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Modelling Walleye Population and Its Cannibalism Effect

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Abstract

Walleye is a very common recreational fish in Canada with a strong cannibalism tendency, such that walleyes with larger sizes will consume their smaller counterparts when food sources are limited or a surplus of adults is present. Cannibalism may be a factor promoting population oscillation. As fish reach a certain age or biological stage (i.e. biological maturity), the number of fish achieving that stage is known as fish recruitment. The objective of this thesis is to model the walleye population with its recruitment and cannibalism effect. A matrix population model has been introduced to characterize the walleye population into three different groups: newborns, juveniles, and adults. A delay differential equation (DDE) model has also been introduced to characterize walleyes into two groups including juveniles and adults. Local and global stabilities of equilibria have been discussed in both models. Furthermore, numerical simulations are present to visualize the effects of both models.

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Chapter 1

Introduction

Walleye is a common fish species found in many waters in Canada and the northern United States. In Canada, it occurs in most parts of Ontario, Manitoba, Saskatchewan, and Alberta. Walleye is one of the most important species to the recreational fisheries in North America[17]. Based on the data from a survey of recreational angling back in 2005, walleye was the primary species caught in Canada [11]. Similarly, in the USA, a national survey was conducted, indicating that 3.8 million anglers spent an average of 13.6 days angling for walleye in 2001 [28]. According to the survey conducted by Fisheries and Oceans Canada in 2010, walleye was the top species harvested by anglers in Ontario, Manitoba, Saskatchewan and Alberta, standing for 23% of the total fish harvested by anglers in the country [12].

1.1 The Life Cycle and Food Sources of Walleye

Growth rates in walleye are highly influenced by a lot of factors including temperature, oxygen level, pH level of the habitat, pollution, food quality, etc [14]. If the water temperature is satisfactory, spawning occurs usually before the end of June; however, spawning is not guaranteed with a low water temperature [27].

After being spawned, eggs only need 4 to 10 days to hatch with different water temperatures [27]. After 40 to 60 days, juvenile walleyes become piscivorous but not yet sexually mature. In fact, walleyes are heterosexual, and male walleyes reach their maturity earlier than females [4].

The age when walleye reaches sexual maturity depends on both the temperature and the habitat fertility [14]. However, in general, juveniles are considered to be immature at 1-3 years of age [17, 4].

Food sources of walleye shift ontogenetically with its different life stages [14]; however, adult walleyes are fully piscivorous [14]. Larval walleyes are usually fed by plankton[16].

When larval walleyes grow, the food source moves rapidly from plankton to invertebrates and zooplankton [16, 4, 14]. As walleye fry grows, they start to eat smaller fish as the primary food source [4].

1.2 Cannibalism

Being piscivorous, walleyes do eat their own species, which is called cannibalism. Frankly, cannibalism is significant enough to affect the population dynamics of walleye. This phenomenon is very noticeable in a lot of lakes [3, 20]. There has been a controversy about the cause of cannibalism. In Polis's paper [25], cannibalism is evaluated by the level of stressful condition including the crowdedness and starvation. Population loss due to cannibalism can be surprisingly high among walleye. In fact, in the Eastern Bering Sea, almost 3/5 of the annual mortality of the total walleye pollock population is caused by cannibalism [9]. Therefore, cannibalism plays a very critical role in population dynamics of walleye. In fact, walleye can survive even when the food sources for the adults are limited, which is called the life boat effect [29].

1.3 Mathematical Models in Population Dynamics

Mathematical models have been well developed to study the population dynamics since the end of eighteen century when Malthus published the book *An Essay on the Principle of Population*. Now, population dynamic is an important branch in Applied Mathematics to study the trend of both human and animal population. Usually, a population can be studied using 4 different models including discreet matrix model, ordinary differential equation (ODE) model, delay differential equation (DDE) model, and partial differential equation (PDE) model. Matrix population models have been used widely to study the population by generations or age structure which involve the so-called Leslie matrix [19] introduced by Patrick Leslie back in 1945. For an age-structured population, another very common way to study is using PDE such as McKendrick-von Foerster equation [23]. In fact, McKendrick-von Foerster equation is the first model introducing age structure in population dynamics [2]. The model considers the population as a function of age and time. There are also a lot of papers studying the behaviour of predator and prey population interactions. For this type of population dynamics, ODE models are usually used. The simplest model was introduced by Alfred Lotka in 1909 [21]. In Lotka-Volterra equations, prey has a logistic growth with no natural death term, and predator has the growth rate only from hunting preys. It is a very simplified model, yet predicts the periodic oscillations of populations. In recent years, DDE's have been studied intensively because of

the nature of delay in birth and reproduction [18, 10, 5, 13, 2]. The most famous example is Nicholson's blowflies equation [5].

Cannibalism is a very common phenomenon for walleyes [3, 20]. Some mathematical models have also been proposed to study the effect of cannibalism in the population dynamics. Cannibalism can be considered as a predator-prey model where both predator and prey are in the same population group. The first model was proposed in 1954 by Ricker [26]. In that paper, cannibalism is considered as density-dependent. The population cycle and chaos are shown in the paper. However, the stability of a positive equilibrium in Ricker model is independent of cannibalism (only dependent on birth rate) [26]. Some discreet models (e.g. [8, 6]) have also been established to study such effect. In the paper by Costantino [6], a nonlinear difference equation model was proposed to study the population dynamics of the flour beetle. The total population is divided into three stages including larvae, pupae, and adults. In the paper, cannibalism plays the role of stabilizing and controlling the population. In fact, without cannibalism, the population is unbounded. That paper showed that there exist periodic solutions and chaos.

Partial differential equation models have been used most frequently to study the structured population models [24, 15]. In Diekmann's model [24], cannibalism is a regulator of density. The cannibalism effect is added into the death terms of the PDE models. Both papers observed the periodic solutions. Also, ordinary differential equations can also be used to study the structured population; however, it is not common to do so.

There are still a few papers using ODE models. In the paper by Magnusson [22], the population of walleyes was characterized into three life stages (adult predators, juvenile predators, and prey). In his model, the population is not bounded. With a sufficiently large natural birth rate, the system may be divergent. The paper shows that cannibalism has a destabilizing effect on positive equilibrium. Periodic solutions may exist with some high level of cannibalism.

1.4   Prospective and Organization of the Project

Since walleye is very important in both recreational and economical fisheries, knowing the cannibalistic mechanism in the walleye population is critical. With the knowledge of such mechanism, possible predictions can be made for the future fish population, and government agencies can make better decisions on fish harvesting and fishing regulations. Decisions on fish conservation are also possible to be made with this study. Some data shows that the population of walleye in Lake Erie has a cycle [1]. With this data, we are trying to model the walleye population with possible periodic solutions with cannibalism. We want to see how cannibalism may affect the population dynamics.

In Chapter 2, we propose a difference equation model to investigate the population cycle

due to the cannibalism effect. The model is motivated by the LPA model [7] because of the similarities of cannibalism mechanism between flour beetles and walleyes. In the model, the population is divided into 3 stages including newborns, juveniles, and adults. We will verify the well-posedness of the model, including the boundedness and positivity of solutions. We will also explore the equilibria and their local stabilities using eigenvalues, and global stability. Then, we will use numerical methods to simulate the model with some parameters to see if the system has a periodic solution and how cannibalism affects the equilibria and their stabilities. In this chapter, the biological implication is that we found that the cannibalism is an affect causing population cycles. Although cannibalism lowers the population level, fish cannibalism also has a stabilizing effect.

In Chapter 3, a delay differential equation model is introduced to study the population dynamics of walleyes. Motivated by the Nicolson's blowflies equation [5], we divide the population into two stages of life cycle, juvenile and adults. For the birth function, we will use Ricker's function [26]. Similar to Chapter 2, we will verify the boundedness and positivity of solutions, and calculate the equilibria. We will also check the stability of each equilibrium. Then we will use software (DDE23 from Matlab) to visualize the population dynamics with different parameters. By some numerical simulations, we investigate whether or not there exists a periodic solution. In this chapter, we discovered that cannibalism has a life boat effect which means fish can still survive when the reproduction rate is at a low level. We also found that cannibalism has a stabilizing effect similar to Chapter 2.

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Chapter 2

Matrix Population Model of Walleye with Cannibalism Effect

2.1 Introduction

Walleyes have four life stages including egg, newborn, juvenile, and adult. After they are born, it only takes 4 to 10 days for walleye eggs to hatch [13]. As newborns, they are fed primarily on plankton and zooplankton. Soon after, they shift their food sources from plankton to invertebrates and some small fish [8]. However, their food can vary by conditions of their habitat. In Lake Erie, the primary food of young walleye is phytoplankton instead of zooplankton [2]. Both juvenile and adult walleye are piscivorous, and they consume not only other fish but also walleye smaller than their own sizes. Therefore, cannibalism is a critical part of the feeding behaviour of walleye and it plays an important role in population dynamics.

Some data shows that the population of recruitments have a periodic fluctuation around 3 years [12]. It is very critical to investigate the cause of such fluctuation phenomena as it contributes to the government policy of fish conservation and harvesting. Most observed recruitments seem to exhibit an irregular cycle sinusoid pattern, and the mechanism of such fluctuations are unknown. It is believed that such pattern likely reflects the influence of environmental factors such as temperature, water quality, etc. It is also conjectured that cannibalism may also be partially responsible for such fluctuations.

2.2 Model Formulation

Difference equations have been intensively used in the field of population dynamics and mathematical biology since the pioneering paper of Leslie [11] 70 years ago. These matrix models

can be generally written as the following form

$$X(t + 1) = P(X(t)) \cdot X \tag{2.1}$$

where P is a $n \times n$ square projection matrix governing the population at time $t + 1$ from the population in the previous time t. Leslie particularly studied this matrix based on age structure. Then, $P(X)$ can be considered as the combination of two parts:

$$P(X) = F(X) + T(X)$$

$$F(X) = \begin{pmatrix} f_1(X) & f_2(X) & f_3(X) & \cdots & f_n(X) \\ 0 & 0 & 0 & \cdots & 0 \\ \vdots & \vdots & \vdots & \ddots & \vdots \\ 0 & 0 & 0 & \cdots & 0 \end{pmatrix}, \quad T(\vec{x}) = \begin{pmatrix} 0 & 0 & \cdots & 0 & 0 \\ \tau_1(X) & 0 & \cdots & 0 & 0 \\ 0 & \tau_2(X) & \cdots & 0 & 0 \\ \vdots & \vdots & \ddots & \vdots & \vdots \\ 0 & 0 & \cdots & \tau_{n-1}(X) & 0 \end{pmatrix}$$

where $F(X)$ is the fertility matrix, and $T(X)$ is the survival matrix. Here, $f_i(X)$ and $\tau_i(X)$ are corresponding to the birth function and death function of generation i.

In this section, a system of difference equations is proposed to study the effect of cannibalism on the population dynamics of walleye. Our model is motivated by the LPA model formulated by Costantino et al. [3, 4] for studying the population of flour beetles. In the LPA model, flour beetles have 4 life stages including egg, larvae, pupa, and adult. Both larval and adult beetles are cannibalistic, yet they tend to consume eggs. Additionally, during the stage of the pupa, pupa does not consume anything, and it can be consumed by adults. Similar to flour beetles, walleyes have the comparable population structure and cannibalism effect. However, walleye do not have the pupa stage. In fact, the juvenile walleye do consume both eggs and newborns. Hence, some modifications have to be done to model the walleye cannibalism from our motivation.

In this step, we need to characterize the fish population in terms of the life stages. In our case, we can consider four stages of the fish population (Eggs, Newborns, Juveniles, and Adults). The stage of the egg is only 2 weeks [13], and it is relatively short compared to other stages. Hence, in this model, we will combine both egg and newborn stages into one stage, and we still call it newborn stage. Newborns are the fish with age less or equal to 1 year, and they do not have the ability to cannibalize the other fish. Juveniles are the fish older than 1 year old and not older than 2 years. For juveniles, they are not biologically mature to lay eggs; however, because most fish is size(age)-dependent cannibalistic, they do have the ability to eat eggs and newborns. The last life stage is adults. In this stage, they are both biologically mature enough

to lay eggs and able to eat eggs, newborns and juveniles.

