

### Summary

Environmental sex determination (ESD) is prevalent among reptiles and fishes. This strategy is believed to reflect an evolutionary adaptation in animals where sex specific differences lead to a skewed sex ratio at birth. Lamprey go through a stage-structured life cycle with the majority of their life spent in the larval stage. It has been shown that larval growth rate is inversely related to the percentage of larvae that grow into male. Our task is to propose the ecosystem and demographic consequences of this varying sex ratio.

First, we develop an **Adaptive Population Control (ACC)** model that explains the skewed sex ratio at high and low levels of resource availability as a control measure by lamprey to maximize their growth rate. We find that the advantage of a variable sex ratio is greatest under extremely poor or extremely suitable environmental conditions.

Next, to account for the male skewed populations of lamprey at high densities, we develop a modified logistic growth model that allows for variable carrying capacity for males and females. **Differential Carrying Capacity (DCC)** model accurately predicts the optimal sex ratio to achieve the maximal growth rate at various population densities.

In line with ACC, we use **Aquatic Nutritional Network (ANN)**, a niche width differential equation model is developed by integrating concepts from Lotka-Volterra equations. to study the dynamics of lamprey and their native prey/predator. We find that variable sex ratios allow time for regeneration of the native prey in Lamprey.

Lastly we study the effect of generation time on the population growth rate in lamprey. Considering the highly variable duration of the larval stage, we model intrinsic growth rate of lamprey as an inverse function of its generation time.

**Keywords:** Lamprey Biofeedback Model (LBM); Lotka-Volterra Equations; Aquatic Nutritional Network (ANN); Generation Time-Control Model (GTM); Differential Carrying Capacity (DCC)

# Contents

<b>1</b>	<b>Introduction</b>	<b>3</b>
1.1	Background . . . . .	3
1.2	Problem Restatement and Analysis . . . . .	3
1.3	Overview of our work . . . . .	4
<b>2</b>	<b>Assumptions</b>	<b>4</b>
<b>3</b>	<b>List of Notation</b>	<b>6</b>
<b>4</b>	<b>Adaptive Population Control (APC)</b>	<b>6</b>
4.1	Lamprey Population Growth . . . . .	6
<b>5</b>	<b>Generation Time Control</b>	<b>9</b>
5.1	Aquatic Nutritional Network . . . . .	10
5.2	Dynamic Equations of ANN . . . . .	10
5.3	ANN Results . . . . .	13
5.4	Differential Carrying Capacity (DCC) Model for Lamprey Populations . . . . .	14
<b>6</b>	<b>Model Simplification and Analysis</b>	<b>14</b>
6.1	Numerical Solution Approach for the APC Model . . . . .	14
<b>7</b>	<b>Sensitivity Analysis</b>	<b>15</b>
7.1	ANN Sensitive Analysis . . . . .	15
7.2	APC Sensitive Analysis . . . . .	17
<b>8</b>	<b>Evaluate of the Model</b>	<b>19</b>
8.1	Strengths and weaknesses . . . . .	19
<b>9</b>	<b>Conclusions</b>	<b>19</b>

# 1 Introduction

Ecosystem equilibrium relies significantly on sex ratios within animal populations. This study investigates the sea lamprey (*Petromyzon marinus*), focusing on the relationship between local resource availability, sex ratio variances, and their ecological effects.

## 1.1 Background

Understanding the life cycle of the sea lamprey is critical to comprehending their ecological role and the impact of sex ratio variation. The sea lamprey exhibits a complex life cycle that is divided into distinct stages, each critical to their development and survival.

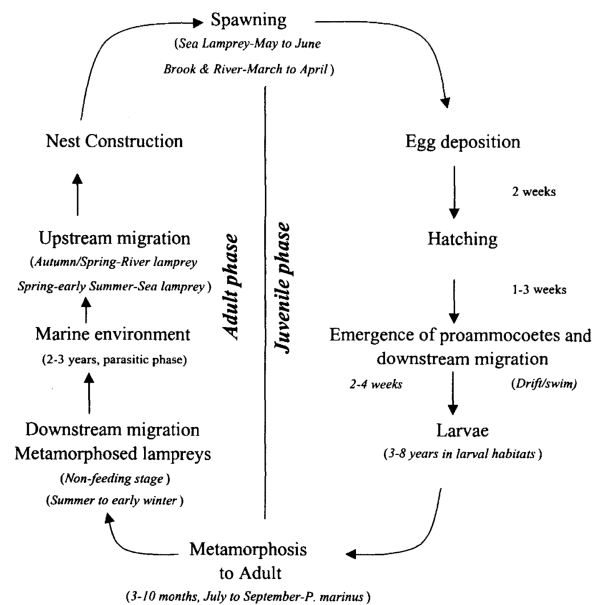


Figure 1: General Life Cycle of Lampreys

Comprehending the sea lamprey's life cycle is pivotal for understanding their ecological impact. The species' complex developmental journey is captured in **Figure 1**, highlighting the critical stages from spawning migration to the culmination of their marine phase.

## 1.2 Problem Restatement and Analysis

We are asked to model the effect of variable sex ratio in lamprey on demographic and ecosystem aspects of this animal. We assume the environmental sex determination in lamprey to be an adaptive strategy that maximizes growth rates at varying resource availability. Building upon this assumption, we measure demographic consequences of this variable sex ratio on lamprey population.

- To understand the ecological consequences of variable sex ratio we build a stage-structured food chain for lamprey and analyzed the behavior at equilibrium for varying sex ratios.

- To reflect the adaptive mechanism of variable sex ratio on population growth, we study the effect of changing sex ratio on population growth rate in lamprey.
- Analyzing the dynamical behavior of lamprey's ecosystem, we identify the stability points and determine if (any) species could gain from a changing sex ratio.
- We propose the long duration of sex indeterminacy and high sensitivity to resource availability as a potential disadvantages of variable sex ratio.

