Impact of sex ratio on ecosystem stability: a Lotka-Volterra model considering sex ratio

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Abstract. This study examined the effects of sex ratio on ecology, using Lamprey as the study population. It was found that there was a close relationship between sex ratio and food availability, with a higher proportion of female Lamprey when food availability was adequate and an increase in the proportion of males when food was scarce. The relationship between sex ratio and population dynamics of Lamprey was established by logistic growth model and Lotka-Volterra predator-prey model, and it was found that the change of sex ratio had a significant effect on the population size of Lamprey, which will affect the number of prey as well as the ecological factors such as water temperature and pH value. These discoveries reveal the important role of gender ratio in the ecosystem, and provide new perspectives and methods to solve the dynamics and resource utilization in the ecosystem.

Keywords: Lamprey, sex ratio, Ecology, Food availability.

1. Introduction

Lamprey populations have fluctuated over the past few decades, and such fluctuations have not only affected the survival of the lampreys themselves, but have also had a significant impact on their ecosystems. In particular, increases and decreases in lamprey populations can affect predator-prey relationships in the water, while also potentially altering important ecological factors such as water temperature and pH. Therefore, it is of great theoretical and practical importance to study the ecological impacts of changes in lamprey populations[1-2].

The ecological impact of changes in lamprey populations is a complex and systematic problem that requires a combination of several factors such as lamprey populations, sex ratios, and predator-prey relationships[3]. In particular, there is a strong correlation between lamprey abundance and sex ratio, which in turn affects lamprey predation behaviour and ecological niche distribution, and hence the aquatic ecosystem.

In order to solve this problem, this study will model the correlation between changes in the number of lampreys and sex ratio and predator-prey relationship. By collecting data on the number of lampreys, sex ratio, and predator population size, and applying mathematical modelling and statistical analysis methods, we will explore the impact mechanism of lamprey population changes on the aquatic ecosystem[4-5]. At the same time, the reliability and accuracy of the model were verified by combining the field survey and experimental data to provide a scientific basis for the management of the lamprey population and ecological environmental protection.

2. The Impact of Sex Ratio on Ecological Environment

2.1. Relationship Model Between Food Supply and Sex Ratio

The relationship between food supply and sex ratio in lampreys changes according to external environmental conditions. Research by the United States Geological Survey (USGS) and Michigan State University has revealed that whether lampreys become male or female depends on their growth
rate during the larval stage. Slower growth in the larval stage increases the likelihood of becoming male, with growth rate influenced by food supply\textsuperscript{[6]}. Based on this, a model relating food supply to growth rate is first established, followed by a model connecting growth rate to sex ratio. Combining these two models ultimately yields the relationship between food supply and sex ratio.

2.1.1. Relationship Model Between Food Supply and Growth Rate

The logistic growth model, typically applied to describe the growth of populations or organisms, is adapted here for individual lamprey growth, particularly under resource-limited conditions. Therefore, the logistic growth model is simplified and a new growth model for a single lamprey was established:

\[
\frac{dL}{dt} = \lambda (L_{\infty} - L) L
\]

\[L(0) = L_0\]  \hspace{1cm} (1)

Where \( L(t) \) represents the length of a lamprey at time \( t \), \( \lambda \) denotes the intrinsic growth rate influenced primarily by food quantity, \( L_{\infty} \) is the lamprey's ultimate length, and \( L_0 \) is the initial length\textsuperscript{[7]}.

For aquatic organisms exhibiting asymptotic growth, growth equations like the Von Bertalanffy Growth (VBG) Equation, Richards Growth Equation, Gompertz Growth Equation, or Robertson Growth Equation are suitable, each bearing physiological significance and indicating a limit to body length.

Where for the Richards growth equation, when \( a < 0 \), the inflection point of the equation increases as \( a \) increases; when \( a > 0 \), there is no inflection point within a meaningful range; when \( a = 1 \), it is equivalent to the VBG; when \( a \) tends to infinite, it is equivalent to the Gompertz growth equation; and when \( a = -1 \), it is equivalent to the Robertson equation. The choice between these models depends on the location of the inflection point of body length growth and differing parameters\textsuperscript{[8]}.

The VBG is identified as the most suitable model for lamprey populations, then the length of individual lampreys varies over time as follows:

\[L(t) = L_{\infty}[1 - e^{-\lambda(t-\tau)}]\]  \hspace{1cm} (2)

In 1965, Holling, based on experimental observations, proposed three distinct types of functional response functions for different species. Among these, the Type II functional response function is characterized as follows:

\[\phi(x) = \frac{x}{m + x}\]  \hspace{1cm} (3)

Assuming that a Type II functional reaction applies to the relationship between food quantity \( f \) and the growth of lampreys is as follows:

\[\lambda = \frac{\theta_1 f}{1 + \theta_2 f}\]  \hspace{1cm} (4)

Where \( \theta_1 \) denotes the coefficient of influence of food on the growth of lampreys, and \( \theta_2 \) denotes the saturation coefficient of the influence of food on lampreys.

