Study on Lamprey Population Growth and Sex Differentiation Models Using Bayesian Methods

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Abstract. This study developed a predictive model to assess the ecological impacts of changing sex ratios in various lamprey populations, categorizing them into parasitic, non-parasitic, anadromous, and potamodromous types. Critical data on temperature tolerance and growth durations for four representative species were collected to analyze the interactions under different sex ratios, focusing on both competitive and mutualistic dynamics within communities. The model explored sex differentiation mechanisms through various adjustment modes, linking lamprey growth rates to environmental factors like temperature and resource availability. Bayesian methods were utilized to integrate prior knowledge and address uncertainties, predicting larvae's sex-based outcomes. Additionally, a Bayesian biomass dynamic model evaluated population dynamics considering birth and death rates. Markov Chain Monte Carlo (MCMC) simulations within this Bayesian framework facilitated robust parameter estimation, significantly enhancing the understanding of how sex ratio changes impact species-specific and regional biodiversity and population dynamics.

Keywords: Logistic Growth Model, Bayesian Estimation, Bayesian Network Inference, Markov Chain Monte Carlo simulation.

1. Introduction

Lampreys, the oldest vertebrates, have survived 300-500 million years and numerous mass extinctions, playing a crucial role in aquatic ecosystems. Their life cycle includes four stages: embryo, larva, juvenile, and adult, with the larval phase being vital. This phase involves key physiological processes like gonadal development and sexual maturation, heavily influenced by environmental factors, particularly water temperature. Adult lampreys show a positive correlation between oxygen consumption and water temperatures, and temperature fluctuations impact their dermal photoreceptors, affecting behaviors like foraging. However, human activities and climate change have inflicted substantial damage on lampreys, yet the complexity of ecosystem interactions makes it challenging to quantify this impact.

Because of the great importance of temperature to aquatic life, understanding how temperature affects individuals is crucial to understanding the basic ecology of a species. To address this, this study built and optimized logical growth models and the Bayesian biomass dynamic model, providing a framework to understand the intricate dynamics of lamprey populations, their responses to environmental stressors, and the broader implications for ecosystem health and conservation strategies. The Bayesian method, integral to biological population assessments, incorporates uncertainty and prior knowledge, aiding in management strategy risk analyses. This statistical approach, based on Thomas Bayes' concept, interprets probability as belief, updating it with new evidence. Nonparametric frequentist estimation techniques are widely used but sensitive to outliers, which can skew results. To better understand the rationale behind selecting Bayesian estimation over other methods, it is essential to consider the distinctions between the available approaches in more detail. The Nonparametric Maximum Likelihood Estimation (NPMLE) method developed by Lindsay estimates species abundances as finite mixtures of point masses without specifying a parametric form [1]. However, NPMLE has limitations; determining the number of point masses relies on criteria like the Bayesian Information Criterion, which can introduce errors. Resampling for

error estimation often leads to a high proportion of outliers, and as Woodroofe noted, NPMLE can produce biased results in truncated data scenarios [2]. Parametric frequentist estimation, as outlined by Bunge, requires specifying species' abundance models and using maximum likelihood, challenging model selection and optimization. Artur J. Lemonte's exponentiated generalized inverse Gaussian distribution, intended for modeling lifetime data, extends approaches like the exponentiated standard gamma distribution [6]. However, its complexity and computational demands in deriving structural properties such as moments can hinder practical application, despite offering robust theoretical insights. Parametric Bayesian estimation, using priors on species numbers and abundance parameters, ensures logical, discrete posterior species counts with asymmetric credible intervals. This method simplifies computation in complex spaces and avoids risky optimization. the approach has been effectively applied in diverse fields. Effectively applied by W. A. Lewins in ecological studies with a zero-truncated negative binomial distribution [7], and by Darren J. Wilkinson in bioinformatics, it enhances data integration and uncertainty management in sophisticated biological modeling [8].

This study developed a predictive model to assess the ecological impacts of changing sex ratios in lamprey populations, categorized as parasitic, non-parasitic, anadromous, and potamodromous. Data on temperature tolerance and growth for four species were analyzed to explore interactions under different sex ratios, focusing on both competitive and mutualistic dynamics. The model linked lamprey growth rates to environmental factors like temperature and resource availability, using Bayesian methods to integrate prior knowledge and address uncertainties. Markov Chain Monte Carlo simulations enhanced parameter estimation, improving the understanding of how sex ratio changes affect biodiversity and population dynamics.