### 1.3 Overview of our work

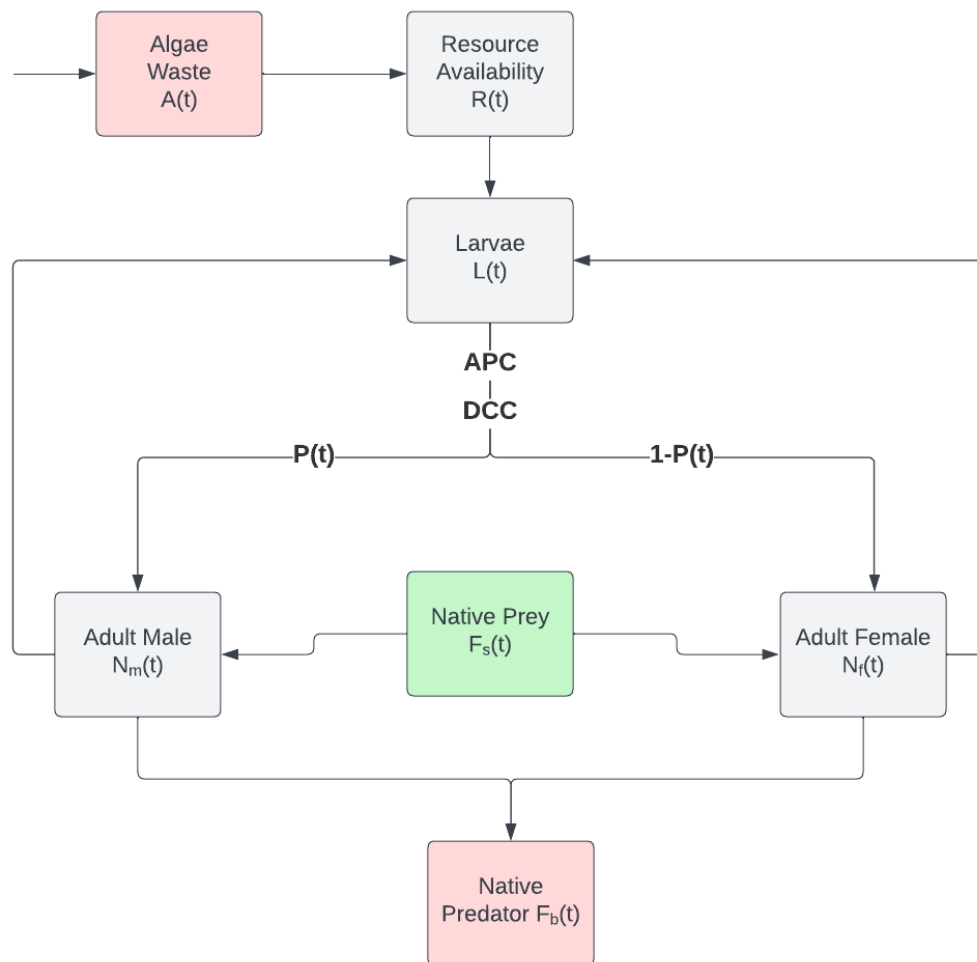


Figure 2: Mindmap

## 2 Assumptions

- In our assumption, we adopt the Lotka-Volterra predator-prey model to describe the interactions within our biological system.

- The mating system in lamprey is polygandrous.
- Lamprey males invest more in a single mating compared to females. Male lampreys develop a nest and produce pheromones before mating and also increase energy input into reproduction in the presence of male competitors (? ), indicating that mating is more expensive to male sex.
- Resource availability affects male and female lamprey fitness differently with male fitness being higher at higher levels of resource availability.
- Carrying Capacity for male lamprey is assumed to be bigger than the carrying capacity for female lamprey. This assumption is based on the direct observation that more dense populations of lamprey are male skewed.
- Both male and female lamprey should reach a certain size (100-120 mm) before metamorphosis. (16)
- The time from developing eggs to hatching is negligible in calculating lamprey generation time

### 3 List of Notation

Table 1: Variables and Parameters in the Ecological Model

Symbol	Description	Units
$L$	Number of larvae	individuals
$\alpha$	Interaction rate between male and female nutrients	1/time
$A$	Amount of algae (or primary resource)	mass
$K_A$	Half-saturation constant for algae effect on birth rate	dimensionless
$N_m$	Number of male nutrients or total number of males	individuals
$N_f$	Number of female nutrients or total number of females	individuals
$K_L$	Carrying capacity for larvae	individuals
$m$	Natural mortality rate of larvae	1/time
$K_m$	Half-saturation constant for algae effect on mortality rate	dimensionless
$c_l$	Natural growth rate of algae	mass/time
$a_l$	Rate at which algae is consumed by larvae	1/time
$F_s$	Number of parasitic objects or small fish	individuals
$c_s$	Intrinsic growth rate of small fish	individuals/time
$K_{F_s}$	Carrying capacity for small fish	individuals
$e_s$	Environmental loss factor for small fish	1/time
$F_b$	Number of native predators or big fish	individuals
$b_m, b_f$	Predation rates on male and female fish, respectively	1/time
$K_{F_b}$	Carrying capacity for big fish	individuals
$c_f$	Mortality of big fish	1/time
$e_b$	Environmental benefit factor for big fish	1/time
$P$	Proportion of larvae maturing into males	dimensionless
$k$	Brody Growth Coefficient	1/year
$K_{N_m}, K_{N_f}$	Carrying capacities for male and female nutrients, respectively	individuals

We have been tasked with evaluating the effects of varying sex ratios in lampreys on demographic aspects and interspecies interactions of this parasite. Given the inverse relationship between larval growth rates and the percentage of males in the population, we consider environmental sex determination (ESD) in lampreys to be an adaptive strategy. Importantly, we hypothesize that higher larval growth rates are indicative of better resource availability

## 4 Adaptive Population Control (APC)

We propose that the lamprey population regulates the sex ratio of developing larvae to maximize the population growth. (Figure 3)

### 4.1 Lamprey Population Growth

- We know that male lamprey invest heavily in a single mating event by producing pheromones and building the nest. based on this assumption we propose that male lamprey would benefit more in productive environment compared to female lamprey.

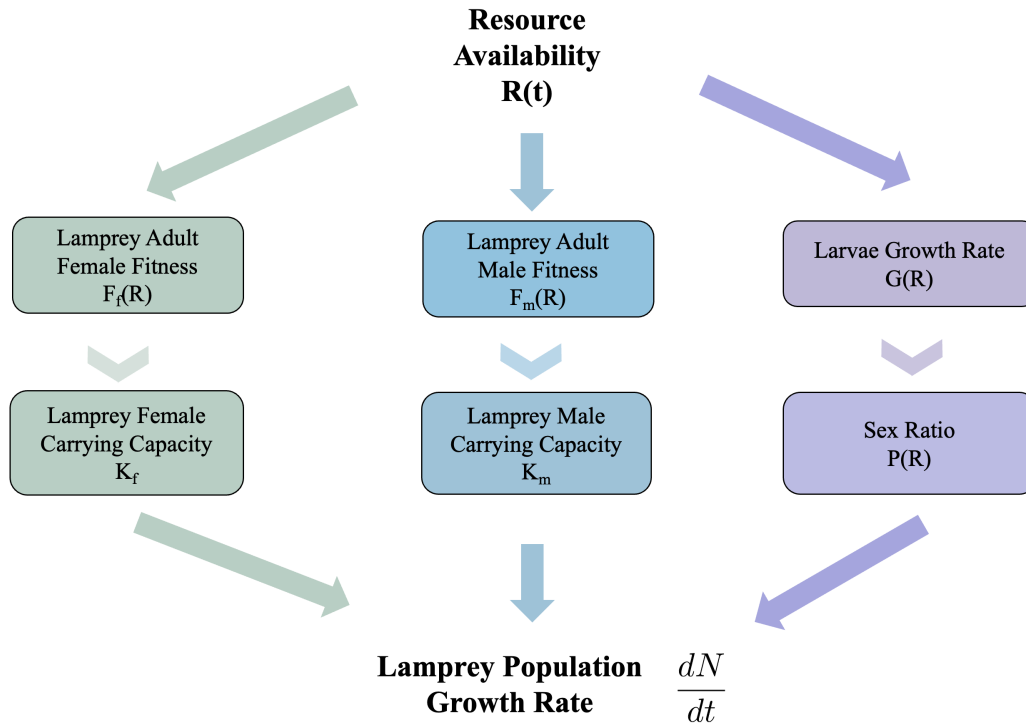


Figure 3: Adaptive Population Control (APC)