Let $N(t)$, $J(t)$, and $A(t)$ be the populations of newborns, juveniles, and adults respectively at time t. Based on the above characteristics at stages, we can have the following system of nonlinear difference equations.

$$\begin{cases} N(t+1) = bA(t)e^{-c_{ej}\cdot J(t)-c_{ea}\cdot A(t)} \\ J(t+1) = (1-\mu_n)N(t)e^{-c_{nj}\cdot J(t)-c_{na}\cdot A(t)} \\ A(t+1) = (1-\mu_j)J(t)e^{-c_{ja}\cdot A(t)} + (1-\mu_a)\cdot A(t) \end{cases} \qquad (2.2)$$

For the exponential term, such as $J(t+1) = N(t)\cdot\exp(-c_{nj}\cdot J(t))$, if $J(t)$ is 0, there would be no cannibalism occurred, and $J(t+1)$ would just be $N(t)$. In fact, the reason we use exponential form is from the Poisson process including encounters of individuals [6]. The positive parameter b ($b > 0$) is the natural birth rate for the fish. c_{ej}, c_{ea}, c_{nj}, c_{na}, and c_{ja} are the cannibalism coefficients, meaning that they are the cannibalistic encounter rates for eggs and juveniles, eggs and adults, newborns and juveniles, newborns and adults, and juveniles and adults. Finally, μ_a denotes the death rate for the adult population satisfying $0 < \mu_a < 1$.

This system can also be written in the matrix form $X(t+1) = L(N(t), J(t), A(t))X(t)$.

$$X(t) = \begin{pmatrix} N(t) \\ J(t) \\ A(t) \end{pmatrix}$$

$$L(N(t), J(t), A(t)) = \begin{pmatrix} 0 & 0 & be^{-c_{ej}\cdot J(t)-c_{ea}\cdot A(t)} \\ (1-\mu_n)e^{-c_{nj}\cdot J(t)-c_{na}\cdot A(t)} & 0 & 0 \\ 0 & (1-\mu_j)e^{-c_{ja}\cdot A(t)} & (1-\mu_a) \end{pmatrix}$$

There are assumptions made in this model. The time intervals of newborns and juveniles are identical, and deaths due to cannibalism occur before being adults. The reason we adapt this assumption is that in most government research papers, they consider juveniles as walleye younger than 3 years old [9]. In our case, new borns are the fish of 1 year old, and juveniles are the fish of 2 years old.

2.3   Well-posedness

In order to check if the model is well-posed, the first thing we need to investigate is the non-negativity. In population dynamics, only a non-negative population has a biological meaning.

For the system (2.2), because $b > 0$ and $1 - \mu_a > 0$, the entries of the Leslie matrix L are always non-negative. This implies that

$$\begin{pmatrix} N(0) \\ J(0) \\ A(0) \end{pmatrix} \geq \begin{pmatrix} 0 \\ 0 \\ 0 \end{pmatrix} \implies \begin{pmatrix} N(t) \\ J(t) \\ A(t) \end{pmatrix} \geq \begin{pmatrix} 0 \\ 0 \\ 0 \end{pmatrix}$$

for $t = 1, 2, 3, ...$ We thus conclude that the system is non-negative invariant. Further more, we want to investigate whether the solutions of the system are bounded.

From (2.2), we have

$$0 \leq N(t+1) = bA(t)e^{-c_{ej} \cdot J(t) - c_{ea} \cdot A(t)} \leq b \cdot A(t)e^{-c_{ea} \cdot A(t)} \leq \frac{b}{c_{ea}e}.$$

We can also obtain the boundedness of $J(t)$ shown as following:

$$J(t+1) = (1 - \mu_n)N(t)e^{-c_{nj} \cdot J(t) - c_{na} \cdot A(t)} \leq (1 - \mu_n)N(t) \leq (1 - \mu_n)\frac{b}{c_{ea}e} \qquad t = 1, 2, 3, ...$$

Finally, for $A(t)$, we have

$$A(t+1) = (1 - \mu_j)J(t)e^{-c_{ja} \cdot A(t)} + (1 - \mu_a) \cdot A(t) \leq (1 - \mu_n)(1 - \mu_j)\frac{b}{c_{ea}e} + (1 - \mu_a) \cdot A(t)$$

$$= \alpha + \beta A(t)$$

where $\alpha = (1 - \mu_n)(1 - \mu_j)\frac{b}{c_{ea}e}$, and $\beta = (1 - \mu_a)$.

By the above inequality, we further obtain

$$A(t) \leq \alpha + \beta \left(\alpha + \beta A (t-1) \right)$$

$$= \alpha + \beta\alpha + \beta^2 \left(\alpha + \beta A(t-2) \right)$$

$$= \alpha(1 + \beta + \beta^2 + ... + \beta^t)A(0)$$

$$= \alpha \frac{1 - \beta^{t+1}}{1 - \beta}A(0)$$

$$\leq \frac{\alpha}{1 - \beta}A(0)$$

$$= \frac{1}{\mu_a}(1 - \mu_n)(1 - \mu_j)\frac{b}{c_{ea}e}A(0).$$

Thus, we can conclude that all $N(t)$, $J(t)$, and $A(t)$ are bounded.

On the other hand, from (2.2), the following inequalities hold:

$$
\begin{aligned}
0 &\le N(t+1) &\le bA(t) \\
0 &\le J(t+1) &\le (1 - \mu_n)N(t) \\
0 &\le A(t+1) &\le (1 - \mu_j)J(t) + (1 - \mu_a)A(t)
\end{aligned}
$$

This means that the model is bounded by the following linear system

$$
\begin{cases}
x(t+1) = bz(t) \\
y(t+1) = (1 - \mu_n)x(t) \\
z(t+1) = (1 - \mu_j)y(t) + (1 - \mu_a)z(t)
\end{cases}
\tag{2.3}
$$

with initial conditions $x(0) = N(0) \ge 0, y(0) = J(0) \ge 0$, and $z(0) = A(0) \ge 0$. We can rewrite the linear system (2.3) in the matrix form:

$$
\begin{pmatrix} x(t+1) \\ y(t+1) \\ z(t+1) \end{pmatrix} = \begin{pmatrix} 0 & 0 & b \\ 1 - \mu_n & 0 & 0 \\ 0 & 1 - \mu_j & 1 - \mu_a \end{pmatrix} \begin{pmatrix} x(t) \\ y(t) \\ z(t) \end{pmatrix}
$$

which is equivalent to

$$
X(t+1) = L(0,0,0)X(t)
$$

2.3.1   Basic Reproduction Number

There are several ways to obtain the basic reproduction number. Here, we will go by the spectral radius of the next generation operator.

Let

$$
A = F + T, \ \text{where } F = \begin{pmatrix} 0 & 0 & b \\ 0 & 0 & 0 \\ 0 & 0 & 0 \end{pmatrix}, \text{and } T = \begin{pmatrix} 0 & 0 & 0 \\ 1 - \mu_n & 0 & 0 \\ 0 & 1 - \mu_j & 1 - \mu_a \end{pmatrix}.
$$

Then, by Leenheer's formula [10], the basic reproduction number is given by

$$
R_0 = \rho\left(F(I - T)^{-1}\right),
$$

where $\rho(M)$ represents the dominant eigenvalue of the matrix M. Then, we can calculate R_0 by plugging in F and T to obtain

$$
\begin{aligned}
R_0 =&\rho\left(\begin{pmatrix} 0 & 0 & b \\ 0 & 0 & 0 \\ 0 & 0 & 0 \end{pmatrix}\begin{pmatrix} 1 & 0 & 0 \\ 1-\mu_n & 1 & 0 \\ \frac{(1-\mu_n)(1-\mu_j)}{\mu_a} & \frac{1-\mu_j}{\mu_a} & \frac{1}{\mu_a} \end{pmatrix}\right) \\
=&\rho\begin{pmatrix} \frac{b(1-\mu_n)(1-\mu_j)}{\mu_a} & \frac{b(1-\mu_j)}{\mu_a} & \frac{b}{\mu_a} \\ 0 & 0 & 0 \\ 0 & 0 & 0 \end{pmatrix} \\
=& \frac{b(1-\mu_n)(1-\mu_j)}{\mu_a}.
\end{aligned}
$$

By the definition of the basic reproduction rate and its biological meaning[10], we expect that the population will go extinct if the basic reproduction rate is less than 1:

$$
\begin{pmatrix} x(t) \\ y(t) \\ z(t) \end{pmatrix} \rightarrow \begin{pmatrix} 0 \\ 0 \\ 0 \end{pmatrix} \text{ as } t \rightarrow \infty \quad \text{if} \quad R_0 = \frac{b(1-\mu_n)(1-\mu_j)}{\mu_a} < 1. \tag{2.4}
$$

Actually, this can be verified as below. First, note that

$$
\begin{aligned}
X(t+1) &= L(Z(t))X(t) \\
&\leq L(0,0,0)X(t) \\
&\leq L^2(0,0,0)X(t-1) \\
&\leq \dots \\
&\leq L^{t+1}(0,0,0)X(0).
\end{aligned} \tag{2.5}
$$

Let r be the strictly dominant eigenvalue of $L(0,0,0)$. Then, by Theorem 1.1.2 and Theorem 1.1.3 in Cushing's book [6], we have the following:

$$
\begin{cases} (i)\ r < 1 \Leftrightarrow R_0 < 1 \\ (ii)\ \text{If } r < 1, L^t(0,0,0)X(0) \rightarrow 0 \text{ as } t \rightarrow \infty \end{cases}
$$

Biologically, in the difference equation model, if the basic reproduction number is less than 1, the population will go extinction eventually. Additionally, we can consider this basic

reproduction number as the net reproduction number per unit time per capita.

2.4 Equilibria

In this section, we consider the equilibriums of the system. An equilibrium is a time-independent solution for the systems of difference equations $X(t + 1) = F(X(t))$. And the equilibrium is defined by

$$X = F(X) \qquad (i.e.\ x_i = f_i(x_1, ..., x_n) \quad i = 1, 2, ...)$$

For the system (2.2), we can find the equilibrium by solving the following equations:

$$N = bAe^{-c_{ej}\cdot J(t) - c_{ea}\cdot A}, \tag{2.6}$$

$$J = (1 - \mu_n)Ne^{-c_{nj}\cdot J - c_{na}\cdot A}, \tag{2.7}$$

$$A = (1 - \mu_j)Je^{-c_{ja}\cdot A} + (1 - \mu_a) \cdot A. \tag{2.8}$$

The first thing we notice is that there exist a trivial equilibrium $X_0 = (0, 0, 0)$. At the trivial equilibrium, because the population in each stage is zero, we can also call this extinction equilibrium.

Besides the trivial equilibrium, we are able to investigate if a positive equilibrium exists by solving the system (2.6)-(2.8) for non-zero values of the variables. From (2.8) and (2.7), we get the following

$$J = \frac{\mu_a A}{1 - \mu_j}e^{c_{ja}A}, \qquad N = \frac{\mu_a}{(1 - \mu_n)(1 - \mu_j)}Ae^{c_{ja}A + c_{na}A + c_{nj}J}. \tag{2.9}$$

Substituting (2.9) back in (2.6) yields

$$\frac{\mu_a}{(1 - \mu_n)(1 - \mu_j)}Ae^{c_{ja}A + c_{na}A + c_{nj}J} = bAe^{-c_{ej}\cdot J - c_{ea}\cdot A}. \tag{2.10}$$

Since we look for positive solutions, cancelling A in (2.10) and rearranging the equation lead to

$$exp(c_{ja}A + c_{na}A + c_{ea} \cdot A + c_{nj}J + c_{ej} \cdot J) = \frac{b(1 - \mu_n)(1 - \mu_j)}{\mu_a} = R_0. \tag{2.11}$$

Now, we can take logarithm of both sides to obtain the following equation

$$c_{ja}A + c_{na}A + c_{ea} \cdot A + c_{nj}J + c_{ej} \cdot J = \ln R_0. \tag{2.12}$$

We now further substitute (2.9) into the equation (2.12) to get

$$(c_{ja} + c_{na} + c_{ea})A + (c_{nj} + c_{ej})\frac{\mu_a A}{1 - \mu_j}e^{c_{ja}A} = \ln R_0. \qquad (2.13)$$

Let $g(A)$ denote the left hand side, as a function of A. Then, it is easy to see that $g(A)$ is monotonically increasing for $A > 0$ satisfying $g(0) = 0$ and $g(\infty) = \infty$. Hence, equation (2.13) has a positive solution for A if and only if $R_0 > 1$.