2. Growth and Sex Differentiation in Lampreys

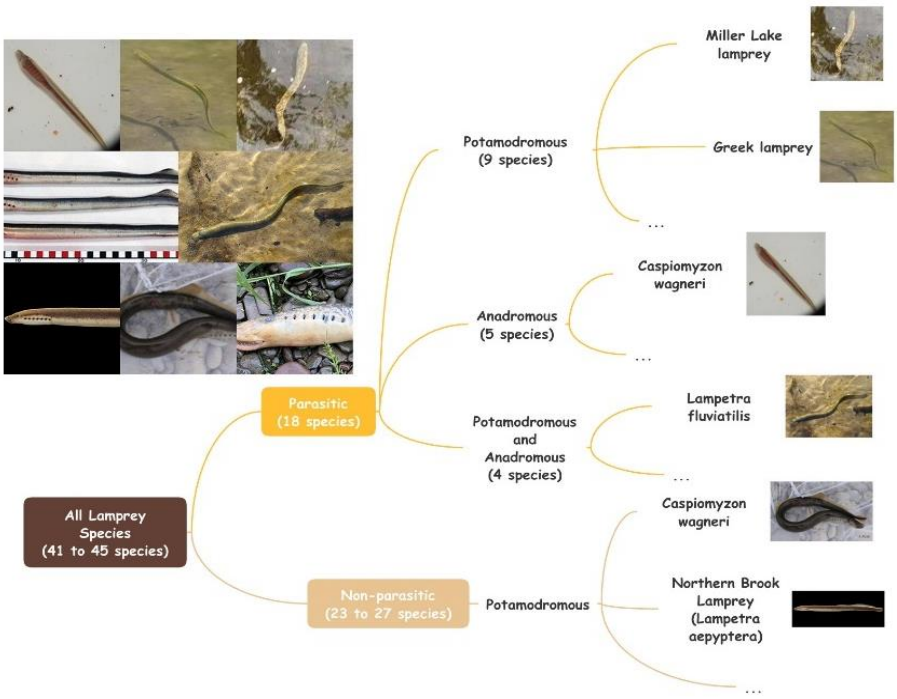


Figure 1: The situation of 45 species of Lampreys

As known from the review, the differential characteristics among different varieties are significant, especially between parasitic and non-parasitic types, as well as between Anadromous and Potamodromous types (Figure 1).

Therefore, based on these two characteristics, this study selected four representative species and collected their basic information from relevant literature, such as temperature range, average growth years, etc. (Table 1) Timothy A. Whitesel (2022) provides data on lethal and sublethal temperature thresholds for Pacific lamprey larvae, noting survival rates at a range of temperatures for chronic and

acute exposure experiments, highlighting significant mortality at temperatures of 30.7°C and above. Paul M. Sankovich and Timothy A [3]. Whitesel (2023) details the effects of stream temperature on larval growth and behavior, with data ranging from 16.2°C to 30.4°C for different regions, and assesses physiological responses such as hepatic body index. In addition, Michael H. Meeuwig et al. (2005) measured the length and mass of Pacific and West Stream lampreys under different temperature conditions, allowing analysis of developmental changes associated with temperature fluctuations. This study also utilized data from Johnson et al. (2014, 2016) on larval sea lampreys, focusing on survival and metamorphosis rates [12]. The studies provided specific growth metrics, such as the Brody growth coefficient and the length at which 50% of larvae undergo metamorphosis, differentiated by stream and lentic environments. The data also included survival percentages and density-dependent growth effects across various habitats.

Lethenteron camtschaticum is commonly found in Lake Superior, partly anadromous, feeding on fish like salmon and lake trout, and is the Arctic's most prevalent lamprey.

(2) Eudontomyzon Mariae, primarily in Lake Erie, has a parasitic adult phase targeting fish such as salmon and is Europe's most common lamprey [9].

(3) Ichthyomyzon gagei occupies Lake Huron, clings to large fish for sustenance, and feeds on plankton and algae [4].