- Based on records of sex composition of lampreys from two different locations, a positive correlation between the number of males and population abundance was found. (17) Considering the strikingly similar slopes for functions of  $N_m(N)$  for the two locations (0.74 and 0.71) we assume  $N_m(N)$  to increase linearly with total abundance.
- As  $N$  approaches very large values,  $P(N)$  stabilizes at 0.74, closely aligning with the male larvae ratio of 0.78 in unproductive environments mentioned in the problem. This correlation validates the use of larval growth rates as reliable indicators of adult lamprey populations, endorsing the adaptive population control model.
- To quantify this we assume a linear increase of fitness for both male and female lamprey with male fitness increasing faster. Here we set  $\alpha_m$  and  $\alpha_f$  as the fitness of male and female lamprey at  $R$  level of resource availability. setting  $\alpha_m > \alpha_f$  and  $g_m < g_f$  to reflect the higher fitness of males at productive environments, we have :

$$\alpha_m(R) = g_m \cdot R + h_m \quad (1)$$

$$\alpha_f(R) = g_f \cdot R + h_f \quad (2)$$

- Resource availability is an index between 0 and 1 reflecting the suitability of environment. at  $R = 1$  lamprey grow exponentially and at  $R = 0$  growth = 0. Building on the classical exponential growth model, we replace the  $N$  term with  $F(x)$ .  $F(x)$  is the mating function

reflecting the number of matings.

$$\frac{dN}{dt} = r \cdot F(x) \cdot \left(1 - \frac{N}{K}\right) \tag{3}$$

where

$$F(x) = \min \left\{ \begin{array}{l} \alpha_m \cdot P(N) \cdot N, \\ \alpha_f \cdot (1 - P(N)) \cdot N \end{array} \right\} \tag{4}$$

- Number of males that survive to the age of reproduction, succeed in finding a mate, and produce gametes is  $N_m \cdot \alpha_m(R)$ . Similarly for females, this value is  $N_f \cdot \alpha_f(R)$ . Since the total number of offsprings are the same for male and female : (13).

$$P(N) \cdot N \cdot \alpha_m(R) = P(N) \cdot N \cdot \alpha_f(R). \tag{5}$$

- Here we derive an inverse relationship between ratio of male lampreys in the population and their fitness. This suggests the variable sex ratio allows lamprey to maximize the population growth by increasing the number of mating events.

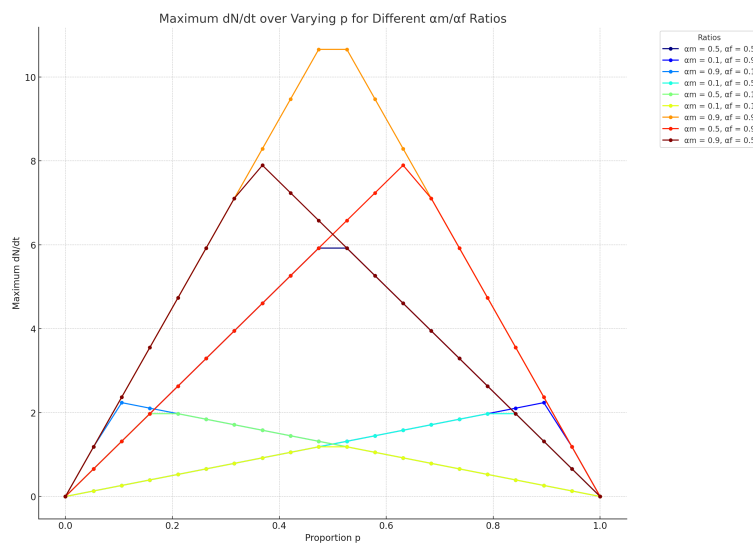


Figure 4: Maximal dN/dt over different sex ratios.

- The behavior of the model under two extreme spectrum of environment suitability is depicted in **Figure 4**. As depicted, as we deviate towards the end spectrum of resource availability, more skewed sex ratios are favored.
- The bimodal shape of **Figure 5** depicts the maximal growth rate at the two ends of resource availability is achieved when there is a skewed sex ratio in population.



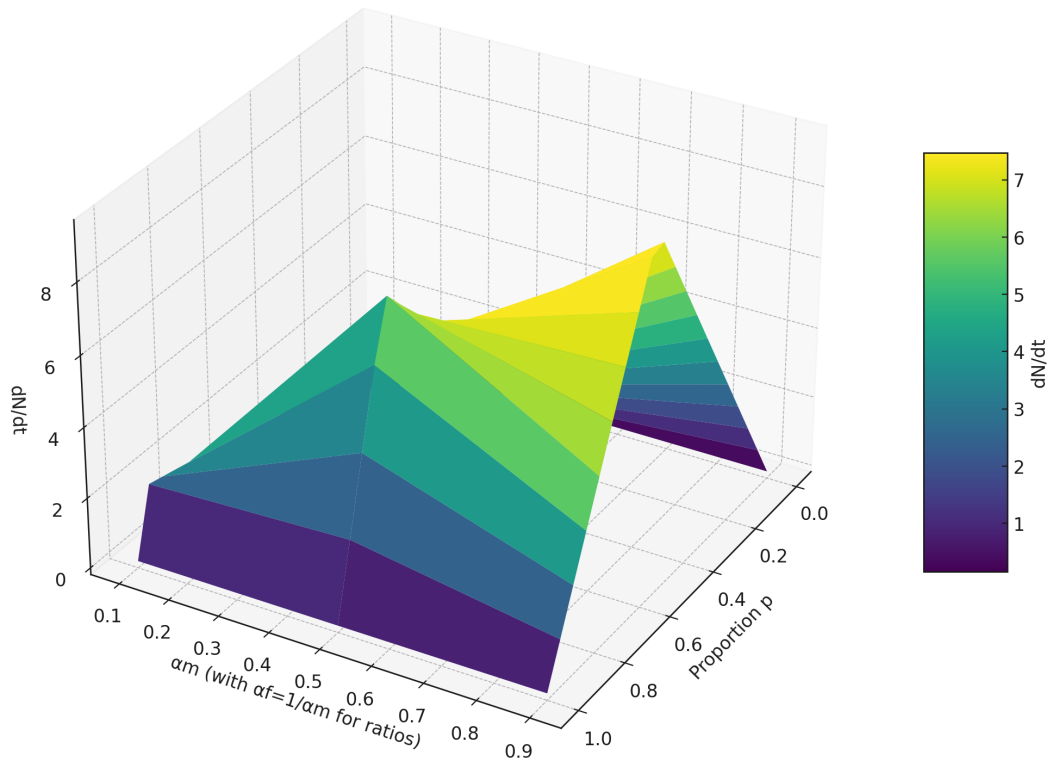


Figure 5: Maximal  $dN/dt$  over different sex ratios.