2.1.2. Relationship Model Between Growth Rate and Sex Ratio

Drawing on literature and relevant data, the expanded literature model reveals that a Bayesian hierarchical logistic regression model is utilized to estimate the sex distribution of adult sea lampreys released into various streams and stillwater areas. The model treats the sex of adult sea lampreys captured in a specific year as a Bernoulli random variable\textsuperscript{[9]}. The probability of the lampreys being male is modeled as follows:
Where \( i \) is indexing a separate stream or type, i.e., whether it is a river or a stillwater area, \( z \) is the number of years to maturity after stocking \((0 \leq y \leq 5)\), type indexes whether a location is a river or a stillwater area, \( \alpha^{\text{type}}_i \) and \( \nu^{\text{type}}_i \) are location-specific intercepts and slopes, respectively, which are associated with the probability of being a male (on a logit scale) with \( y \).

\[
\begin{align*}
\alpha^{\text{type}}_i &= \alpha^{\text{type}}_0 + \delta^{\text{type}}_{\alpha i} \\
\nu^{\text{type}}_i &= \nu^{\text{type}}_0 + \delta^{\text{type}}_{\nu i}
\end{align*}
\]  

(6)

Where \( \alpha^{\text{type}}_0 \) and \( \nu^{\text{type}}_0 \) are the type-specific population averages for the parameters, \( \delta_{\alpha i} \) and \( \delta_{\nu i} \) are location-specific deviations from \( \alpha^{\text{type}}_0 \) and \( \nu^{\text{type}}_0 \), respectively.

The following vague priors were specified for the model:

\[
\begin{align*}
\alpha^{\text{type}}_0, \nu^{\text{type}}_0 &\sim MVN(0, \Sigma^{\text{type}}) \\
\delta_{\alpha i} &\sim N(0, \sigma_{\alpha i}) \\
\delta_{\nu i} &\sim N(0, \sigma_{\nu i}) \\
\Sigma^{\text{type}} &\sim \text{Wish}(2*2\text{identitymatrix}, 3) \\
\sigma_{\alpha i} &\sim \text{Unif}(0, 100) \\
\sigma_{\nu i} &\sim \text{Unif}(0, 100)
\end{align*}
\]

2.2. The Impact on Biological Factors

2.2.1. Predator-prey Model Considering Sex Ratio

The sex ratio within lamprey populations directly influences their own population dynamics, as lampreys require water and food for growth, primarily consisting of plankton and fish. Therefore, changes in the sex ratio of lamprey populations can affect the quantity of prey available, potentially leading to alterations in water temperature and pH values.

Around the year 1925, American mathematician Alfred J. Lotka and Italian mathematician Vito Volterra independently proposed a similar model capable of describing the fluctuation patterns observed in natural populations. This model, subsequently named the Lotka-Volterra model in honor of its creators, is also commonly referred to as the predator-prey model. It has evolved to become a seminal model in the study of ecological systems, characterizing the dynamic interactions between predators and their prey. The specific form is as follows:

\[
\begin{align*}
\frac{dU}{dt} &= \alpha U - \gamma UV \\
\frac{dV}{dt} &= -\beta V + e\gamma UV
\end{align*}
\]  

(7)

Where \( U(t) \) denotes the population density of prey at time \( t \) and \( V(t) \) denotes the population density of predators at time \( t \), viewed as the natural growth rate of prey, i.e., the difference between their natural birth rate and their natural death rate. \( e \) denotes the coefficient of conversion between the number of prey and the number of newborn predators, and denotes the proportion of prey captured by predators per unit of time.

According to relevant literature\(^9\), assuming that the population of lampreys is small and there is some difficulty in finding mates, we develop a model that takes the Allee effect\(^10\) into account.
\[
\begin{align*}
\frac{dF}{dt} &= r(t)CF - \frac{M}{\tau + M} \left(1 - \frac{F + M}{K}\right) - \mu_F F \\
\frac{dM}{dt} &= (1 - r(t))CF - \frac{M}{\tau + M} \left(1 - \frac{F + M}{K}\right) - \mu_M M
\end{align*}
\]

(8)

Where \( F(t) \) denotes the population size of female lampreys at time \( t \), \( M(t) \) denotes the population size of male lampreys at time \( t \); \( r(t) \) corresponds to the proportion of female lampreys at time \( t \); \( C \) is the average number of offspring per female lamprey per unit of time from all matings. \( \mu_F \) and \( \mu_M \) refer to the mortality rates of female and male lampreys, respectively; \( K \) is the overall environmental holding capacity of the lamprey, \( \tau \) quantifies the number of male lampreys unable to find a mate at time \( t \).