(4) Petromyzon marinus, located in Lake Michigan, has a unique migratory pattern, parasitizes cold-water fish, and serves as a key food source during its breeding season.

Table 1: Information on Four Representative Lamprey Species in the Great Lakes Region

Species	Habitat	Parasitic	Anadromous
Lampreys	Lake Superior	Yes	No
Ukrainian Brook Lamprey	Lake Erie	No	Yes
Southern Brook Lamprey	Lake Huron	No	No
Sea Lamprey	Lake Michigan	Yes	Yes

2.1. Ecosystem Effects on Growth Rates

2.1.1 Expression for LGR Influenced by Temperature

Temperature is a critical environmental factor that can significantly impact the metabolic rate of poikilothermic organisms, thereby influencing their growth rate[10]. In our ecological growth model, this study incorporates the function $f(T)$ to understand how environmental temperature influences Lamprey growth, as Equation 1.

$$LGR(t) = \left(\frac{LGR_{max} \cdot R(t)}{K + R(t)}\right) \cdot f(T(t)) \tag{1}$$

Where T_{max} and $T_{\min}$ represent the upper and lower horizontal asymptotes of the curve, respectively, b control the slope of the curve, and c is the midpoint of the curve. $LGR_{\max}$ represents the maximum larval growth rate under ideal conditions. K denotes the ecological carrying capacity. $R(t)$ is the resource availability at time t, and $LGR(t)$ is the growth rate at time t, which approaches $LGR_{\max}$ as resources exceed K. This expression is based on a symmetric S-shaped regression model, which is particularly useful in describing biological responses that exhibit threshold effects.

This study collected data on temperature and growth conditions from existing studies [4], using nonlinear least squares to estimate unknown parameters. The temperature Limits and parameter estimation results for representative Lamprey varieties are shown in Table 2:

Table 2: Temperature Limits and Estimation Results of Parameters for Four Representative Species

Species	Category	T_{max}	b	c
Lampreys	Lethenteron camtschaticum	29.3	9.69	25.32
Eudontomyzon mariae	Ukrainian Brook Lamprey	28.8	24.4	9
Ichthyomyzon gagei	Southern Brook Lamprey	28.9	16	
Petromyzon marinus	Sea Lamprey	28.6	10.4	9

2.1.2 Expression for LGR Influenced by Resource Availability

The logistic growth rate function $LGR(t)$ is a variation of the standard logistic growth model, adapted to explicitly incorporate the role of a resource variable $R(t)$ over time, this study has Equation 2.

$$LGR(t) = \frac{LGR_{max} \cdot R(t)}{K + R(t)} \tag{2}$$

where The growth rate increases $R(t)$, reflecting more resources leading to faster growth. The growth rate approaches $LGR_{\max}$ as $R(t)$ becomes much larger K, indicating a saturation point. Equation 2 reflects the biological reality that while increased food leads to faster growth, there's a limit to how much growth can be accelerated, even with abundant food.

2.1.3 Model the Growth of Larvae Over Time

To transition from the conceptual framework of growth rates to the empirical quantification of actual growth, this study conceptualized the growth rate as the derivative of size concerning time, thereby formulating a differential equation to model the growth dynamics of larvae。

To find the size of the larvae as a function of time, integrate the growth rate over time, as equation 3:

$$\frac{dL(t)}{dt} = LGR(t) + C \tag{3}$$

$$L(t) = \int_0^A LGR(t)dt + C \tag{4}$$

Where A represents the species' average age at maturity. $L(t)$ represents the length of larvae at a time t. According to existing research, there is significant variation in the age at maturity among varieties, so this study chose to use the average age at maturity within each variety as the upper limit of integration [5]. Growth Simulation Results for Lamprey are shown in Figure 2.