## 5 Generation Time Control

Lamprey life cycle has major implications on its growth rate. Lamprey spend the majority of their lifetime in the larval stage. While differences in larval size at metamorphosis is seen for larvae growing with access to different resources, these differences are not significant for male and females in the same environment.

- Assuming both sexes have to reach a critical size before metamorphosis, the growth rate at the larval stage directly affects the larval stage duration.
- Considering the widely variable larval duration in lamprey growing in different environment, (14), we assume the shift towards a female-skewed sex ratio to be a form of population control by changing the overall generation time of the animal.
- if we assume the net reproductive rate of lamprey in each generation be  $R_0$ , we have :

$$G = (\ln R_0)/r \quad (6)$$

- where  $G$  = Generation time. From empirical data we have that the average larval age for males = 7-10 and females = 3-5, combining this with the time lamprey stay in the parasitic stage, we predict the the total generation time of larvae growing into female to be almost half of those growing into male, thus :

## 5.1 Aquatic Nutritional Network

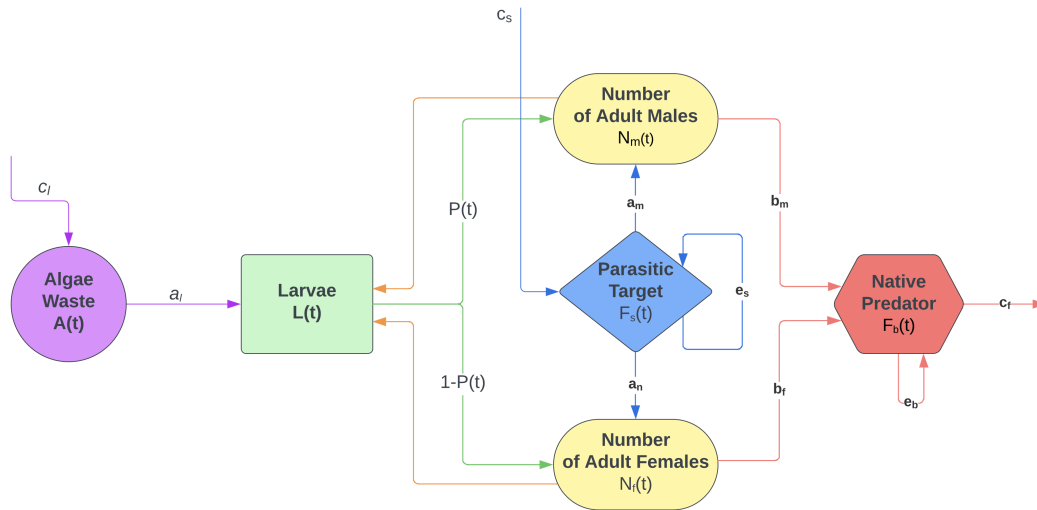


Figure 6: Aquatic Nutritional Network (ANN)

In order to model the lamprey ecosystem, we build a generalized network of biotic and abiotic factors that influence lamprey ecosystem. We build time dependent changes for these agents and predict the equilibrium points based on varying sex ratios of lamprey. (Figure 6)

## 5.2 Dynamic Equations of ANN

### 5.2.1 Larvae Growth Equation

$$\frac{dL}{dt} = \alpha \left( \frac{A}{A + K_A} \right) N_m N_f \left( 1 - \frac{L}{K_L} \right) - m \left( \frac{L}{A + K_m} \right) L \quad (7)$$

This equation models the growth of larvae ( $L$ ), considering both the birth rate influenced by interactions between male ( $N_m$ ) and female ( $N_f$ ) nutrients, and the mortality rate. The birth rate is modulated by the availability of algae ( $A$ ), and both the birth and mortality rates are adjusted for carrying capacity and resource availability.

### 5.2.2 Algae Dynamics Equation

$$\frac{dA}{dt} = c_l - a_l A \quad (8)$$

This equation represents the dynamics of algae ( $A$ ), with its natural growth rate ( $c_l$ ) and consumption by larvae ( $a_l A$ ).

### 5.2.3 Small Fish Dynamics Equation

$$\frac{dF_s}{dt} = c_s F_s \left( 1 - \frac{F_s}{K_{F_s}} \right) - (a_m + a_f) F_s + e_s F_s \quad (9)$$

The small fish population ( $F_s$ ) grows intrinsically at a rate ( $c_s$ ) limited by carrying capacity ( $K_{F_s}$ ), is affected by parasitism (represented by  $a_m$  and  $a_f$ ), and experiences environmental losses ( $e_s$ ).

#### 5.2.4 Big Fish Dynamics Equation

$$\frac{dF_b}{dt} = (b_m N_m + b_f N_f) \left(1 - \frac{F_b}{K_{F_b}}\right) - c_f F_b + e_b F_b \quad (10)$$

Big fish ( $F_b$ ) predation on male and female populations is balanced by its mortality rate ( $c_f$ ), with growth also influenced by environmental benefits ( $e_b$ ) and limited by its carrying capacity ( $K_{F_b}$ ).

#### 5.2.5 Male Nutrients Dynamics Equation

$$\frac{dN_m}{dt} = a_m F_s + PL \left(1 - \frac{N_m}{K_{N_m}}\right) - b_m N_m \quad (11)$$

The male nutrient population ( $N_m$ ) grows due to parasitism on small fish ( $a_m F_s$ ) and maturation from larvae ( $PL$ ), with natural death rate ( $b_m$ ) and limited by carrying capacity ( $K_{N_m}$ ).

#### 5.2.6 Female Nutrients Dynamics Equation

$$\frac{dN_f}{dt} = a_f F_s + (1 - P)L \left(1 - \frac{N_f}{K_{N_f}}\right) - b_f N_f \quad (12)$$

Female nutrient population ( $N_f$ ) dynamics are similar to males', with growth from parasitism and larval maturation, adjusted for the proportion not becoming males ( $1 - P$ ), and limited by carrying capacity ( $K_{N_f}$ ).

#### 5.2.7 Sex Ratio Dynamic Equation

$$\frac{dP}{dN} = \frac{\gamma}{N^2} \quad (13)$$

Ratio of males to total population. Derived from empirical data (17).

#### 5.2.8 Approaches for Analyzing ANN

#### 5.2.9 Equilibrium in the ANN Ecological Model

Equilibrium points in the ecological ANN model indicate stable population states and are found by setting growth rates to zero in our ordinary differential equations (ODEs). We express this mathematically for a set of populations  $\mathbf{X} = \{X_1, X_2, \dots, X_n\}$ , with equilibrium achieved when  $\frac{dX_i}{dt} = 0$  for all  $i$ . These translate into algebraic equations that define the equilibrium states, providing the solutions where the system's dynamics are in balance.

$$\frac{dX_i}{dt} = 0, \quad \forall i \in \{1, 2, \dots, n\} \quad (14)$$

Solving these equations yields the equilibrium points of the system, critical to understanding its long-term behavior.