Combining the Lotka-Volterra model with a model that adds the effect of sex ratio to the population growth of male and female lampreys, we can assume the following relationship:

\[ C = e\gamma U(F + M) \]

then we obtain the following predator-prey model for lampreys:

\[
\begin{align*}
\frac{dF}{dt} &= r(t)F e\gamma U(F + M) - \frac{M}{\tau + M} \left(1 - \frac{F + M}{K}\right) - \mu_F F \\
\frac{dM}{dt} &= (1 - r(t))F e\gamma U(F + M) - \frac{M}{\tau + M} \left(1 - \frac{F + M}{K}\right) - \mu_M M \\
\frac{dU}{dt} &= \beta U - \gamma UF - \gamma UM
\end{align*}
\]

(10)

Assuming that a type II functional response also applies to the sex ratio change function, let the function be:

\[ r(t) = \frac{v_0 + v_1 e_{\gamma t}}{1 + e_{\gamma t}} \]

(11)

Where \( v_0 \) is the proportion of females in the total population at the initial time, \( v_1 \) is the sex ratio after stabilization of the population, \( e_0 \) is the coefficient of the effect of food on the sex ratio, and \( e_1 \) is the saturation coefficient of the effect of food on the sex ratio.

Since the environmental holding capacity is determined by the amount of food available during the larval period of the lamprey, the higher the amount of food, the higher the environmental holding capacity. It is assumed that the amount of food is positively proportional to the environmental holding capacity, that is:

\[ K = pf \]

(12)

Where \( p > 0 \) is a proportionality coefficient, it is a constant.

In addition, the amount of food determines the sex ratio at the initial moment, so we replace the amount of food with the proportion of overall female lampreys at the initial moment, that is:

\[ \tau = q(M(0) - F(0)) \]

(13)

Where \( q > 0 \) is a proportionality coefficient, it is a constant.

2.2.2. Solution of the Model

The model we ultimately require to solve is as follows:
Our parameter settings are described in Table 1.

<table>
<thead>
<tr>
<th>Parameter</th>
<th>$U_0$</th>
<th>$e$</th>
<th>$\gamma$</th>
<th>$\beta$</th>
<th>$p$</th>
<th>$q$</th>
<th>$\mu_F$</th>
<th>$\mu_M$</th>
</tr>
</thead>
<tbody>
<tr>
<td>Value</td>
<td>200</td>
<td>0.005</td>
<td>0.1</td>
<td>1.2</td>
<td>0.5</td>
<td>350</td>
<td>0.2</td>
<td>0.2</td>
</tr>
</tbody>
</table>

To investigate the impact of sex ratio on the ecosystem, we observe changes in the ecosystem by modifying parameters within the sex ratio change function. Given that in environments with insufficient food supply, the male ratio can reach up to 78%, whereas in environments with an abundance of food, the male ratio stands at 56%, our sex ratio function should aim for an eventual convergence towards 44%.

$$
\lim_{t \to \infty} r(t) = \lim_{t \to \infty} \frac{V_0 + v_1 \varepsilon_0 f}{1 + \varepsilon_1 t} = \lim_{t \to \infty} \frac{v_1 \varepsilon_0}{t} = \frac{v_1 \varepsilon_0}{\varepsilon_1} = 0.44
$$

In order to facilitate parameter adjustment, we set $v_1$, $\varepsilon_0$, and $\varepsilon_1$ as fixed values, only changing the proportion of female lampreys and the corresponding number of male and female lampreys at the initial time. All the parameter settings are shown in Table 2. Based on this, the solution results under five scenarios are displayed in Figure 1.