To illustrate (2.13), a plot (Figure 2.1) has been generated with some random parameters.
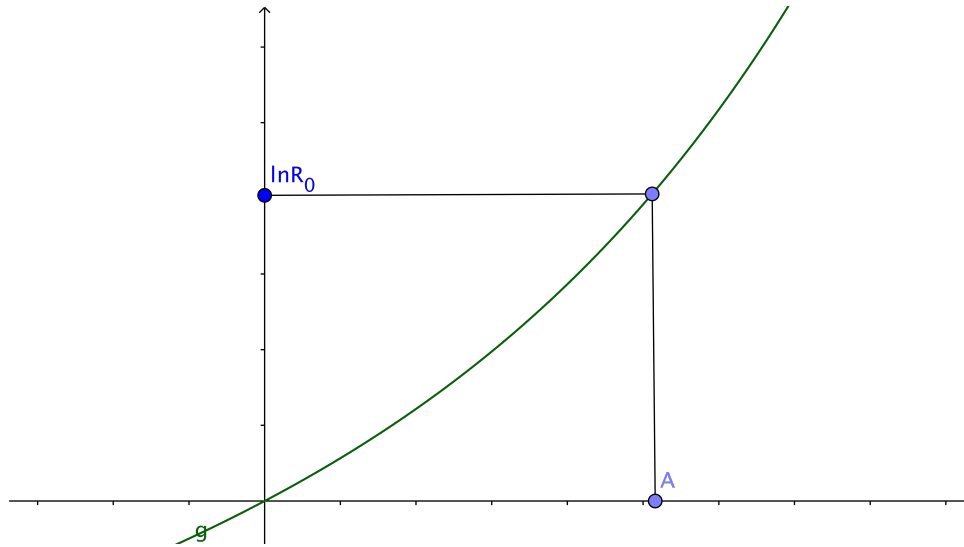

Figure 2.1: $R_0 - A$ relationship

When $R_0 > 1$, let A^* be the unique positive solution of (2.13).

$$J^* = \frac{\mu_a A^*}{1 - \mu_j}e^{c_{ja}A^*},$$

$$N^* = \frac{\mu_a}{(1 - \mu_n)(1 - \mu_j)}A^* e^{c_{ja}A^* + c_{na}A^* + c_{nj}\frac{\mu_a A^*}{1-\mu_j}e^{c_{ja}A^*}},$$

then (N^*, J^*, A^*) is the unique positive equilibrium of the system (2.2).

2.5 Stability Analysis

2.5.1 Stability of Trivial Equilibrium

To check the local stability of the trivial equilibrium X_0, we have to check the eigenvalues of the Jacobian of the system (2.2) at X_0. Calculating the Jacobian gives

$$M(N, J, A) = \begin{pmatrix} 0 & -c_{ej}bA(t)e^{-c_{ej}J(t)-c_{ea}A(t)} & (b-c_{ea}bA(t))e^{-c_{ej}J(t)-c_{ea}A(t)} \\ (1-\mu_n)e^{-c_{nj}J(t)-c_{na}A(t)} & -c_{nj}(1-\mu_n)N(t)e^{-c_{nj}J(t)-c_{na}A(t)} & -c_{na}(1-\mu_n)N(t)e^{-c_{nj}J(t)-c_{na}A(t)} \\ 0 & (1-\mu_j)e^{-c_{ja}A(t)} & (1-\mu_j)J(t)e^{-c_{ja}A(t)} + (1-\mu_a) \end{pmatrix}.$$

$$(2.14)$$

Evaluating (2.14) at E_0 yields

$$M(0,0,0) = \begin{pmatrix} 0 & 0 & b \\ 1-\mu_n & 0 & 0 \\ 0 & 1-\mu_j & 1-\mu_a \end{pmatrix}.$$

which is precisely the matrix $L(0,0,0)$ in section 2.3. In order to check the stability, we need to find the eigenvalues of the matrix above. If all the eigenvalues have the norm less than 1, we can conclude that the equilibrium is stable. The eigenvalues are the cubic roots of the following equation.

$$\det\begin{pmatrix} -\lambda & 0 & b \\ 1-\mu_n & -\lambda & 0 \\ 0 & 1-\mu_j & 1-\mu_a-\lambda \end{pmatrix} = -\lambda\Big(-\lambda(1-\mu_a-\lambda)\Big) + b(1-\mu_n)(1-\mu_j) \qquad (2.15)$$

$$= -\lambda^3 + (1-\mu_a)\lambda^2 + b(1-\mu_n)(1-\mu_j) \qquad (2.16)$$

$$= \lambda^3 - (1-\mu_a)\lambda^2 - b(1-\mu_n)(1-\mu_j) = 0 \qquad (2.17)$$

Then, we can use the Jury criterion [1] for cubic equations to get the following necessary and sufficient conditions for the roots to satisfy $|\lambda| < 1$:

$$\begin{cases} 1 - (1-\mu_a) - b(1-\mu_n)(1-\mu_j) > 0 & (2.18) \\ 1 + (1-\mu_a) + b(1-\mu_n)(1-\mu_j) > 0 & (2.19) \\ 3 - (1-\mu_a) + 3b(1-\mu_n)(1-\mu_j) > 0 & (2.20) \\ 1 - (1-\mu_a)b(1-\mu_n)(1-\mu_j) - \big(b(1-\mu_n)(1-\mu_j)\big)^2 > 0 & (2.21) \end{cases}$$

Rearranging (2.18), we get $\mu_a > b(1-\mu_n)(1-\mu_j) \iff R_0 < 1$. Hence, (2.18) holds iff $R_0 < 1$. Because both $1-\mu_a$ and $b(1-\mu_n(1-\mu_j))$ are non-negative, (2.19) and (2.20) are naturally true

if $R_0 < 1$.

For (2.21), if $R_0 < 1$, then $\delta \triangleq b(1 - \mu_n)(1 - \mu_j) < \mu_a < 1$. Hence,

$$1 - (1 - \mu_a)\underbrace{b(1 - \mu_n)(1 - \mu_j)}_{\delta} - \left(\underbrace{b(1 - \mu_n)(1 - \mu_j)}_{\delta}\right)^2 = 1 + (\mu_a - 1)\delta - \delta^2$$

$$> 1 + (\delta - 1)\delta - \delta^2$$

$$= 1 - \delta$$

$$> 0 \qquad (\delta < 1)$$

We conclude that as long as (2.18) holds (i.e. $R_0 < 1$), then (2.19)-(2.21) hold as well, and have all the roots satisfying the condition $|\lambda| < 1$.

Now, we can conclude that the absolute value of the dominant eigenvalue is less than 1 if $R_0 < 1$, and greater than 1 is $R_0 > 1$, confirming the result in [7] for our system (2.2)

Note that we have actually shown in section 2.3 that if $R_0 < 1$, then $L^*(0, 0, 0)X(0) \to 0$ as $t \to \infty$. By (2.5), and the local stability of E_0 proved above, we have established the globally stability of E_0 under $R_0 < 1$. Note that when $R_0 > 1$, E_0 loses its stability and becomes unstable

We can also interpret the result biologically. Note that $R_0 = \frac{(1-\mu_n)(1-\mu_j)}{\mu_a}b < 1$ is equivalent to $(1 - \mu_n)(1 - \mu_j)b < \mu_a$ which indicates that gaining is less than losing, implying that the birth rate multiplied by the survival rate from newborns to juveniles and from juveniles to adults is smaller than the death rate for adults. Thus, not surprisingly, the whole population will eventually die out.

2.5.2 Stability of Positive Equilibrium

In addition to the extinction equilibrium, we know that when $R_0 > 1$, there exists a unique positive equilibrium $X^* = (N^*, J^*, A^*)$. Similar to Cushing's LPA model, the exchange of stability occurs [5]. To check the stability of X^*, we consider the Jacobian matrix (2.14) evaluated at X^*. By plugging equation (2.9) into (2.14), we can get the following simplified Jacobian matrix at the positive equilibrium $X^* = (N^*, J^*, A^*)$. Since we are considering the positive equilibrium X^*, we know that $R_0 > 1$ and $A > 0$. Note that this simplified Jacobian matrix does not apply to the zero equilibrium because $A = 0$ when $R_0 < 1$.

$$M(X^*) = M(N^*, J^*, A^*) = \begin{pmatrix} 0 & -c_{ej}N^* & -c_{ea}N^* + \frac{N^*}{A^*} \\ \frac{J^*}{N^*} & -c_{nj}J^* & -c_{na}J^* \\ 0 & \frac{\mu_a A^*}{J^*} & -c_{ja}\mu_a A^* - \mu_a + 1 \end{pmatrix}$$

and the characteristic equation of $M(X^*)$ is

$$
\begin{aligned}
p(\lambda, A) = &\lambda^3 \\
&+ \frac{(c_{nj}\mu_a A e^{c_{ja}A} - c_{ja}\mu_a A\mu_j + c_{ja}\mu_a A - \mu_a\mu_j + \mu_a + \mu_j - 1)}{1 - \mu_j}\lambda^2 \\
&+ \frac{\mu_a A(Ae^{c_{ja}A}c_{ja}c_{nj}\mu_a + e^{c_{ja}A}c_{nj}\mu_a + e^{c_{ja}A}c_{ej} - e^{c_{ja}A}c_{nj} - c_{na}\mu_j + c_{na})}{1 - \mu_j}\lambda \\
&+ \frac{\mu_a(A^2 e^{c_{ja}A}c_{ej}c_{ja}\mu_a + \mu_a Ae^{c_{ja}A}c_{ej} - Ae^{c_{ja}A}c_{ej} - Ac_{ea}\mu_j + Ac_{ea} + \mu_j - 1)}{1 - \mu_j} \\
= &\, 0,
\end{aligned}
\tag{2.22}
$$

where $A = A^*$.

It is obvious that solving this characteristic equation is extremely complicated. Instead of solving this equation, we can solve the equation when $A = 0$ (i.e. trivial equilibrium), and see if λ would change with respect to A. Then, the problem will be solving the characteristic equation (2.22)

First of all, we need to solve $\lambda^3 - (1 - \mu_a)\lambda^2 - b(1 - \mu_n)(1 - \mu_j) = 0$. In this case, we have one real dominant eigenvalue λ_0 and a complex conjugate pair of eigenvalues $\lambda_\pm$.

$$
\lambda_\pm = \alpha \pm \beta i,
$$

$$
\alpha = \frac{1}{3}s_a - \frac{1}{2}\gamma - \frac{1}{18}\frac{s_a^2}{\gamma},
$$

$$
\beta = \frac{\sqrt{3}}{2}\frac{1}{\gamma}\left(\gamma^2 - \frac{1}{9}s_a^2\right) > 0,
$$

where

$$
\gamma := \left(\frac{1}{2}bs_{nl} + \frac{1}{27}s_a^3 + \left(\frac{1}{27}bs_{nl}s_a^3 + \frac{1}{4}b^2 s_{nl}^2\right)^{\frac{1}{2}}\right)^{\frac{1}{3}} > 0,
$$

$$
s_{nl} = (-1 + \mu_n)(-1 + \mu_j) = (1 - \mu_n)(1 - \mu_j) > 0,
$$

$$
s_a = 1 - \mu_a > 0.
$$

Similar to the results from Cushing's paper [5], the pair of complex conjugate eigenvalues must satisfy the followings

$$
|\lambda_\pm| < 1, \quad \text{when} \quad \mu_a < 1.
$$

$$
|\lambda_\pm| = (bs_{nl})^{2/3} = (b(1 - \mu_n)(1 - \mu_j))^{2/3} = R_0^{2/3}, \quad \text{when} \quad \mu_a = 1.
\tag{2.23}
$$

Note when $R_0 = 1$, the positive equilibrium collapses to the extinction equilibrium. Naturally, the Jacobian becomes the Leslie matrix $L(0,0,0)$. From 2.3.1, we know the dominant

eigenvalue of $L(0,0,0)$ is $\lambda = R_0 = 1$.