### 5.2.10 Setting Up the Equilibrium System

To establish equilibrium within an ecological model, we must transform the system's differential equations into algebraic equations. This allows us to pinpoint equilibrium points where the change in population over time is zero, indicating a potential state of balance in the ecosystem. Each algebraic equation represents a balance of forces within a specific ecological niche, factoring in interaction rates, intrinsic growth, and decay processes.

$$\begin{cases} \alpha \left( \frac{A}{A+K_A} \right) N_m N_f \left( 1 - \frac{L}{K_L} \right) - m \left( \frac{L}{A+K_m} \right) L = 0, \\ c_l - a_l A = 0, \\ c_s F_s \left( 1 - \frac{F_s}{K_{F_s}} \right) - (a_m + a_f) F_s + e_s F_s = 0, \\ (b_m N_m + b_f N_f) \left( 1 - \frac{F_b}{K_{F_b}} \right) - c_f F_b + e_b F_b = 0, \\ a_m F_s + PL \left( 1 - \frac{N_m}{K_{N_m}} \right) - b_m N_m = 0, \\ a_f F_s + (1 - P)L \left( 1 - \frac{N_f}{K_{N_f}} \right) - b_f N_f = 0. \end{cases}$$

### 5.2.11 Numerical Solution of the Equilibrium System

Given the complexity of the system, analytical solutions may not be feasible. Hence, we resort to numerical methods to solve the system of equations. This involves the use of computational algorithms designed to find the roots of nonlinear equation systems subject to the aforementioned constraints.

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#### Algorithm 1 Numerical Solution for the Equilibrium System using a Python-like approach

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- 1: Define the system of equations as  $F(x)$ , where  $x$  is a vector of variables (e.g.,  $A, L, F_s, F_b, N_m, N_f$ ).
  - 2: Define the Jacobian matrix  $J(x)$ , containing partial derivatives of  $F(x)$ .
  - 3: Initialize  $x$  with an initial guess  $x_0$ .
  - 4: Set convergence tolerance  $\text{tol}$  and max iterations  $\text{maxIter}$ .
  - 5: Set  $\text{iter} = 0$ .
  - 6: **while**  $\text{iter} < \text{maxIter}$  and  $\|\Delta x\| \geq \text{tol}$  **do**
  - 7:     Compute  $F(x_0)$ .
  - 8:     Compute  $J(x_0)$ .
  - 9:     Solve  $J(x_0)\Delta x = -F(x_0)$  for  $\Delta x$ .
  - 10:    Update  $x_0 \leftarrow x_0 + \Delta x$ .
  - 11:    Check convergence: if  $\|\Delta x\| < \text{tol}$ , exit loop.
  - 12:     $\text{iter} \leftarrow \text{iter} + 1$ .
  - 13: **end while**
  - 14: **if**  $\text{iter} = \text{maxIter}$  **then**
  - 15:    Indicate non-convergence.
  - 16: **else**
  - 17:    Return  $x_0$  as the solution.
-

### 5.3 ANN Results

In our ecological model, key parameters such as the interaction rate ( $\alpha$ ), algae consumption rate ( $a_l$ ), and natural mortality of larvae ( $m$ ) significantly influence the simulated dynamics of the aquatic ecosystem. The interaction rate ( $\alpha$ ) modulates how effectively populations interact, crucial for understanding reproductive success and species interplay. The updated algae consumption rate ( $a_{l\text{updated}}$ ) reflects the larvae’s dependency on algae, a primary food source, indicating resource utilization efficiency. Mortality rate ( $m$ ) represents the larvae’s vulnerability to non-predatory factors, impacting population sustainability. Together with the growth rates of algae ( $c_l$ ) and small fish ( $c_s$ ), these parameters delineate the foundation of food web interactions and energy flow. The inclusion of carrying capacities ( $K_L, K_{Fs}, K_{Fb}, K_{Nm}, K_{Nf}$ ) ensures the model respects ecological limits, portraying a balanced ecosystem where each species’ growth is regulated by available resources and interaction strengths. This intricate parameterization enables our model to forecast equilibrium points, providing insights into the stability and resilience of the ecosystem under study. (15)

#### 5.3.1 ANN Model Simulation

The updated graphs from the ecological model simulation display the dynamics of various components within an aquatic ecosystem over time, specifically focusing on lampreys (in different life stages), their prey (small fish), predators (big fish), and a primary food source (algae).

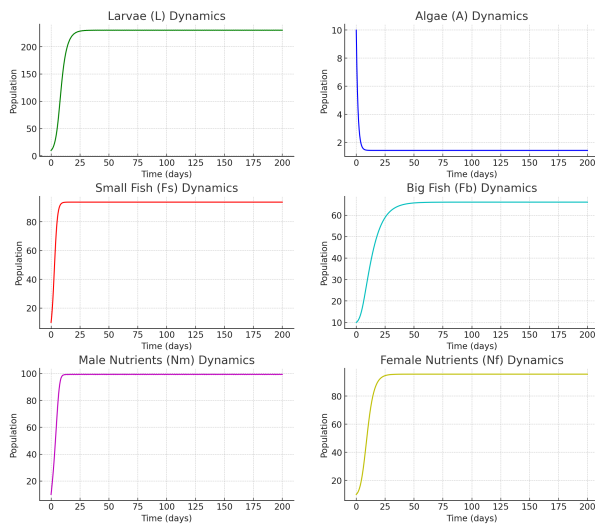


Figure 7: Dynamic of ANN When P = 0.5

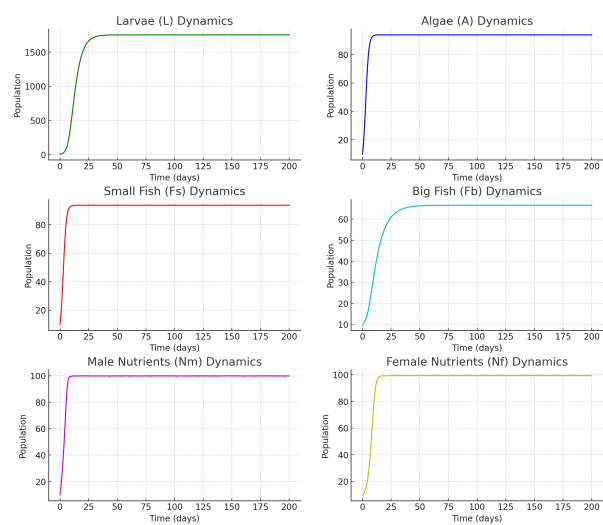


Figure 8: Dynamic of ANN When P = 0.8

Note that Lampreys overused their primary source of food (Algae) of equal sex ratios. However, variable sex ratio allowed enough time for the regeneration of algae, potential preventing extinction.