<table>
<thead>
<tr>
<th>Scenario</th>
<th>$v_0$</th>
<th>$F_0$</th>
<th>$M_0$</th>
<th>$K$</th>
<th>$\tau$</th>
<th>$v_1$</th>
<th>$\varepsilon_0$</th>
<th>$\varepsilon_1$</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>0.44</td>
<td>44</td>
<td>56</td>
<td>150</td>
<td>6</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>2</td>
<td>0.385</td>
<td>38</td>
<td>62</td>
<td>135</td>
<td>12</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>3</td>
<td>0.33</td>
<td>33</td>
<td>67</td>
<td>120</td>
<td>17</td>
<td>0.44</td>
<td>1</td>
<td>1</td>
</tr>
<tr>
<td>4</td>
<td>0.275</td>
<td>28</td>
<td>72</td>
<td>105</td>
<td>22</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>5</td>
<td>0.22</td>
<td>22</td>
<td>78</td>
<td>90</td>
<td>28</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
Through the results presented in Figure 1, it is observable that in conditions of ample food supply, marked by a higher proportion of female lampreys at the onset, both male and female lamprey populations increase almost synchronously, leading to a rise in the overall population size and a significant decline in the number of preys. As the population reaches a certain level, the scarcity of food sources, evidenced by a drastic reduction in prey, triggers a decline in lamprey numbers. As the prey's living conditions improve and their numbers begin to rise, the population of lampreys also starts to increase rapidly, following a cyclic pattern where the abundance of food leads to population growth, and this cycle repeats with lamprey numbers showing a lag of approximately a quarter period compared to the prey.
In contrast, when food is scarce, indicated by a lower proportion of female lampreys initially, the lack of sufficient food in the ecological environment leads to a decrease in prey numbers during the initial period. Consequently, both female and male lamprey populations exhibit a downward trend, with the overall lamprey population decreasing, and the rate of decline being faster for males. As a result, the proportion of female lampreys increases, eventually stabilizing. When the lamprey population diminishes to a certain extent, the prey's living conditions improve, and their numbers begin to rebound, showing cyclic variations in population sizes for both species, similar to the pattern observed under abundant food conditions.

With ample food supply, where the proportion of female lampreys approaches 0.5, the sex ratio-related predation model shows minimal influence from the sex ratio, and the overall trend is similar to that of a predation model that does not consider sex ratio. However, the lamprey population overall tends to decrease, a trend attributed to the female proportion nearing but not exceeding 0.5, influencing the overall trend in predator numbers.

Under conditions of food scarcity, significant differences in the sex ratio of the lamprey population lead to a sharp decline in total numbers, reflecting an adaptive response to environmental conditions. A larger disparity in sex ratio reduces competition within the species for food, allowing for better adaptation to the environment.

2.3. The Impact on Abiotic Factors

Many species exhibit significant sexual dimorphism in body size and other traits related to ecological function. However, according to the literature, the only morphological distinction in lampreys is that males are typically slightly larger than females, but this difference is not particularly pronounced. Consequently, we consider the potential impact of changes in the sex ratio of lampreys on communities and ecosystems.

Lampreys play a crucial role in the food chain, acting as parasites that can cause significant loss to fishery resources in ecosystems. In some parts of the world, such as France, Spain, and Portugal, they are also considered a food source. Changes in the sex ratio of lampreys can affect their predation pressure, thereby influencing the population numbers of their prey. This impact can propagate along the food chain, affecting higher trophic levels and even the stability of entire ecosystems.

As part of the ecosystem, lampreys contribute to various ecosystem services, providing feedback on their habitats, such as water purification and the stability of food webs. Changes in their sex ratio can alter lampreys' activity patterns and behaviors in ecosystems, subsequently affecting water flow and quality. These feedback effects can further influence environmental factors such as water temperature and pH values. Similarly, changes in the sex ratio of lampreys can affect the temperature and pH values in the ecosystems, as illustrated in Figure 2.

The influence of lamprey sex ratios on temperature and pH levels in ecological settings as illustrated in Figure 2, ecosystems with a male-biased sex ratio, where the proportion of males is higher, exhibit lower pH values and temperatures.

Male lampreys, compared to females, possess enhanced predatory capabilities, higher overall feeding rates, and greater nutrient excretion rates. This leads them to utilize resources more efficiently than females, including preying on prey and dominating territories. Consequently, their activities result in the excessive exploitation of resources and the discharge of more waste and metabolic products into ecosystems. This may contribute to a reduction in the water body's pH levels and temperatures.
3. Conclusions

Firstly, there is a close correlation between changes in lamprey populations and sex ratios, and changes in sex ratios will directly affect the ecological behavior and ecological niche distribution of lamprey populations. Therefore, in the management and protection of lamprey populations, the effects of changes in sex ratios on the ecosystem must be fully considered. Secondly, the increase or decrease of the lamprey population will directly affect the predator-prey relationship in the aquatic ecosystem. An increase in the number of lampreys may lead to an increase in the number of predators, thus affecting the survival status and ecological balance of other aquatic populations. Finally, the correlation model and data analyses established in this study can more accurately predict the impacts of lamprey population changes on the ecological environment, and provide scientific basis and decision-making reference for lamprey population management and ecological conservation.

In conclusion, the present study is of great significance for understanding the mechanism of the impact of lampreys’ population changes on the ecological environment, and provides a certain reference value for future related research and practical work.

References