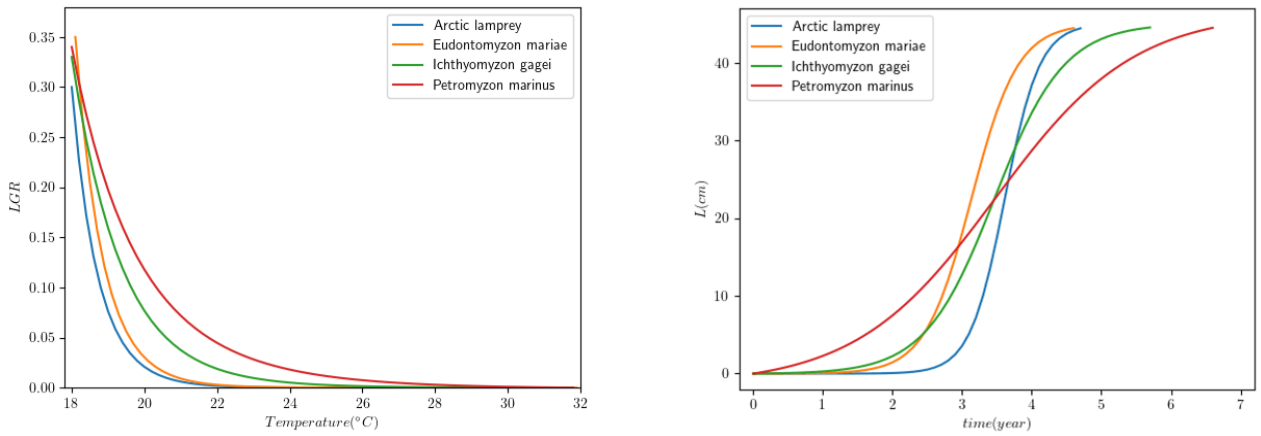


Figure 2: Growth Simulation Results of Lamprey in the Great Lakes Region

Initially, all species grew slowly, peaking at 3-4 years, then stabilizing at 5-6 years. Lampreys began smaller but exceeded Eudontomyzon mariae in size after 3 years. Eudontomyzon mariae and Ichthyomyzon gagei showed similar growth, while Petromyzon marinus, starting largest, grew steadily, indicating the highest potential asymptotic length among them.

2.2. Ecosystem effects on sex differentiation

The objective of sex differentiation modeling is to understand the mechanisms of sex differentiation in Lampreys. The study has focused on:

(1)The Modes of Sex Ratio Differentiation

(2) The Outcomes of Sex Ratio Differentiation

(3) The Variations of Sex Ratio Differentiation

2.2.1 The Modes of Sex Ratio Differentiation

The mode of sex differentiation dictates the form of the function. In studying biological principles, this study discovered that sex differentiation in Lampreys is a typical binary outcome (i.e., individuals ultimately manifest as either female or male). Hence, the logistic regression function is an ideal analytical tool, as its output is a probability value that lies between 0 and 1, closely with the actual situation in Lampreys.

2.2.2 The Outcomes of Sex Ratio Differentiation

After defining the function, it's crucial to account for ecosystem factors affecting sex differentiation likelihood in lampreys.

Research indicates larval growth rate is a key determinant of sex [5]. This model excludes genetic and hormonal influences, focusing on the relationship between growth rate and sex probability, as equation 5.

$$P(\text{Male}|LGR, A) = \frac{1}{1 + e^{-(\beta_0 + \beta_1 \times LGR + \beta_2 \times A)}} \tag{5}$$

In Equation(5), $P(\text{Male}|LGR, A)$ P(Male |LGR, A) denotes the chance of larval male development based on growth rate and age, bounded between 0 and 1 by the Sigmoid function. Parameters β_0 β_1 , β_2 are data-derived, LGR indicating larval growth rate and A representing maturity age, marking sex differentiation timing.

2.2.3 The Variations of Sex Ratio Differentiation

Studies indicate varying sex differentiation sensitivity across species; Arctic lamprey's sex probability is more growth rate-dependent than Eudontomyzon Mariae [9], implying multifaceted factors in sex change probability. A species interaction term S is introduced to the model to address these species-specific influences.

$$P(\text{Male}|LGR, A, S) = \frac{1}{1 + e^{-(\beta_0 + \beta_1 \times LGR + \beta_2 \times A + \beta_3 \times S + \beta_4 \times LGR \times S}} \tag{6}$$