#### 5.3.2 Equilibrium Points

- Larvae (L): 94.88 individuals
- Algae (A): 1.43 mass units

- Small fish ( $F_s$ ): 93.75 individuals
- Big fish ( $F_b$ ): 66.15 individuals
- Male nutrients/Total number of males ( $N_m$ ): 97.69 individuals
- Female nutrients/Total number of females ( $N_f$ ): 97.69 individuals

The equilibrium points, with larvae at 94.88, algae at 1.43 units, small fish at 93.75, big fish at 66.15, and both male and female nutrients at 97.69 individuals, indicate a balanced ecosystem. These values show that lampreys and their interactions with algae and fish are key to maintaining stable populations. The balance between algae availability and fish populations reflects successful nutrient cycling and predation dynamics, crucial for ecosystem management and conservation efforts.

## 5.4 Differential Carrying Capacity (DCC) Model for Lamprey Populations

### 5.4.1 Model Overview

We develop the DCC model to reflect the the effect of sex ratio (P) on :

$$\frac{dN}{dt} = r \cdot N(t) \cdot f[P(t)] \cdot \left[ P(t) \left( 1 - \frac{N(t)}{k_m(R)} \right) + (1 - P(t)) \left( 1 - \frac{N(t)}{k_f(R)} \right) \right] \quad (15)$$

Here,  $N(t)$  is the population size at time  $t$ ,  $r$  is the intrinsic growth rate,  $P(t)$  represents the proportion of males in the population,  $k_m$  is the carrying capacity for males, and  $k_f$  is the carrying capacity for females.

$$f[P(t)] = \alpha \cdot P(t) \cdot (1 - P(t)) \quad (16)$$

In lamprey populations, males may require larger territories or different environmental conditions than females(1). The DCC model accounts for these differences by incorporating separate carrying capacities for each sex.  $f$  function is multiplied to the function to transforms  $p = 0.0$  and  $p = 1$  to zero. we assume that  $k_m > k_f$ , the

## 6 Model Simplification and Analysis

### 6.1 Numerical Solution Approach for the APC Model

Differential Carrying Capacity (APC) model, which takes into account the different environmental capacities for males and females in a lamprey population, can be numerically solved using the Runge-Kutta fourth order method (RK4). The RK4 method is highly regarded for its balance between numerical stability and computational efficiency. It works by approximating the slope of the population curve at several points within each time step and then combining these approximations to predict the population at the next time step.

### 6.1.1 The Runge-Kutta Fourth Order Method

The RK4 method improves upon simpler numerical methods by evaluating the instantaneous rate of change (the derivative) at four points within each time step. These evaluations are then combined to produce an estimate of the average derivative over the time step. This estimate is used to project the population forward in time.

Given our model's differential equation:

$$\frac{dN}{dt} = r \cdot N(t) \cdot f[P(t)] \cdot \left[ P(t) \left( 1 - \frac{N(t)}{k_m(R)} \right) + (1 - P(t)) \left( 1 - \frac{N(t)}{k_f(R)} \right) \right] \quad (17)$$

RK4 method proceeds as follows for each time step from  $t$  to  $t + dt$ :

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#### Algorithm 2 Runge-Kutta Method for the DCC Model

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1: function RK4STEP( $N, r, P, k_m, k_f, dt$ )
2:    $f(t, N) \leftarrow r \cdot N \cdot \left[ P \cdot \left( 1 - \frac{N}{k_m} \right) + (1 - P) \cdot \left( 1 - \frac{N}{k_f} \right) \right]$ 
3:    $k1 \leftarrow dt \cdot f(t, N)$ 
4:    $k2 \leftarrow dt \cdot f\left(t + \frac{dt}{2}, N + \frac{k1}{2}\right)$ 
5:    $k3 \leftarrow dt \cdot f\left(t + \frac{dt}{2}, N + \frac{k2}{2}\right)$ 
6:    $k4 \leftarrow dt \cdot f(t + dt, N + k3)$ 
7:    $N_{next} \leftarrow N + \frac{1}{6} \cdot (k1 + 2 \cdot k2 + 2 \cdot k3 + k4)$ 
8:   return  $N_{next}$ 
9: end function

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The intermediate variables  $k1$ ,  $k2$ ,  $k3$ , and  $k4$  represent the slopes at the beginning, the midpoint, and the end of the interval, respectively. The final population size at  $t + dt$  is then estimated by taking a weighted average of these slopes, which accounts for the nonlinear nature of the population's growth.

### 6.1.2 Implementation and Conservation Implications

The RK4Step function is used iteratively to simulate the lamprey population over time. The model takes the initial population size  $N(0)$ , growth rate  $r$ , carrying capacities  $k_m$  and  $k_f$ , and initial proportion of males  $P(0)$ , all of which must be derived from empirical data or scientific estimation.

By applying this model with appropriately chosen parameters, conservationists and scientists can forecast the effects of environmental changes on lamprey populations with separate considerations for males and females. This nuanced approach allows for more targeted conservation efforts that can better support the stability and health of the species.

## 7 Sensitivity Analysis

### 7.1 ANN Sensitive Analysis

To understand the resilience and adaptability of our ecological system model, particularly focusing on the lamprey population and its interaction with other species, we performed a comprehensive

sensitivity analysis. This analysis was aimed at investigating the influence of varying rates of parasitism by larvae on small fish, represented by parameters  $a_m$  and  $a_f$ , on the equilibrium states of six critical components of the ecosystem: larvae ( $L$ ), algae ( $A$ ), small fish ( $F_s$ ), big fish ( $F_b$ ), male nutrients ( $N_m$ ), and female nutrients ( $N_f$ ).

### 7.1.1 Methodology

The sensitivity analysis was structured around systematically varying the parasitism rates  $a_m$  and  $a_f$  from 0.01 to 0.05 in steps of 0.01. This range was chosen to reflect realistic variations in parasitism intensity that could occur within the ecosystem without disrupting its foundational dynamics. For each combination of  $a_m$  and  $a_f$ , we recalculated the model's equilibrium points, enabling us to observe how these two parameters influence the overall balance within the ecosystem.