Denote A^* and the principal eigenvalue for $R_0 > 1$ by A_{R_0} and λ_{R_0} respectively. Now, we can take the implicit differentiation of the function $p(\lambda_{R_0}, A_{R_0}) = 0$ with respect to R_0, and we can obtain the following

$$\frac{\partial}{\partial \lambda} p(\lambda_{R_0}, A_{R_0}) \frac{d\lambda_{R_0}}{dR_0} + \frac{\partial}{\partial A} p(\lambda_{R_0}, A_{R_0}) \frac{dA_{R_0}}{dR_0} = 0$$

and

$$\frac{d\lambda_{R_0}}{dR_0} = -\frac{\frac{\partial}{\partial A} p(\lambda_{R_0}, A_{R_0})}{\frac{\partial}{\partial \lambda} p(\lambda_{R_0}, A_{R_0})} \frac{dA_{R_0}}{dR_0}. \tag{2.24}$$

We know that $\frac{dA_{R_0}}{dR_0}$ is positive at $R_0 = 1$, and in order to ensure that $\frac{d\lambda_{R_0}}{dR_0}$ is negative, we need to check if $\frac{\frac{\partial}{\partial A} p(\lambda_{R_0}, A_{R_0})}{\frac{\partial}{\partial \lambda} p(\lambda_{R_0}, A_{R_0})}$ is positive. This requires both $\frac{\partial}{\partial A} p(\lambda_{R_0}, A_{R_0})$ and $\frac{\partial}{\partial \lambda} p(\lambda_{R_0}, A_{R_0})$ having the same sign. Calculating these two partial derivatives at $A = 0$ and $\lambda = 1$, we obtain

$$\frac{\partial p}{\partial \lambda} = 3 - 2 \frac{-\mu_a \mu_j + \mu_a + \mu_j - 1}{-1 + \mu_j}$$
$$= 2\mu_a + 1 > 0, \tag{2.25}$$

$$\begin{aligned}
\frac{\partial p}{\partial A} &= -\frac{c_{nj}\mu_a - \mu_a\mu_j + \mu_a}{-1 + \mu_j} - \frac{\mu_a\left(-c_{na}\mu_j + c_{nj}\mu_a + c_{ej} + c_{na} - c_{nj}\right)}{-1 + \mu_j} - \frac{\mu_a\left(-c_{ea}\mu_j + c_{ej}\mu_a + c_{ea} - c_{ej}\right)}{-1 + \mu_j} \\
&= \frac{((c_{ea} + c_{na} + 1)\mu_j + (-c_{ej} - c_{nj})\mu_a - c_{ea} - c_{na} - 1)\mu_a}{-1 + \mu_j} \\
&= \frac{\mu_a}{1 - \mu_j}\left(-(c_{ea} + c_{na} + 1)\mu_j - (-c_{ej} - c_{nj})\mu_a + c_{ea} + c_{na} + 1\right) \\
&= \frac{\mu_a}{1 - \mu_j}\left((c_{ea} + c_{na} + 1)(1 - \mu_j) - (-c_{ej} - c_{nj})\mu_a\right) \\
&= \frac{\mu_a}{1 - \mu_j}\left((c_{ea} + c_{na} + 1)(1 - \mu_j) + (c_{ej} + c_{nj})\mu_a\right) \\
&> 0.
\end{aligned} \tag{2.26}$$

Thus, by (2.24), (2.25), and (2.26), we have

$$\frac{d\lambda_{R_0}}{dR_0}\bigg|_{R_0=1} < 0.$$

Because $\lambda_{R_0} = 1$ when $R_0 = 1$, we obtain that $\lambda_{R_0} < 1$ for $R_0 > 1$ if R_0 is sufficiently close to 1 ($A = 0$).

If $\mu_a < 1$, the two complex eigenvalues are close to the complex eigenvalues $\lambda^{\pm}$ which are less than 1 if n is close to 1. In this case, all the three eigenvalues of J have magnitudes smaller than 1 if $n > 1$ is sufficiently close to 1. Because all the eigenvalues are smaller than 1, the positive equilibrium is locally asymptotically stable. This can also be explained by the bifurcation diagram below:
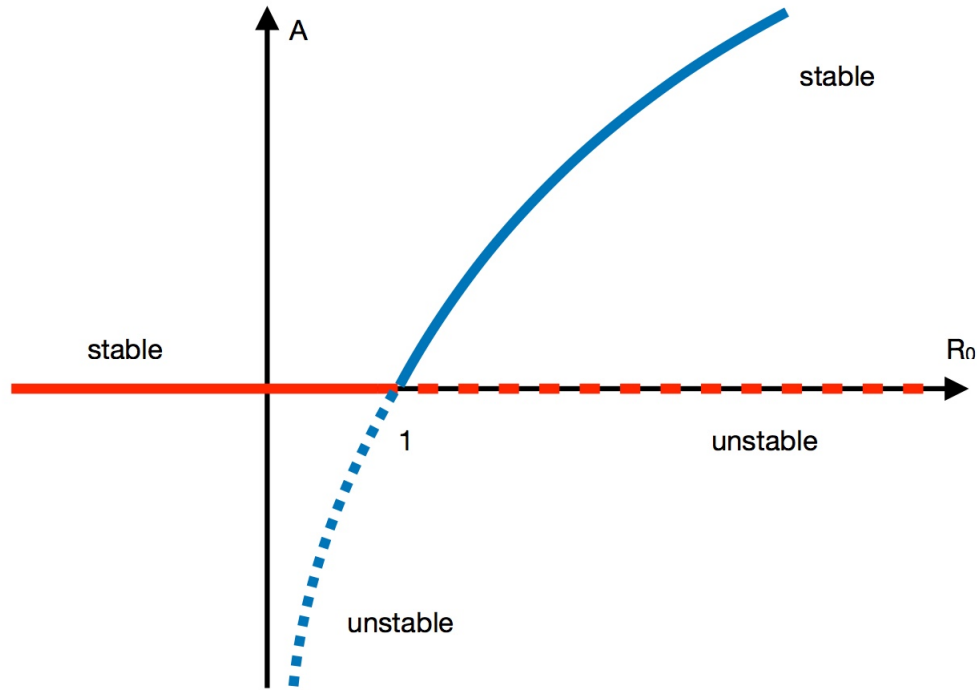

Figure 2.2: Exchange of Stability

Note that for the red branch, the dominant eigenvalue is governed by $\lambda = R_0$ from 2.3.1. However, for the blue branch, the dominant eigenvalue is governed by the characteristic polynomial (2.22). When $R_0 = 1$, two branches collapse, and the corresponding dominant eigenvalues collapse as well.

When $R_0 < 1$, the extinction equilibrium is globally stable. When $R_0 = 1$, the blue branch crosses R_0-axis, and it collapses to the red branch. From 2.3.1, we know the dominant eigenvalue $\lambda_{R_0} = 1$ when $R_0 = 1$. Because $\frac{d\lambda_{R_0}}{dR_0}\Big|_{R_0=1} < 0$ along the blue branch, we conclude that when R_0 is sufficiently close to 1, the dominant eigenvalue $\lambda_{R_0} < 1$. Hence, the blue branch is stable when R_0 is sufficiently close to 1.

If $\mu_a = 1$, biologically speaking, adults will die after one year. However, in reality, our system would have biological meanings only if $0 < \mu_a < 1$.

Theorem 2.5.1 *The following hold for the model (2.2)-(2.4)*

(a) If $\left(N(0), J(0), A(0)\right)$ is non-negative, $\left(N(t), J(t), A(t)\right)$ will remain bounded in the non-negative cone.

(b) If $R_0 < 1$, then the extinction equilibrium (origin) is locally asymptotically stable and globally attracting in the nonnegative cone.

(c) If $R_0 > 1$, there exists a unique non-negative positive equilibrium, and the model is uniformly persistent.

(d) The positive equilibrium is locally asymptotically stable for $R_0 > 1$ sufficiently close to 1.

2.6   Numerical Simulation

In this section, we will keep b as a variable and see how the stability changes with respect to b. For each case of different birth rate b, we run the simulation with both low cannibalism rate and high cannibalism rate to compare the results as well. The following parameters are used for the simulation.

Table 2.1: Low Cannibalism Coefficients Table

Coefficients	Value
C_{ej}	0.015
C_{ea}	0.014
C_{nj}	0.013
C_{na}	0.012
C_{ja}	0.011
μ_n	0.9
μ_j	0.7
μ_a	0.3

Table 2.2: High Cannibalism Coefficients Table

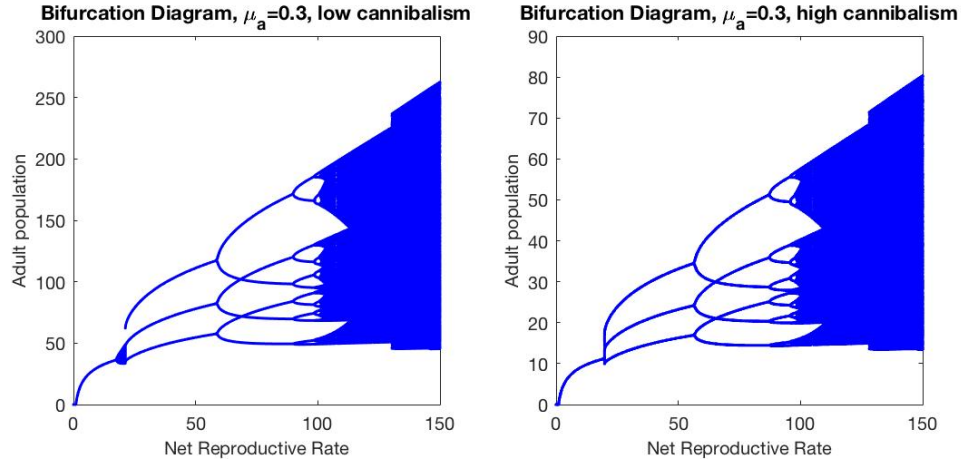| Coefficients	Value
C_{ej}	0.045
C_{ea}	0.044
C_{nj}	0.043
C_{na}	0.042
C_{ja}	0.041
μ_n	0.9
μ_j	0.7
μ_a	0.3

2.6.1   Bifurcation Diagram

Figure 2.3: Bifurcation with respect to b, $\mu_a = 0.3$

From the Figure 2.3, we observe that the extinction equilibrium is stable for a very small interval when R_0 is small. Then, there exists a stable positive equilibrium. After that, there will be a small chaos and a 3-cycle periodic solution following. When the R_0 keeps getting larger, a 3n-cycle periodic solution will occur. We are going to show some examples to illustrate this phenomenon more. One thing worth mentioning is that when R_0 is around 70, there is an overlapping occur in the bifurcation diagram. We can see that it is a 4-cycle solution which is not 3n-cycle. The reason for that is there are actually 2 pairs of overlapping which make the 6-cycle 4-cycle. However, whether it is continuous between the chaos and the 3-cycle periodic solution is unclear. Then we run another simulation with a small range of net reproduction rate.
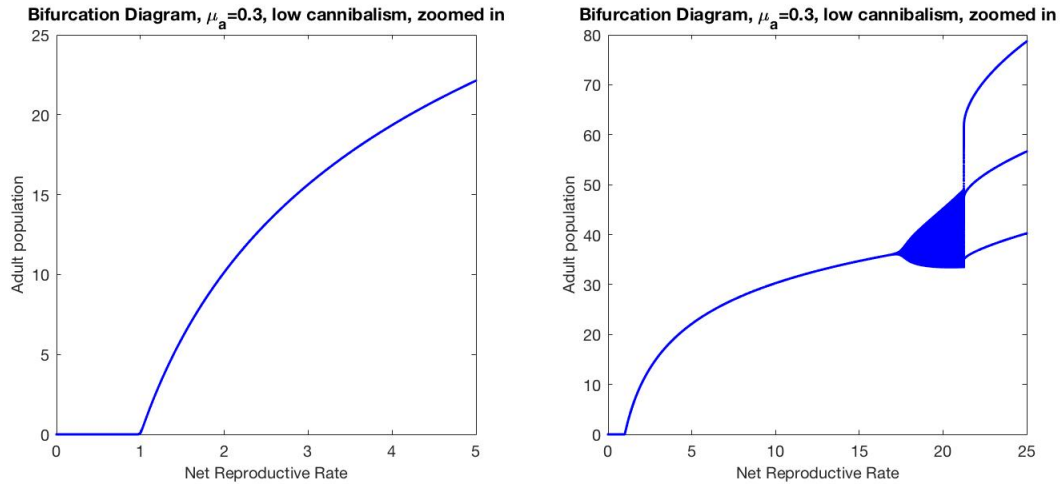

Figure 2.4: Bifurcation with respect to b, $\mu_a = 0.3$, zoomed in

In the zoomed-in diagram, Figure 2.4 shows that the extinction equilibrium is stable when $R_0 < 1$. Also, it is continuous between the chaos and the 3-cycle periodic solution.