3. Bayesian Modeling of Lamprey Population Dynamics

3.1. The Introduction of the Central Limit Theorem

The study aims to assess the probability of Lamprey larvae becoming males, influenced by growth rates and environmental factors, using Bayesian methods to incorporate prior knowledge and address data uncertainties. It proposes a model based on the assumption that individuals in the population are independent, using the Central Limit Theorem to calculate the sex ratio, where each larva's development into a male is considered a Bernoulli trial. As Equation (7):

$$X = X_1 + X_2 + \cdots + X_n \tag{7}$$

Where X_i is a Bernoulli random variable representing whether the ith individual is male (1 for male, 0 for female). The expected value $E[X]$ and variance $Var[X]$ of the Lamprey population can be expressed as:

$$E[X] = \sum_{i=1}^{n} E[X_i] = \sum_{i=1}^{n} p_i, Var[X] = \sum_{i=1}^{n} Var[X_i] = \sum_{i=1}^{n} p_i(1-p_i) \tag{8}$$

Therefore, X is approximated as normally distributed with:

$$X \sim \mathcal{N}\left(\sum_{i=1}^{n} p_i, \sum_{i=1}^{n} p_i(1-p_i)\right) \tag{9}$$

Assuming that p_i is the same for all individuals (i.e. $p_i = p$), it simplifies to: $X \sim \mathcal{N}(np, np(1-p))$ Define the sex ratio as $SR = N_{(Male)}/N$, where $N_{(Male)}$ is the number of males and n is the total population size. Based on the definition of sex ratio, the expected and variance of the population gender ratio are expressed as:

$$E[SR] = \frac{E[N_{(Male)}]}{N} = p, Var[SR] = \frac{Var[N_{(Male)}]}{N^2} = \frac{p(1-p)}{N} \tag{10}$$

Therefore, the distribution of gender ratio SR $SR \sim \mathcal{N}\left(p, \frac{p(1-p)}{N}\right)$ is. Given the condition of $LGRAS$, the expected male proportion SR in the population as Equation (11)

$$SR = p = \frac{1}{1 + e^{-(\beta_0 + \beta_1 \times LGR + \beta_2 \times A + \beta_3 \times S + \beta_4 \times LGR \times S}} \tag{11}$$

Using the above model, the sex ratio of lamprey races in the Great Lakes of the United States was derived (Fig 3).

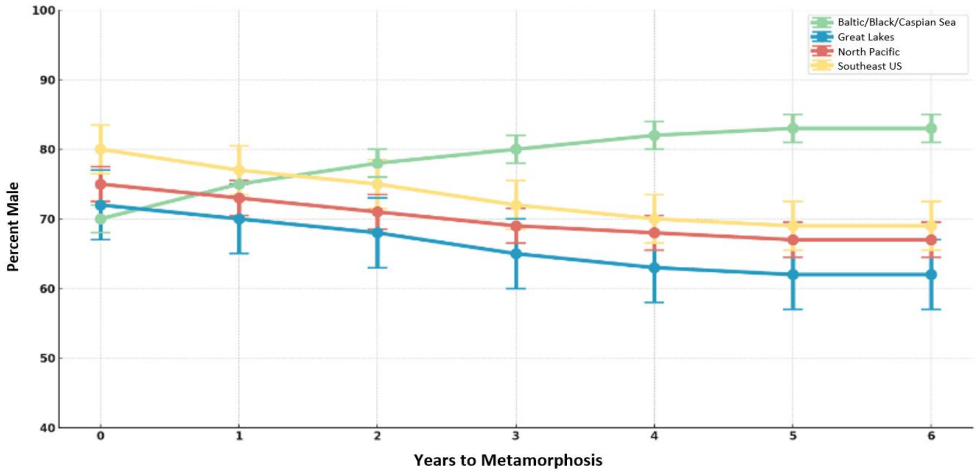


Figure 3: Sex Ratio Changes in the Lamprey Population in the Great Lakes region

3.1.1 Dynamics of Population Size

This study uses a Bayesian biomass dynamic model to analyze and predict population dynamics, considering the impact of birth rate, death rate, and environmental factors on changes in population size. The model parameters are estimated using Bayesian statistical methods to provide a probabilistic description of the future development of the population.