$a_m$	$a_f$	$L_{eq}$	$A_{eq}$	$F_{seq}$	$F_{beq}$	$N_{meq}$	$N_{feq}$
0.01	0.01	60.81	0.71	98.67	63.47	80.92	94.24
0.01	0.02	61.85	0.71	97.47	63.78	81.12	96.14
0.01	0.03	62.75	0.71	96.19	64.06	81.28	97.94
0.01	0.04	63.56	0.71	94.89	64.31	81.41	99.65
0.01	0.05	64.28	0.71	93.61	64.54	81.52	101.28
0.02	0.01	64.38	0.71	97.47	64.46	87.64	94.52
0.02	0.02	65.16	0.71	96.19	64.70	87.62	96.29
0.02	0.03	65.85	0.71	94.89	64.91	87.59	97.98
0.02	0.04	66.46	0.71	93.61	65.11	87.54	99.59
0.02	0.05	67.02	0.71	92.47	65.30	87.48	101.10
0.03	0.01	66.96	0.71	96.19	65.25	93.52	94.71
0.03	0.02	67.58	0.71	94.89	65.44	93.36	96.38
0.03	0.03	68.13	0.71	93.61	65.62	93.19	97.99
0.03	0.04	68.62	0.71	92.47	65.79	93.01	99.50
0.03	0.05	69.07	0.71	91.23	65.94	92.84	100.96
0.04	0.01	68.96	0.71	94.89	65.93	98.87	94.83
0.04	0.02	69.47	0.71	93.61	66.08	98.60	96.44
0.04	0.03	69.92	0.71	92.47	66.23	98.32	97.96
0.04	0.04	70.33	0.71	91.23	66.37	98.04	99.41
0.04	0.05	70.69	0.71	90.06	66.49	97.77	100.81
0.05	0.01	70.58	0.71	93.61	66.52	104.00	94.91
0.05	0.02	70.99	0.71	92.47	66.65	103.62	96.47
0.05	0.03	71.36	0.71	91.23	66.77	103.24	97.95
0.05	0.04	71.69	0.71	90.06	66.89	102.86	99.38
0.05	0.05	72.00	0.71	88.92	67.00	102.49	100.76

Table 2: Sensitivity Analysis Results for Varying Parasitism Rates  $a_m$  and  $a_f$

### 7.1.2 Findings

Our analysis revealed a nuanced response of the ecosystem to changes in parasitism rates. Specifically, according to **Table 2** we noted that:



- Larvae Population ( $L$ ) showed a progressive increase with higher parasitism rates, indicating that more effective parasitism facilitates greater larvae survival and growth.
- Algae Population ( $A$ ) exhibited slight fluctuations, underscoring its resilience and the balanced nature of its consumption by larvae.
- Small Fish Population ( $F_s$ ) decreased as parasitism rates increased, reflecting the direct impact of lamprey larvae on their prey.
- Big Fish Population ( $F_b$ ) also showed a decline, albeit more moderately, suggesting indirect effects through the food web.
- Nutrient Populations ( $N_m$  and  $N_f$ ) for both male and female lampreys increased, pointing to successful conversion of parasitized fish into reproductive adults.

## 7.2 APC Sensitive Analysis

### 7.2.1 Initial Observation

Begin by noting the initial findings: As **Table 3** and **Figure 89**, the differences in population sizes across the various parameter sets were too small to draw meaningful conclusions.

Set Number	$g_m$	$h_m$	$g_f$	$h_f$	Mean Population Size	Final Population Size
Set 1	0.5	-50	0.55	-65	11.44	13.03
Set 2	0.55	-45	0.6	-60	11.47	13.12
Set 3	0.5	-50	0.6	-60	11.45	13.06
Set 4	0.45	-55	0.6	-55	11.45	13.05
Set 5	0.5	-55	0.65	-50	11.47	13.30

Table 3: Sensitivity Analysis Results

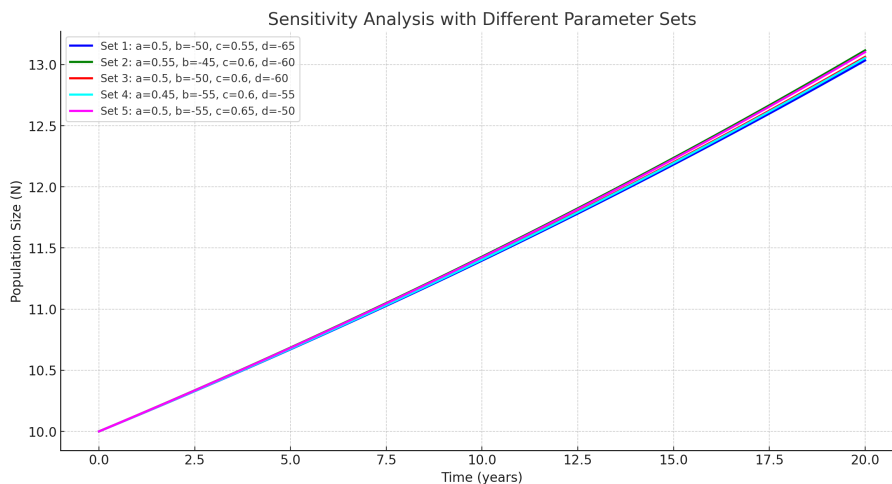


Figure 9: Adaptive Population Control (APC)

Small differences may fall within the natural variability of the system and may not be statistically significant or biologically meaningful.

## 7.2.2 Adjustment Method

Larger changes in output suggest that the model is indeed sensitive to these parameters. This can help in identifying which parameters are most critical to the system's dynamics and should therefore be estimated with greater precision.

After we changing the values for key parameters, the updated graph displays the sensitivity analysis with a larger variation in the parameters, as **Table 4** and **Figure 10**, resulting in more distinct differences between the curves.

Set Number	$g_m$	$h_m$	$g_f$	$h_f$	Mean Population Size	Final Population Size
Set 1	0.3	-70	0.8	-40	11.49	13.16
Set 2	0.6	-30	0.7	-50	11.63	13.50
Set 3	0.5	-50	0.6	-60	11.45	13.06
Set 4	0.4	-60	0.9	-30	11.64	13.52
Set 5	0.7	-20	0.5	-70	11.86	14.06

Table 4: Sensitivity Analysis Results

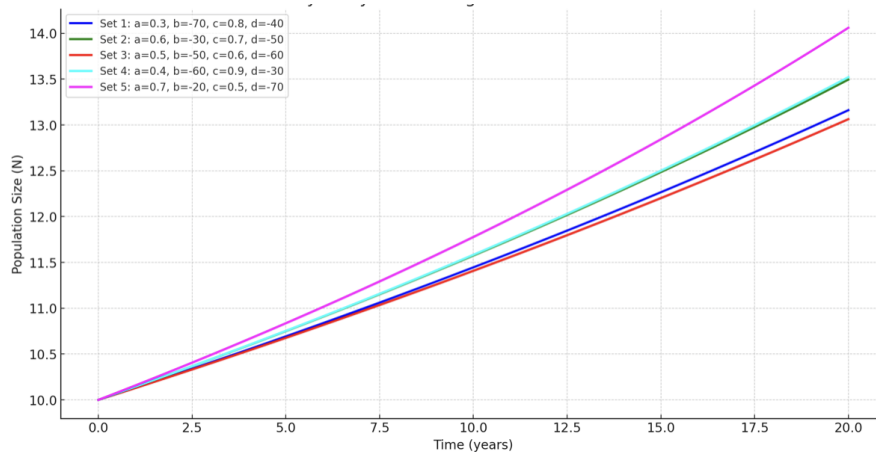


Figure 10: Adaptive Population Control (APC)

## 7.2.3 Results of Adjustments

With the new parameters, we can see more significant differences in the model's outcomes:

- Set 1 has the smallest increase in both mean and final population size compared to the original parameters.
- Set 5 shows the largest increase, indicating that the higher 'a' and 'c' values and less negative 'b' and 'd' values lead to a much larger population size under these model conditions.
- The red curve (Set 3) remains our baseline for comparison as it uses the original parameter values.