2.6.2   Case 1: $R_0 = 0.8$

For case 1, we check the case when $b = 8$ with both low and high cannibalism rates. When $b = 8$, we can calculate $R_0 = 0.8$. From the bifurcation diagram, we should get a diagram that the total population is going extinct.
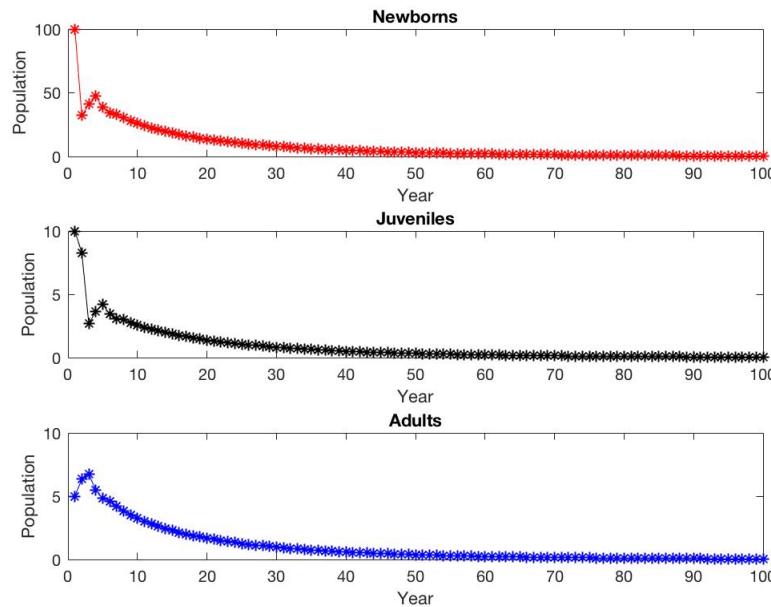
Figure 2.5: $R_0 = 0.8$, $b = 8$, low cannibalism

In Figure 2.5, it is shown that the population of all 3 stages is declining to zero although there is an oscillation happening in the beginning. It is natural to think about R_0 as the net reproductive rate. If the net reproductive rate is below 1, for discreet models, it shows that the next generation will have less population in general than the previous generation. In this scenario, the walleye will go extinct. Next, we want to check if a high level of cannibalism will have any effect on the population dynamics.
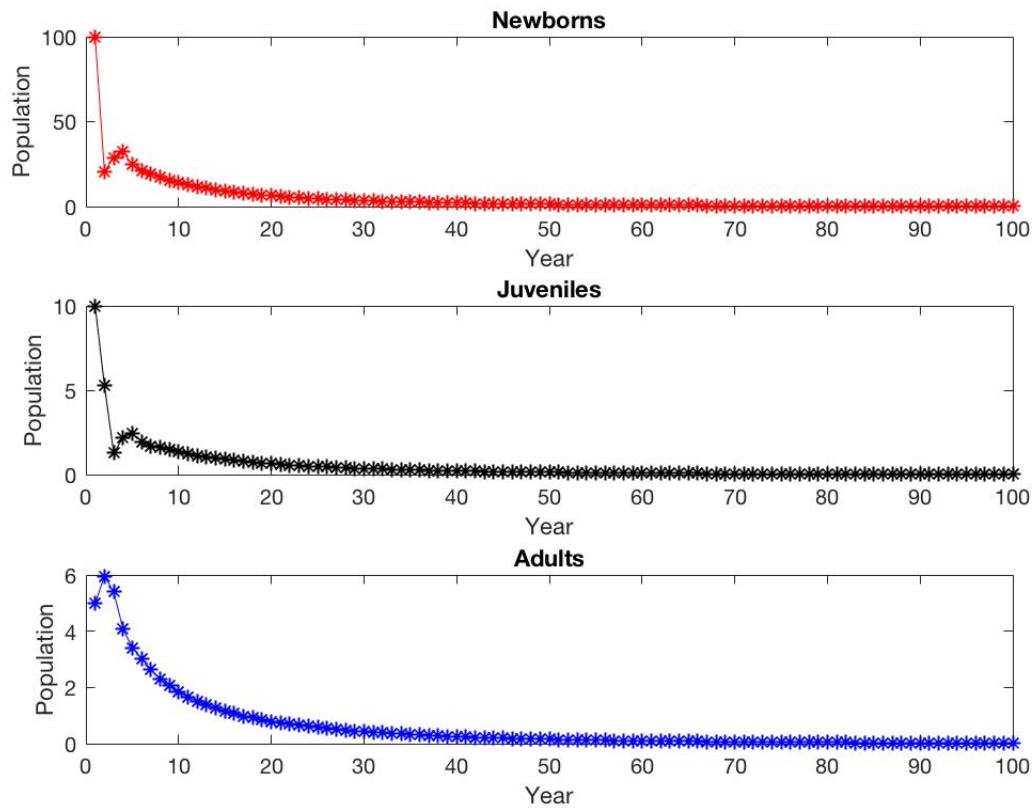
Figure 2.6: $R_0 = 0.8$, $b = 8$, high cannibalism

In Figure 2.6, there is not a noticeable difference from Figure 2.5. However, if we look closely, especially for juveniles we found that the population is convergent to 0 with the faster rate. Hence, we are questioning whether cannibalism is stabilizing the system or speeding up the convergence of the population.

2.6.3   Case 2: $R_0 = 12$

For case 2, we check the case when $b = 120$ with both low and high cannibalism rates. When $b = 120$, we can calculate $R_0 = 12$. From the bifurcation diagram, we should get a diagram that the total population has a stable positive equilibrium.
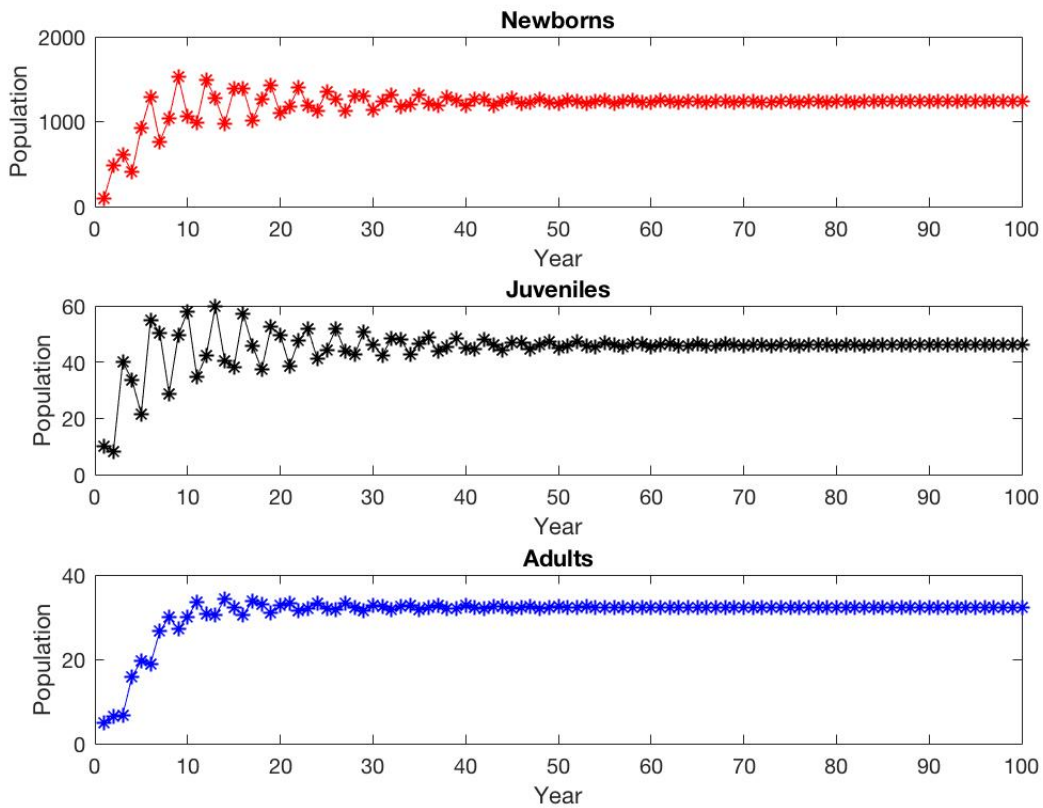
Figure 2.7: $R_0 = 12$, $b = 120$, low cannibalism

In Figure 2.7, $R_0 = 12$, and a positive equilibrium exists, which matches the result from the bifurcation diagram. For the first 40 years, we can clearly see there is an oscillation cased by the negative eigenvalues with the magnitude less than 1. However, since the dominant eigenvalue has the magnitude less than 1, and all three stages are reaching their own equilibrium. Again, we are going to increase the cannibalism rate to see what cannibalism does to the population dynamics.
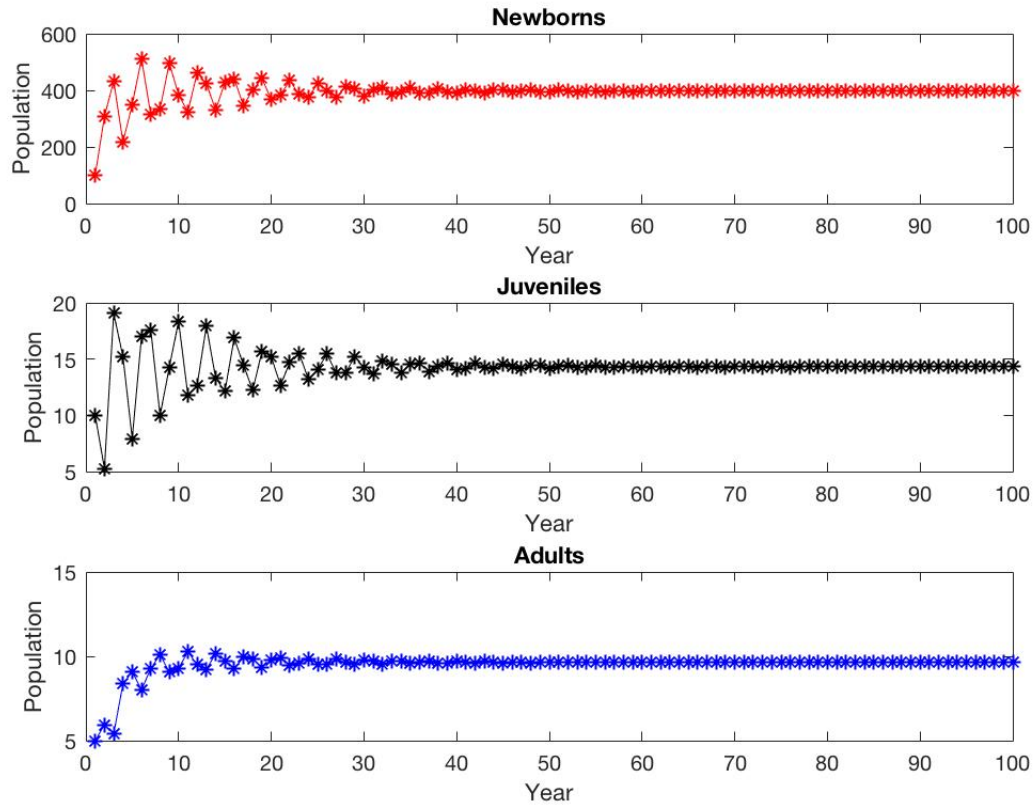
Figure 2.8: $R_0 = 12$, $b = 120$, high cannibalism

In the Figure 2.8, $R_0 = 12$. Comparing Figure 2.7 and Figure 2.8, we notice that there is not a big difference in the general trend of the convergence of population. However, we do notice a decreasing amplitude of the oscillation. For Newborns, the peak value of the population with low cannibalism is around 1800, and around 580 with high cannibalism. Also, we notice a decreasing value of the equilibria for both adult and juvenile population.