3.1.2 The dynamic impact of sex ratio on population size

As this paper hypothesizes, the birth rate is proportional to the number of female individuals and inversely proportional to the sex ratio. The birth rate of the population is given by Equation (12):

$$B = k\frac{N_t \times (1 - SR)}{1 + SR} \tag{12}$$

Where the sex ratio SR is defined as the ratio of the number of male individuals to female individuals, N is the total population, and k represents the maximum fertility of each female individual when the sex ratio is balanced. It is usually between 65% and 85%. This paper takes the average of the existing research conclusions, 75%[10].

$$r_{t+1} = B_t - D_t \tag{13}$$

D_t: The death rate from time t to $t+1$. B_t: The birth rate from time t to $t+1$.

3.1.3 Concept of Stratification for Regional and Species Differences

This paper introduces the concept of a Bayesian hierarchical model based on the Bayesian biomass dynamic model, allowing lampreys to show their variability at different levels, and to assess the impact of the effects of specific locations and specific species on population dynamics.

(1) First level (global level): Define global parameters that describe the dynamics of the population.

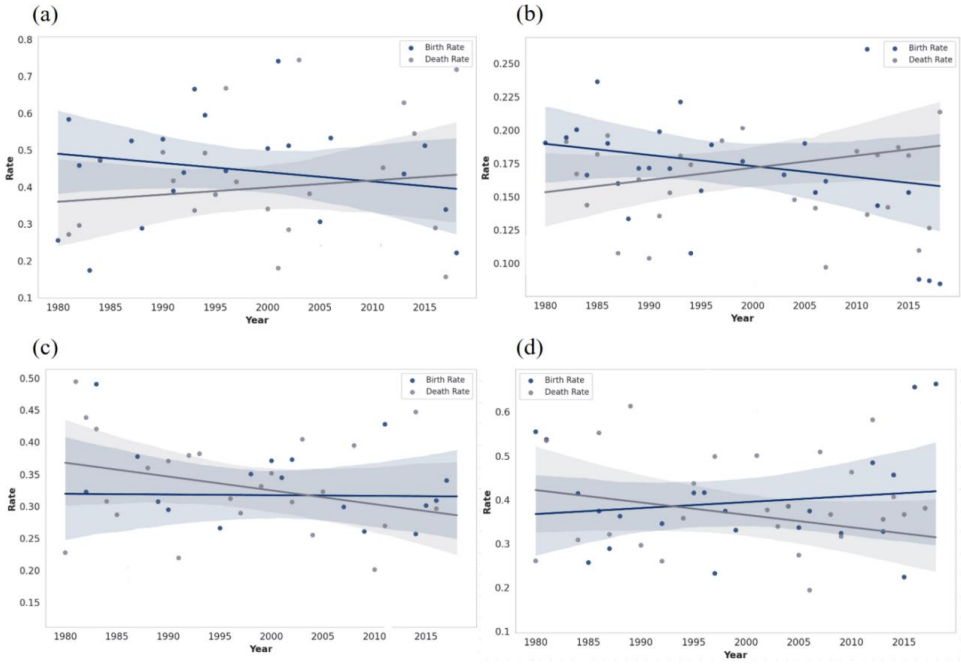


Figure 4: Birth and Death Rates Over Time for Four Representative Species

For each species j, the global birth rate and death rate follow a normal distribution(figure 4):

$$B_{global,j} \sim \mathcal{N}(\alpha_{B,j}, \beta_{B,j}) \tag{14}$$

$$D_{global,j} \sim \mathcal{N}(\alpha_{D,j}, \beta_{D,j}) \tag{15}$$

(2) Second level: Define parameters for each species j, representing birth and death rate deviations as normal distributions:

$$\Delta B_j \sim \mathcal{N}(0, \sigma_{B,j}^2) \tag{16}$$

$$\Delta D_j \sim \mathcal{N}(0, \sigma_{D,j}^2) \tag{17}$$

Integrating the global parameters and species-specific parameters, the actual birth rate and death rate of each species:

$$B_j = B_{global} + \Delta B_j \tag{18}$$

For each species j, this study establishes a Bayesian hierarchical dynamic model Equation (19):

$$N_{t+1,j} = N_{t,j} + (B_j - D_j)N_{t,j}\left(1 - \frac{N_{t,j}}{K_j}\right) + \varepsilon_{t,j}, \varepsilon_t \sim \mathcal{N}(0, \sigma^2) \tag{19}$$

Where, $N_{t+1,j}$ is the population size of species j at a time $t+1$. K_j is the ecological carrying capacity of species j. $(B_j - D_j)$ represents the intrinsic growth rate of the species. $\varepsilon_{t,j}$ is the difference between the model and actual observations.