These results highlight how sensitive the model is to changes in the parameters defining the resource-dependent carrying capacities  $k_m(R)$  and  $k_f(R)$ . This sensitivity analysis is crucial for understanding which parameters are most influential and should be estimated with greater accuracy.

## 8 Evaluate of the Model

### 8.1 Strengths and weaknesses

#### 8.1.1 Strengths

- **Adaptive Strategy**

The APC model proposes an immediate adaptive benefit to changing sex ratio in lamprey. Skewed sex ratio is selected more strongly when resource levels are at the two spectrum of the average values. This sensitive responsiveness is optimal for an animal whose sex is environmentally determined.

#### 8.1.2 Weakness

- **R cannot be measured directly**

Throughout this paper we used R as a measure of resource availability, even though we don't have a solution on how to measure this value directly

- **Improve the quality of the airport service**

Balancing the cost of the cost and the benefit, it will bring in more convenient for airport and passengers. It also saves many human resources for the airline.

## 9 Conclusions

In this paper we analyzed the ecological and demographic consequences of variable sex ratio. Looking from an evolutionary adaptive perspective, we propose that the APC model best reflects this strategy. We further analyze this concept using the DCC model that is based on the fact that male-skewed populations are prevalent in higher densities. Finally we analyze the dynamical behavior of lamprey, their native prey and predator to find the role of variable sex ratio. We found that variable sex ratio allows time for regeneration of resources that is essential for keeping the population from becoming in danger of extinction.

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## Report on Use of AI

[18] OpenAI ChatGPT (Feb 1, 2024 version, ChatGPT-4)

Query1: do you know the larva of lampreys, what food do they usually eat

Output: Lamprey larvae, also known as ammocoetes, primarily feed on a diet of microorganisms. They live in freshwater environments and burrow into soft sediment where they filter-feed. Their diet consists mainly of detritus (organic matter), algae, and microorganisms present in the water. They draw water over their gills through their mouths, filtering out food particles with their gill rakers. This feeding behavior is in stark contrast to the parasitic lifestyle of many adult lampreys, which attach themselves to other fish to feed on their blood and bodily fluids. The larval stage can last several years before they metamorphose into their adult form and, for those species that are parasitic, begin their life feeding on the blood of other fish.

[19] OpenAI ChatGPT (Feb 1, 2024 version, ChatGPT-4)

Query1: how to test the stability of nature

Output: Testing the stability of nature involves a broad and complex set of methodologies, as "nature" encompasses a vast array of systems, including ecological, atmospheric, geological, and biological systems. The approach to testing stability can differ significantly depending on the specific aspect of nature being studied. Here's a general overview of how stability might be assessed in various natural systems:

**Ecological Stability Biodiversity:** Tracking the diversity of species within an ecosystem can provide insights into its stability. A decline in species diversity can indicate a loss of resilience.

**Population Dynamics:** Observing fluctuations in population sizes of various species over time helps in understanding the stability of food webs and ecological interactions.

**Resilience Testing:** Assessing how quickly an ecosystem recovers after a disturbance (such as a fire, flood, or human activity) can indicate its stability and resilience.

**Atmospheric Stability Climate Modeling:** Simulations with climate models to predict future climate conditions under various scenarios can test the stability of atmospheric systems.

**Historical Climate Data Analysis:** Examining past climate patterns and comparing them with current data to detect shifts in temperature, precipitation patterns, and extreme weather events.

**Geological Stability Seismic Monitoring:** The monitoring of seismic activity can help in assessing the stability of the earth's crust, predicting earthquakes, and understanding tectonic movements. **Erosion and Sedimentation Rates:** Measuring how quickly landscapes are eroding or accumulating sediments provides insight into the geological stability of an area.

**Biological Stability Genetic Diversity:** Assessing the genetic diversity within and across populations of species can offer clues to their long-term viability and adaptability. **Ecophysiological Metrics:** Measuring the physiological responses of organisms to environmental changes can help in assessing their resilience and the stability of their habitats.

**General Methodologies Long-Term Ecological Research (LTER):** Conducting long-term studies to gather comprehensive data sets over extended periods, often decades, to assess changes and trends in ecosystems.

**Remote Sensing and Satellite Imagery:** Using remote sensing technologies to monitor changes in land use, vegetation cover, and other indicators of ecological and geological stability.

**Experimental Manipulations:** In some cases, controlled experiments are conducted to test the

responses of systems to various factors, helping in understanding thresholds and tipping points. Each of these methods requires a careful approach to data collection, analysis, and interpretation. Understanding the stability of natural systems is critical for conservation efforts, predicting the impacts of climate change, and managing natural resources sustainably.

[20] OpenAI ChatGPT (Feb 1, 2024 version, ChatGPT-4)

Query1: can you introduce the whole food chain related to lampreys for me?

Output: Lampreys are interesting creatures with a unique position in their ecosystems, and they participate in a diverse food chain. There are many species of lampreys, and their roles in the food chain can vary between being parasitic or non-parasitic (non-feeding as adults). Here's a general overview of the food chain related to lampreys, keeping in mind that specific relationships can vary based on the species and the ecosystem:

**Top of the Food Chain (Predators of Lampreys)**  
**Fish:** Larger predatory fish such as trout, bass, and pike may prey on juvenile lampreys or smaller lamprey species.  
**Birds:** Certain bird species, like herons and cormorants, can feed on lampreys, especially when they are near the surface of the water or in shallower areas.  
**Mammals:** Some mammals, including otters and seals, might prey on lampreys in freshwater and marine environments.

**Middle of the Food Chain (Lampreys)**  
**Parasitic Lampreys:** Adult parasitic lampreys attach to and feed on the blood and body fluids of fish. Species like the sea lamprey (*Petromyzon marinus*) are well-known for this behavior and can significantly impact fish populations in freshwater and marine environments.  
**Non-parasitic Lampreys:** These lampreys do not feed as adults; they live off reserves accumulated as larvae. After metamorphosis, their digestive systems degenerate, and they do not eat before spawning and dying.

**Bottom of the Food Chain (Prey for Lampreys)**  
**Fish:** For parasitic lampreys, various fish species serve as hosts. Lampreys can attach to almost any type of fish but typically prefer those with soft, penetrable skin.  
**Detritus and Microorganisms:** Lamprey larvae, known as ammocoetes, feed by filtering detritus, algae, and microorganisms from the water. They live burrowed in sediment for several years before metamorphosing into adults.

**Beyond the Direct Food Chain**  
**Humans:** Humans have historically fished for lampreys for food in some cultures. In modern times, lampreys are also managed or controlled in areas where they are considered invasive, such as the Great Lakes region, where sea lampreys have had a significant impact on native fish populations. This overview simplifies the complex interactions lampreys have within their ecosystems, highlighting their roles as both predator and prey. The impact of lampreys, particularly invasive species like the sea lamprey, has led to substantial ecological and economic consequences, prompting significant management efforts to control their populations in affected waterways.