2.6.4 Case 3: $R_0 = 20$

For case 3, we increased the natural birth rate b to 200 (i.e. $R_0 = 20$). From the bifurcation diagram Figure 2.4, we know that the the scenario falls into the chaos part of the diagram.

Figure 2.9: $R_0 = 20$, $b = 200$, low cannibalism

In Figure 2.9, $R_0 = 20$, It corresponds to the chaos part from the 2.3. We observe the existence of periodic solutions; however, the frequency of this period is unknown. The solution is eventually oscillating within their own upper and lowers bounds.

Next, we are increasing the cannibalism rates.
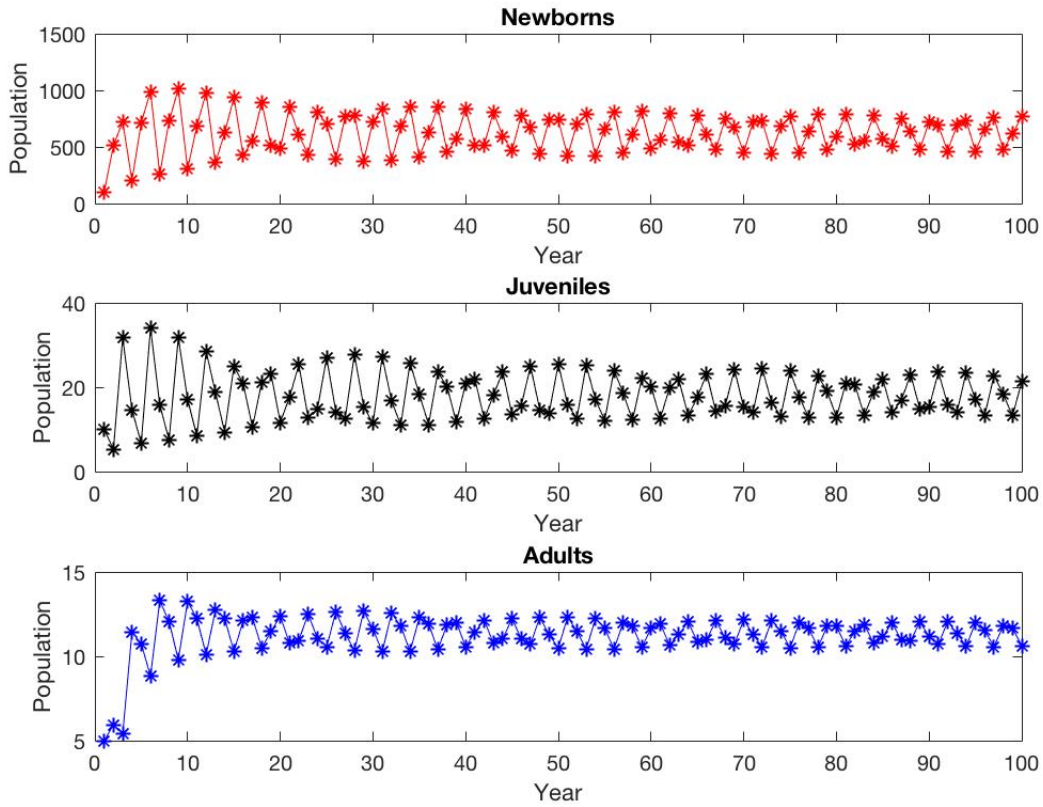
Figure 2.10: $R_0 = 20$, $b = 200$, high cannibalism

With a higher level of cannibalism rates, the oscillation of the system decreases. Although the high cannibalism rates do not change the stability of the positive equilibrium, it still stabilizes the solution to the system by decreasing the amplitude of the oscillation. Similar to 2.8, 2.10 is oscillating within a lower range of population levels. In order to check if a higher level of cannibalism does stabilize the system, we need to increase the level of cannibalism.
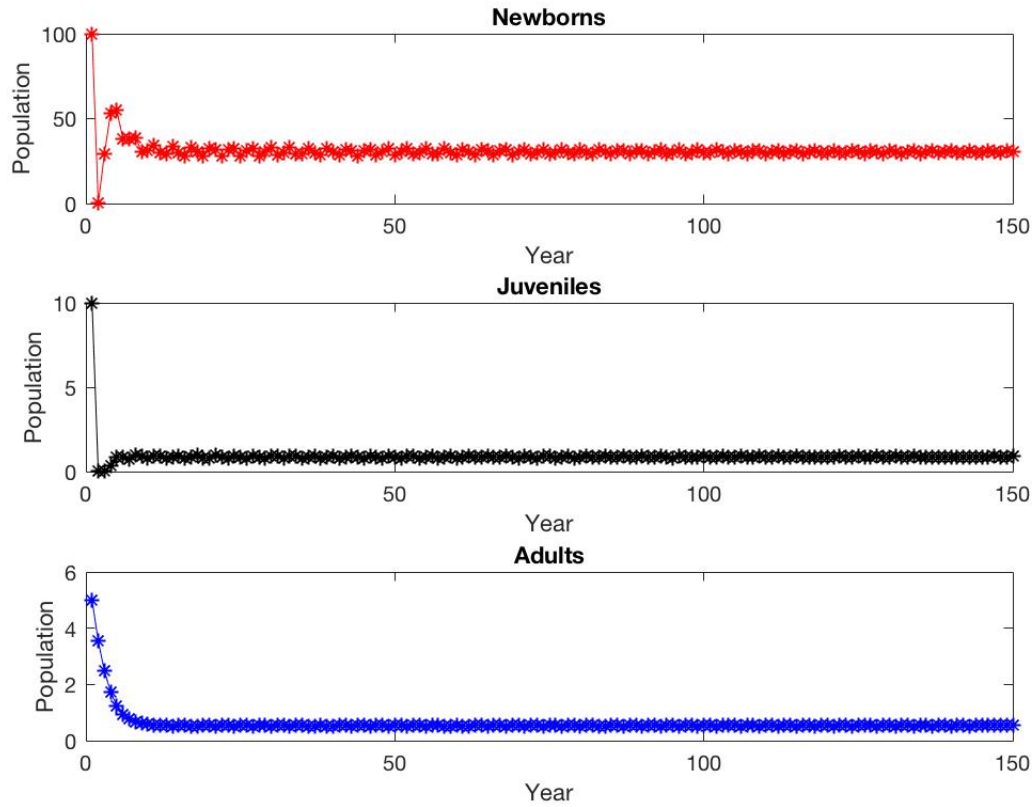
Figure 2.11: $R_0 = 20$, $b = 200$, $c_{ej} = c_{ea} = c_{nj} = c_{na} = c_{ja} = 0.9$

With an even higher level of cannibalism, we notice that the positive equilibrium becomes stable. Now, we can conclude that a higher level of cannibalism can actually stabilize the system by decreasing the amplitude of oscillations and possibly stabilizing the positive equilibrium.

2.6.5   Case 4: $R_0 = 30$

For case 4, we increased the natural birth rate b to 200 (i.e. $R_0 = 20$). From the bifurcation diagram Figure 2.4, we know that the scenario falls into the chaos part of the diagram.
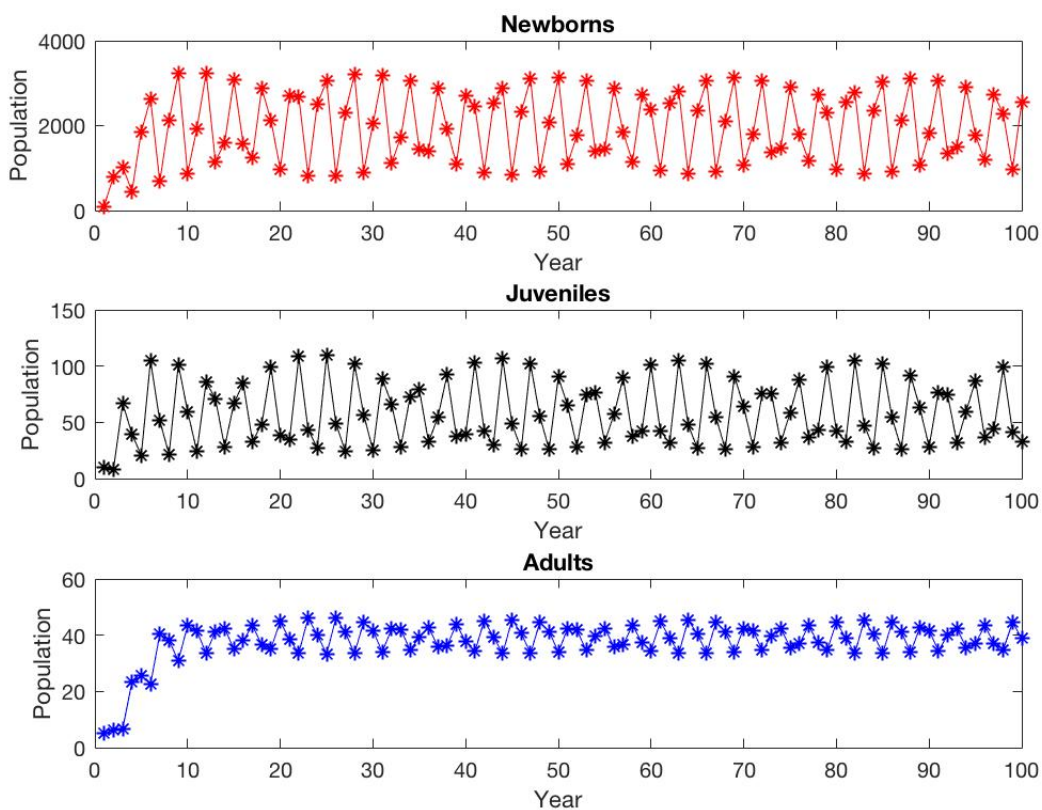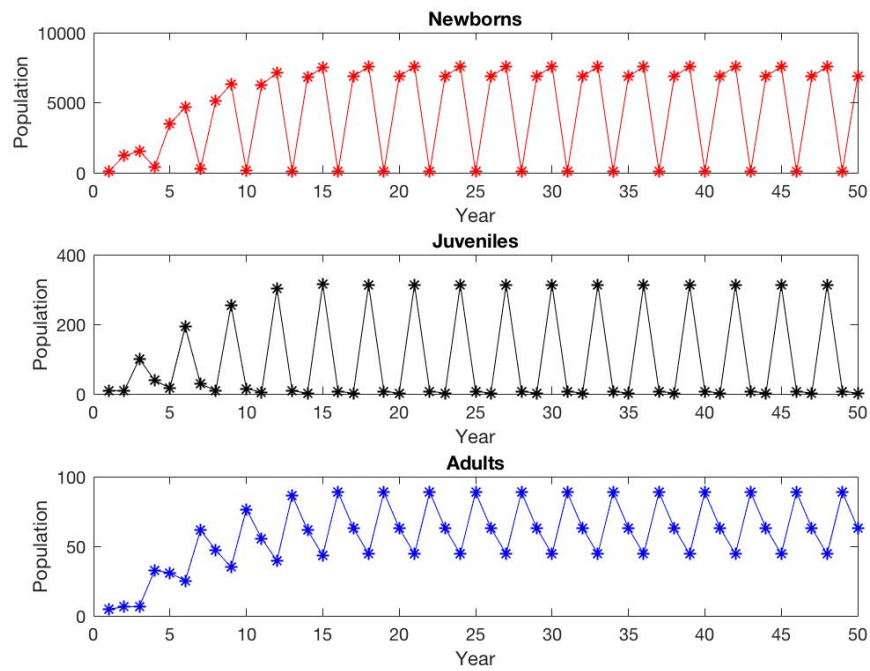
Figure 2.12: $R_0 = 20$, $b = 200$, low cannibalism
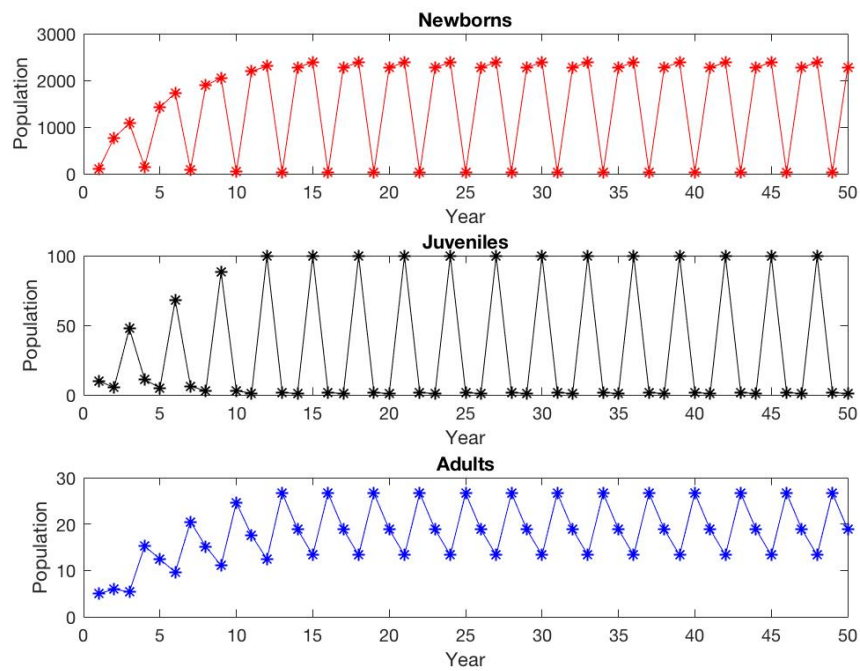
Figure 2.13: $R_0 = 20$, $b = 200$, high cannibalism