3.2. Parameter Estimation in the Bayesian Framework

3.2.1 Setting of Prior Distribution for Parameters

The population distribution, influenced by many small, independent biological and environmental factors, typically forms a normal distribution around the mean. Based on lamprey studies[7][9], the prior distributions for parameters B_t D_t, and K are detailed in Table 3.

Table 3: Prior probability distribution of population dynamic model parameters *B*, *D*, and *K*

Species	Carrying capacity K	Birth rate B	Dead rate D
Arctic lamprey	$K_{i=1} \sim \mathcal{N}(0.63, 0.06)$	$B_{i=1} \sim \mathcal{N}(0.51, 0.15)$	$D_{i=1} \sim \mathcal{N}(0.11, 0.09)$
Eudontomyzon Mariae	$K_{i=2} \sim \mathcal{N}(0.65, 0.0.09)$	$B_{j=2} \sim \mathcal{N}(0.49, 0.09)$	$D_{i=2} \sim \mathcal{N}(0.34, 0.0.1)$
Ichthyomyzon gagei	$K_{i=3} \sim \mathcal{N}(0.63, 0.17)$	$B_{i=3} \sim \mathcal{N}(0.35, 0.15)$	$D_{i=3} \sim \mathcal{N}(0.29, 0.07)$
Petromyzon marinus	$K_{i=4} \sim \mathcal{N}(0.38, 0.12)$	$B_{i=4} \sim \mathcal{N}(0.57, 0.06)$	$D_{i=4} \sim \mathcal{N}(0.53, 0.09)$

3.2.2 Establishment of Likelihood Function

The likelihood function, comparing observed to predicted population sizes, is constructed from the normal distribution's probability density function, given $N_{t,j}, B_j, D_j, K_j, \sigma^2$.

$$L = \prod_{t,j} \frac{1}{\sqrt{2\pi\sigma^2}} \exp\left(-\frac{\left(N_{t+1,j} - \left(N_{t,j} + (B_j - D_j)N_{t,j}\left(1 - \frac{N_{t,j}}{K_j}\right)\right)\right)^2}{2\sigma^2}\right) \tag{20}$$

L represents the probability of all observed data appearing jointly under given model parameters, i.e., the likelihood.

This paper obtained the following changes in the population of Lampreys in the five major lakes on Figure 5.

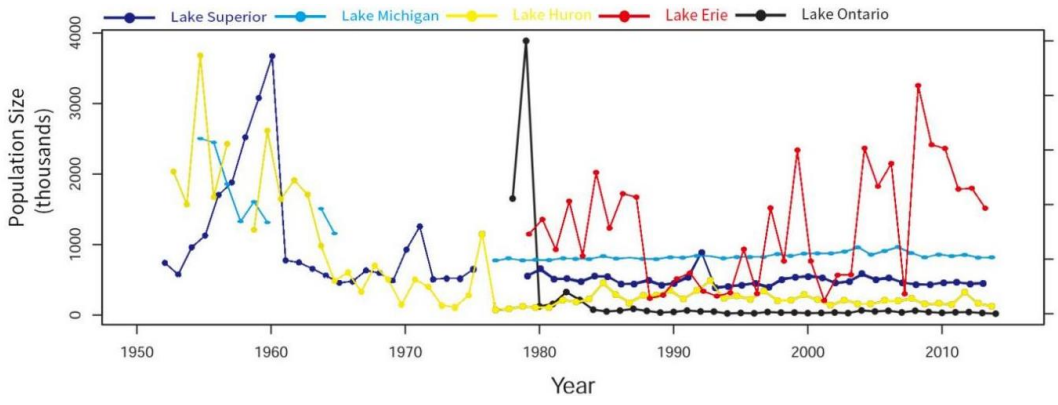


Figure 5: U.S. Great Lakes Lamprey population size numbers

3.2.3 Use of Markov Chain Monte Carlo (MCMC) Simulation

Markov Chain Monte Carlo (MCMC) simulation is a statistical sampling method that generates samples from complex probability distributions by constructing Markov chains. Our MCMC simulation is as follows:

(1) Initialization The initial values for the simulation are $B_{i,j}^0 = 1, D_{i,j}^0 = 0, K_{i,j}^0 = 1$. The prior distribution is set according to Table 4.

