eta}{\eta - 1} \tag{22}$$

RI is the average random consistency index, which can be obtained by Table 3:

Table 3 Average Randomized Consistency Indicator

η	2	3	4	5	6	7	8	9	10
RI	0	0.52	0.89	1.12	1.26	1.36	1.41	1.46	1.52

It's available:

$$\begin{cases} CI_{SD} = 0.0018, CR_{SD} = 0.0036 \\ CI_{CS} = 0.0268, CR_{CS} = 0.0516 \\ CI_{MC} = 0.0013, CR_{CS} = 0.0025 \end{cases} \tag{23}$$

In the above consistency test, the ratio CR<0.1 all holds and the consistency test passes. Next, we normalize the derived vectors to obtain our weights.

We solved by arithmetic mean method (AMM):

$$\omega_i = \frac{1}{n} \sum_{j=1}^{n} \frac{a_{ij}}{\sum_{k=1}^{n} a_{kj}} \tag{24}$$

Where τ_{isD} is the score of the sex ratio on biodiversity (BD), τ_{iCs} is the score of the ith sex ratio on community structure (CS), and τ_{iMC} is the score of the ith sex ratio on material cycling (MC).We were also able to obtain τ_{isD} ,τ_{iCs} and τ_{iMC} by the geometric mean method (GMM) as well as the eigenvalue method (EM), respectively. The formula for the geometric mean is given below:

$$\omega_i = \frac{(\prod_{j=1}^{n} a_{ij})^{\frac{1}{n}}}{\sum_{k=1}^{n} (\prod_{j=1}^{n} a_{ij})^{\frac{1}{n}}} \tag{25}$$

We constructed three tables for the three sets of data in Table 4, 5, 6:

Table 4 Scoring of biodiversity in different sex ratios

BD	AMM	GMM	EM
78%	0.2376	0.2375	0.2375
62%	0.3155	0.3155	0.3155
56%	0..4469	0.447	0.447

Table 5 Scoring of community structure under different sex ratios

CS	AMM	GMM	EM
78%	0.2063	0.2044	0.2044
62%	0.31	0.309	0.309
56%	0..4837	0.4866	0.4866

Table 6 Scoring of material cycling in different sex ratios

MC	AMM	GMM	EM
78%	0.3153	0.3153	0.3153
62%	0.2656	0.2655	0.2655
56%	0..4192	0.4192	0.4192

After considering the arithmetic mean method (AMM), geometric mean method (GMM), and eigenvalue method (EM) together, according to:

$$\varphi_i = 0.2\tau_{iSD} + 0.3\tau_{iCS} + 0.5\tau_{iMC} \quad (26)$$

We can get， $\varphi_1 = 0.26647$， $\varphi_2 = 0.28855$, $\varphi_3 = 0.44498$

The score φi first scores the three major indicators of biodiversity (BD), community structure (CS), and material cycling (MC) and then multiplies them with the weights and finally adds them up. The higher the score, the lower the damage to ecosystem stability.

3. Model Evaluation and/or Further Discussion

3.1. Strengths

Considering the complexity of modeling competition, we separated the reproduction model from the competition model and built the Volterra bait-predator model with the reproductive success model, which represents the two stages of growth and reproduction. Since it takes about 4 years for a lamprey to move from juvenile to adult (reproduction), we directly used 4 years as a span when building the model to link the lampreys that were separated by 4 years, which made an intuitive continuity in the number of former progeny lampreys, and thus facilitated the observation of the effect of the sex ratio of lampreys on the number of progeny larvae. In solving the differential equations of the model, we introduce the 4th order Longe-Kuta algorithm to solve its numerical solution with high computational accuracy and stability.

3.2. Weaknesses

In our modeling, we did not model the sexually differentiated lamprey s as separate females and males, but rather treated the growth rates of the male and female stages as the same, based on the fitted model in the data we obtained (the difference in the growth rates of the lamprey s was mainly in the cryptic female and cryptic male stages, which had not yet been differentiated). Due to the small amount of data we have, although we have ensured flexibility in many parameters, proper estimation in the literature may not allow us to be completely accurate. However, we also performed sensitivity analysis on key parameters with satisfactory results. When analyzing the stability of ecosystems using the hierarchical analysis method, the indicators we gave can be based on relevant materials, but it is still too difficult to evaluate them, and the accuracy of the evaluation may need to be improved.

4. Conclusion

We can get the relationship between sex ratio and ecological impact at a certain abundance. As the sex ratio increases, its impact on the ecological environment first gradually increases and then begins to gradually decrease after reaching a certain sex ratio.

In conclusion, our research delves into the adaptive behaviors of the lamprey in its environment and examines the consequential impacts on both the natural ecosystem and human interests. Fundamentally, our study enhances our comprehension of how the lamprey adjusts to varying resource availability. The findings presented here lay a robust foundation for future research and conservation initiatives, enabling a more nuanced and targeted approach to mitigate the potential damage caused by the lamprey to both economic fish stocks and the overall environment.

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