In Figure 2.12, $R_0 = 30$. It corresponds to that a 3-cycle periodic solution exists. Because of this cannibalism effect, it is very noticeable that when the adult population reaches its peak, egg and juvenile population reaches their troughs at the same time. In Figure 2.13, with a higher level of cannibalism, we notice no change in the pattern of the population cycles. However, the cannibalism lowers the population level.

2.6.6   Case 5: $R_0 = 90$
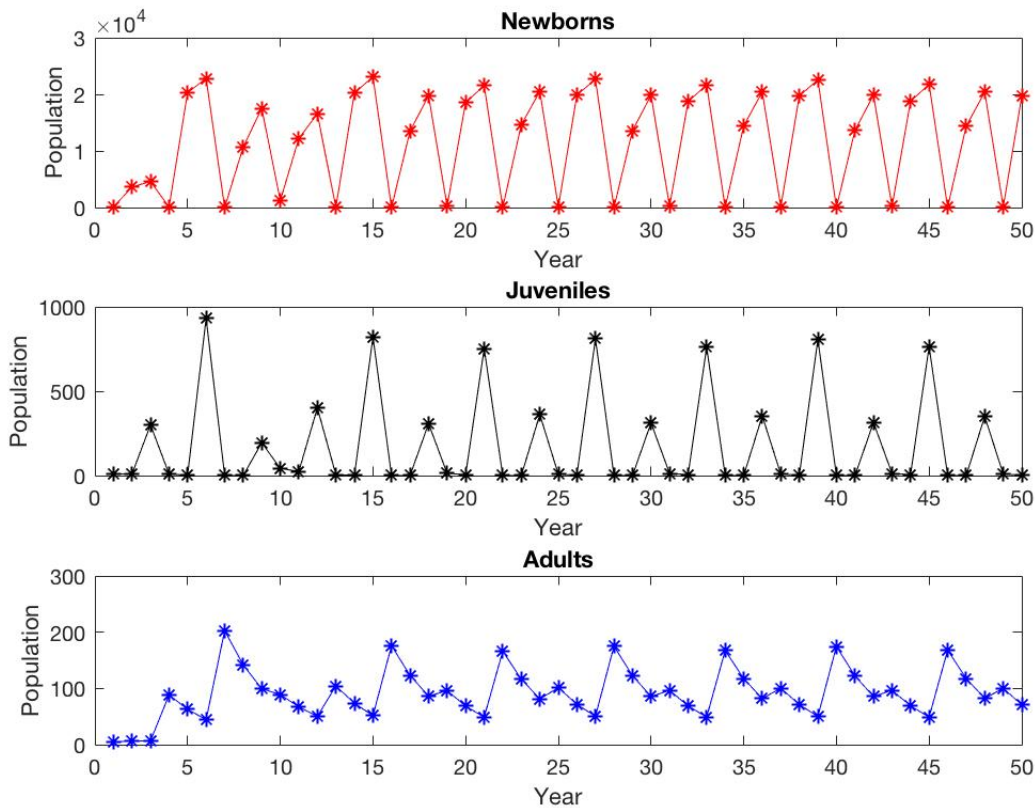
Figure 2.14: $R_0 = 20$, $b = 200$, low cannibalism
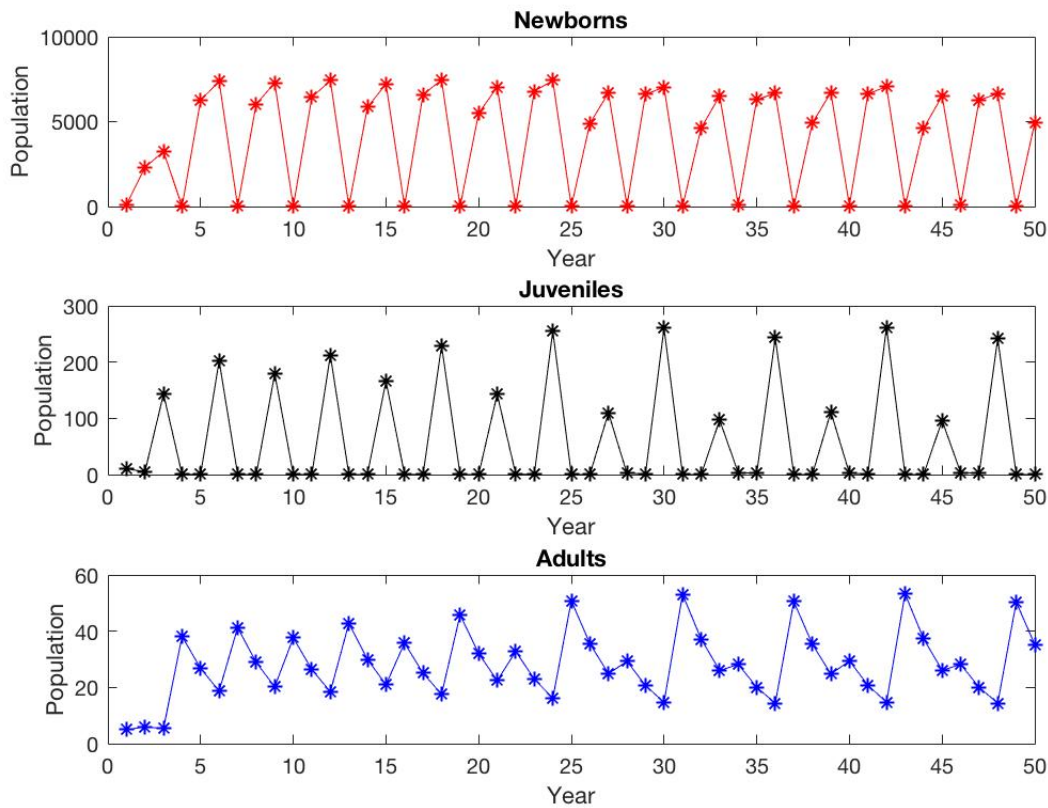
Figure 2.15: $R_0 = 20$, $b = 200$, high cannibalism

Similar to Figure 2.12, Figure 2.14 has the same pattern but with a 6-cycle period. It also has the character that when the adult population reaches its peak, the other two streams are reaching their troughs. One thing worth mentioning is that newborns sometimes reaches zero. However, it is because the population fluctuates too much and the unit is 10^4. The newborn population is not actually zero, and it is just comparably small. In Figure 2.15, with a higher level of cannibalism, the population level is decreased, and it still has a 6-cycle period.