(2) Calculation of Acceptance Probability the Metropolis-Hastings algorithm is used to calculate the acceptance probability. Each parameter's candidate value is accepted or rejected based on this acceptance probability. For example, the acceptance probability for the parameter B_j is:S

$$P(B_j, B_j') = \min\left(1, \frac{L(N_{t+1,j}|B_j', D_j, K_j, \sigma^2) \times P(B_j')}{L(N_{t+1,j}|B_j, D_j, K_j, \sigma^2) \times P(B_j)}\right) \tag{21}$$

(3) Iteration: Repeat the above steps until convergence criteria are met or a predetermined number of iterations are reached.

3.2.4 Parametric Simulation Results for MCMC

Upon the completion of 20,000 iterations, the computational process yields a comprehensive set of estimation results. These results pertain to the key parameters denoted as K (carrying capacity), B (birth rate), and D (death rate). This organized presentation is found in Table 4, where the readers are afforded a clear and systematic overview of the parameter estimates, with different lamprey species in the Great Lakes ecosystem(Table 4).

Table 4: The estimated values of model parameters

Species	Parameter	Mean	CV	2.5% quantile	25% quantile	75% quantile	97.5% quantile
Lampreys	$K_{j=1}$ $B_{j=1}$ $D_{j=1}$	0.31 0.68 0.26	0.14 0.12 0.65	-0.02 0.52 -0.07	-0.06 0.63 0.15	0.39 0.73 0.37	0.62 0.84 0.59
Eudontomyzon mariae	$K_{j=2}$ $B_{j=2}$ $D_{j=2}$	0.29 0.54 0.19	0.65 0.35 0.95	-0.03 0.17 -0.16	-0.02 0.41 0.07	0.47 0.67 0.31	0.39 0.91 0.54
Ichthyomyzon gagei	$K_{j=3}$ $B_{j=3}$ $D_{j=3}$	0.30 0.27 0.41	0.85 0.19 0.49	0.03 0.17 0.02	0.03 0.24 0.28	0.51 0.30 0.54	0.44 0.37 0.80
Petromyzon marinus	$K_{j=4}$ $\boldsymbol{B}_{j=4}$ $D_{j=4}$	0.57 0.38 0.37	0.43 0.32 0.43	0.04 0.30 0.06	0.04 0.30 0.26	0.64 0.46 0.48	0.53 0.62 0.68

4. Conclusions

The Lamprey Population Impact Model thoroughly examines how ecological factors affect lamprey populations, using a sophisticated analytical approach. By integrating a logistic growth model that encompasses both intrinsic growth rates and ecological carrying capacities, this study illuminates the developmental trajectories of lampreys. Enhanced by the inclusion of variable resource availability and temperature fluctuations, the analysis provides a detailed perspective on growth and sex differentiation. Applying this refined model to four distinct Great Lakes lamprey

species uncovers unique evolutionary adaptations, evident even in consistent environmental settings. For broader population analysis, the model employs the Central Limit Theorem to dynamically modify essential ecological indicators such as birth and death rates. Confronting data shortages, Bayesian estimation techniques are used, treating larval transformations into males as probabilistic events and applying hierarchical models to account for differences among species.

This study demonstrates a robust framework for investigating lamprey population growth and sex differentiation using Bayesian methods, underscoring the viability of this approach in population ecology. By treating individual larval developments into males as probabilistic Bernoulli trials and incorporating hierarchical models to address species-level variability, the research provides a novel methodological insight that enhances understanding of ecological dynamics. These findings pave the way for future investigations into the factors influencing lamprey populations, including genetic and environmental interactions that drive sex differentiation. The successful application of Bayesian estimation in this context not only enriches the theoretical landscape of ecological modeling but also offers practical pathways for managing and conserving lamprey populations under diverse environmental conditions. This approach's adaptability and depth could significantly inform conservation strategies and ecological management practices moving forward.

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