2.6.7   Case 6: $R_0 = 170$
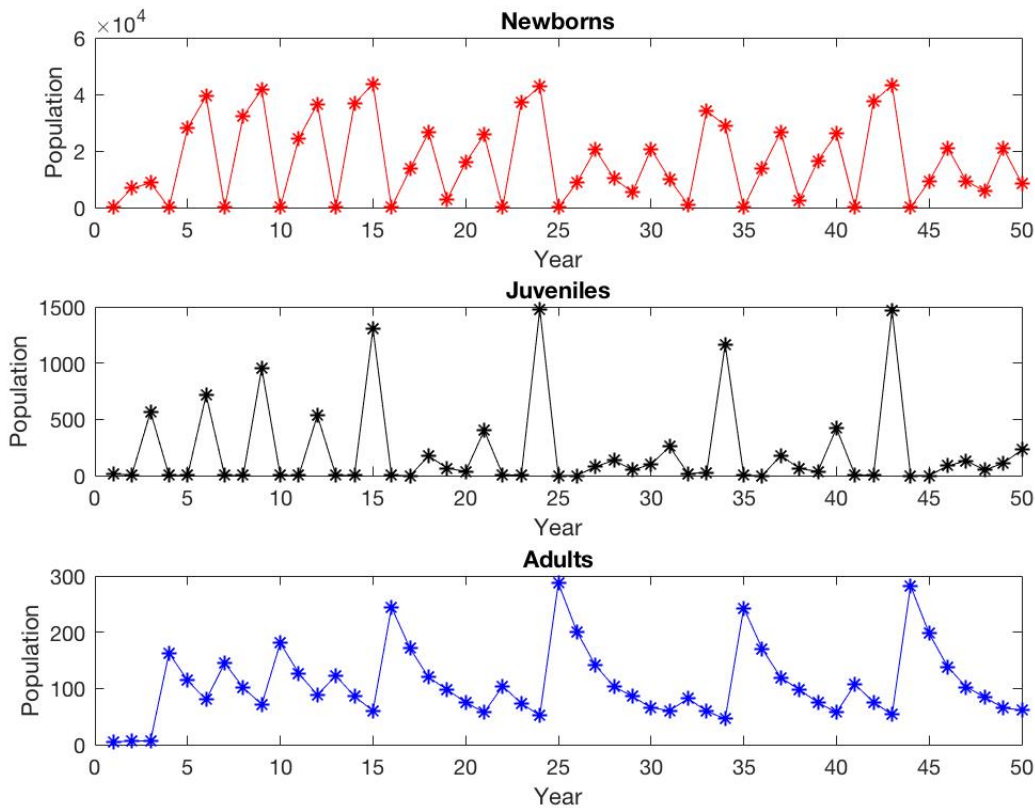
Figure 2.16: $R_0 = 20$, $b = 200$, low cannibalism

In the Figure 2.16, $R_0 = 170$ and reaches the chaos part of the bifurcation. The solutions are still bounded by the non-negative cone obtained from Section 2.3. However, we can not observe a noticeable periodic solution.
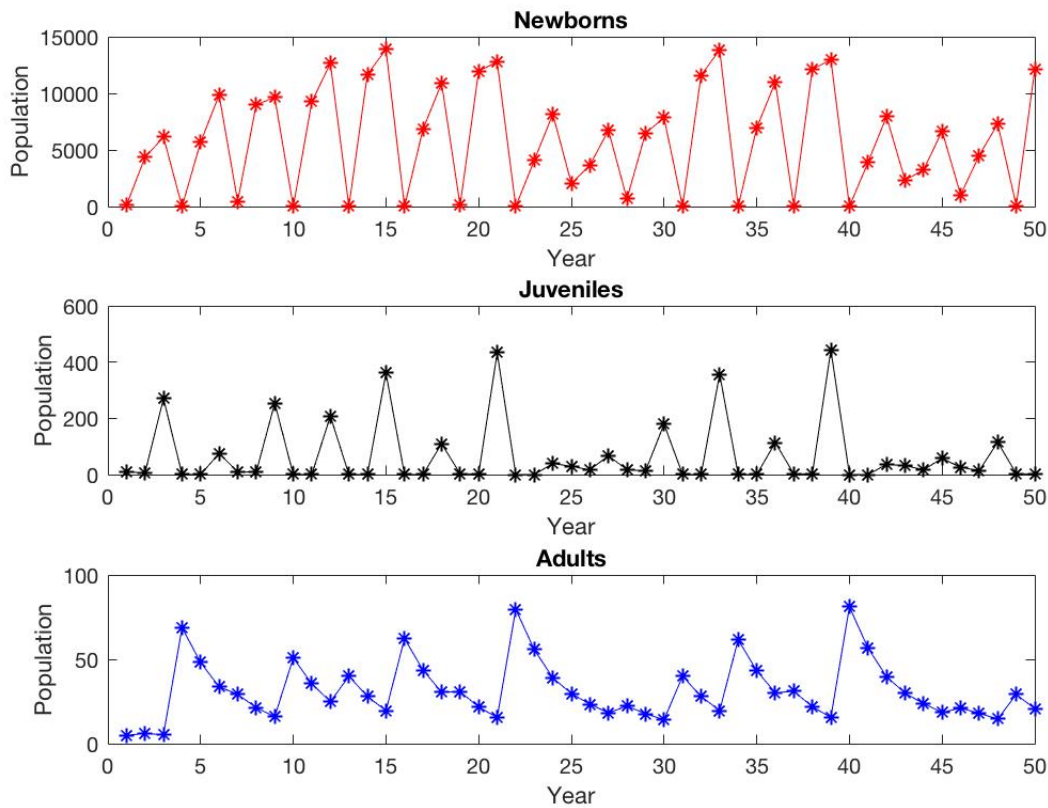
Figure 2.17: $R_0 = 20$, $b = 200$, high cannibalism

Same as other diagrams with higher level of cannibalism, bigger cannibalism rates do not change the stability of the positive equilibrium, but it does lower the level of the population.

2.6.8   Further Study: 4-stage Model

In most dynamical systems, period doubling is usually observed. In the model we studied, the period 1 divides into period 3 at first. Then, the period doubles after. This phenomenon can be understood in a biological way. A relatively low adult population will cause a low birth in the year, and it will take 3 years to affect the adult population again because the model is constructed as 3 age stages. However, mathematically, the reason why the period 1 divides into period 3 is still unknown. In this case, another 4 stage model has been constructed to test if my hypothesis is correct. Another life stage between juvenile and adult has been added into the

system, and we call it $I(t)$ as the intermediate stage. The system is the following

$$
\begin{cases}
N(t+1) = bA(t)e^{-c_{ej} \cdot J(t) - c_{ei} \cdot I(t) - c_{ea} \cdot A(t)} \\
J(t+1) = (1-\mu_n)N(t)e^{-c_{nj} \cdot J(t) - c_{ni} \cdot I(t) - c_{na} \cdot A(t)} \\
I(t+1) = (1-\mu_j)J(t)e^{-c_{ji} \cdot J(t) - c_{ja} \cdot A(t)} \\
A(t+1) = (1-\mu_i)I(t)e^{-c_{ia} \cdot A(t)} + (1-\mu_a) \cdot A(t)
\end{cases}
\tag{2.27}
$$

The way we model this system is similar to the system previously studied. N the only difference is that intermediate stage can consume eggs, newborns, and juveniles. The analytical solution and analysis are very similar too. Instead of solving the cubic characteristic polynomials, a quartic characteristic polynomial has to be solved in order to test the local stability of the equilibria. A bifurcation diagram for this system is generated with some sample parameters.
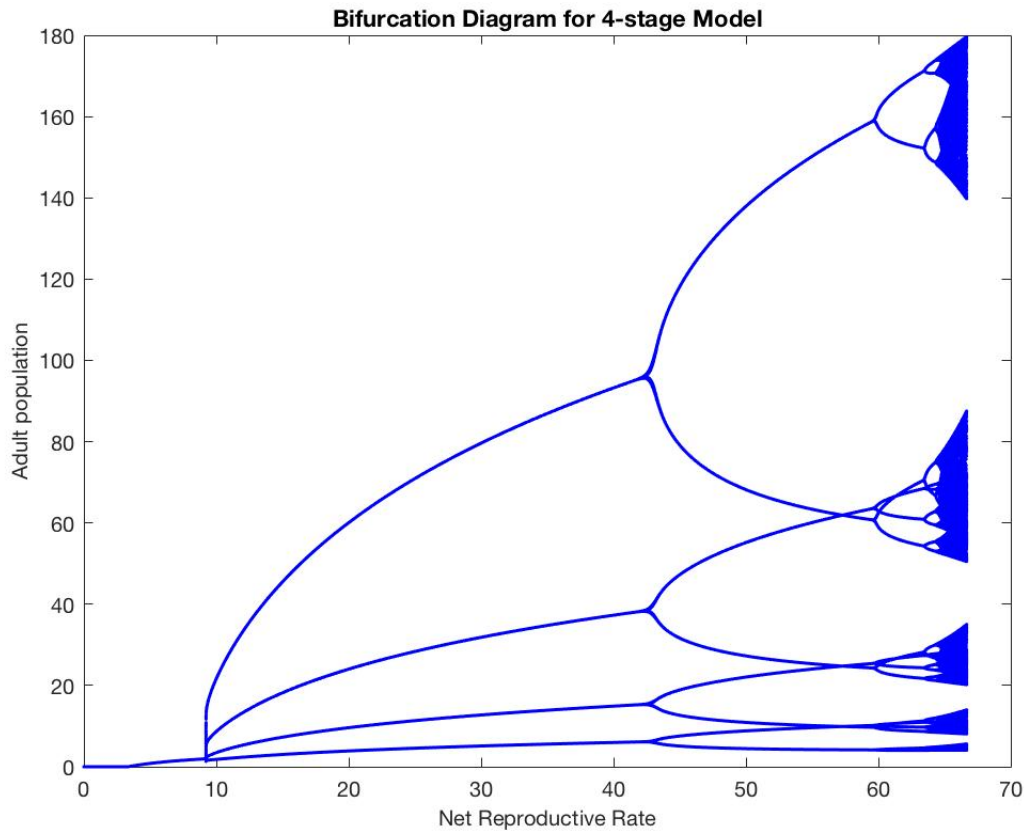
Figure 2.18: $R_0 = 170$, $b = 1700$, $\mu_n = 0.9$, $\mu_j = 0.7$, $\mu_a = 0.3$

As we can see, the period 1 turns into period 4; then, the period doubling occurs. Now, we can conclude that the hypothesis of having period-n is related to how many age groups there

are in the model.

2.7   Conclusion

In Chapter 2, we studied the walleye population by constructing a matrix population model. The population is divided into three stages which are newborns, juveniles, and adults. We assumed that newborns and adults have the same length of the life stage. We defined the basic reproduction rate R_0. When $R_0 < 1$, we found that the extinction equilibrium is globally asymptotically stable. When $R_0 > 1$, there exists a unique positive equilibrium. When R_0 is close enough to 1, the positive equilibrium is locally asymptotically stable. The global stability of the positive equilibrium is still unknown. We numerically simulated the results with two sets of cannibalism rates corresponding to a low and a high level of cannibalism. We found bifurcation exists. With different birth rates, there exists stable equilibrium, periodic solution, and chaos. We also found that with a higher level of cannibalism, the system has a lower level of population. Cannibalism can also stabilize the system by decreasing the amplitude of oscillation and even stabilizing the positive equilibrium.

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Chapter 3

Delay Differential Equation Model of Walleye Population with Cannibalism Effect

3.1 Introduction

In the past few decades, there has been a lot of research conducted in regards to the population dynamics of size-dependent cannibalism [9]. In fact, cannibalism plays a critical role in population dynamics in ecosystems such as fish and insects. Policy makers are able to make the better decision to fish harvesting, pest control and other fields based on the study. As a result, it is very important to understand the dynamics of the cannibalism.

One of the oldest model to study this phenomenon is the Ricker model [15] published back in 1954. As a discrete population model, the Ricker model considers the characters such as victim mortality and size-dependent cannibalism, and it allows stable fixed points, cycles, and chaos. Besides the discrete models, some partial differential equation models have also been studied [8, 13, 7] by adding some cannibalism terms in the death functions and initial conditions to McKendrick-von Foerster equation. Some ordinary differential equation models have also been introduced to explain the phenomenon of the population cycle because of the cannibalism [12].

Cannibalism is related to age structure with individuals of elder ages eating younger individuals. On the other hand, delay differential equations are natural means to describe population growth of structured populations. In this chapter, we propose and analyze a delay differential equation model that characterizes the cannibalism in fish population growth. We hope this model can show some light on the effect of cannibalism on fish population, particularly on

how the cannibalism effect interplays with other model parameters including maturation delay to affect the population dynamics.

3.2 Model Formulation

Motivated by Lotka-Volterra equations [11] and Nicholson's blowflies equation [3, 4, 5], a system of delay differential equations is proposed to study the cannibalism effect of the fish population. From Lotka-Volterra equations, we learned that each equation has its own growth terms and death terms. In the proposed model, we are dividing the fish population into juveniles $J(t)$ which are not biologically mature and adults $A(t)$ which are mature enough to lay eggs. Here, for simplicity, we combine all individuals before maturation into a single class named juveniles. The recruitment of juveniles comes from births by adults, and juveniles take τ years to be adults. This consideration leads to

$$
\begin{cases}
\frac{dJ(t)}{dt} = b\left(A(t)\right) - (d_1 + c_1 A(t))J(t) - b\left(A(t-\tau)\right) e^{-\int_{t-\tau}^{t} d_1 + c_1 A(s) ds} \\
\frac{dA(t)}{dt} = b\left(A(t-\tau)\right) e^{-\int_{t-\tau}^{t} d_1 + c_1 A(s) ds} - (d_2 - c_2 J(t))A(t).
\end{cases}
\tag{3.1}
$$

For the net growth rate of juveniles $J'(t)$, there is a birth term $b(A(t))$ with respect to the adult population $A(t)$, a death term $-d_1 J(t)$, and a cannibalism term $-c_1 A(t)J(t)$ similar to the competition term in Lotka-Volterra equations. The cannibalism here can be considered as the extra death of juveniles. Lastly, there is a term $-b\left(A(t-\tau)\right) e^{-\int_{t-\tau}^{t} d_1 + c_1 A(s) ds}$ accounting for the rate of maturity of juveniles to adults.

The growth term of $A(t)$ depends on the newborns τ years ago, which is $b(A(t-\tau))$. Because of the death terms from juvenile stage, we have a survival proportion to newborns, denoted as $e^{-\int_{t-\tau}^{t} d_1 + c_1 A(s) ds}$. Besides the growth term, there is also a death term $d_2 A(t)$, and a cannibalism term $c_2 A(t)J(t)$. This positive term should not be explained as new production of the fish. Instead, it reflects the fact that the cannibalism reduces the death rate of adult fish.

For the birth function, we use $b(A) = rAe^{-qA}$ from the Ricker model [15], which has been widely adopted in fish population models. With this choice for $b(A)$, (3.1) becomes

$$
\begin{cases}
\frac{dJ(t)}{dt} = rA(t)e^{-qA(t)} - d_1 J(t) - c_1 A(t)J(t) - rA(t-\tau)e^{-qA(t-\tau)} e^{-\int_{t-\tau}^{t} d_1 + c_1 A(s) ds} \\
\frac{dA(t)}{dt} = rA(t-\tau)e^{-qA(t-\tau)} e^{-\int_{t-\tau}^{t} d_1 + c_1 A(s) ds} - d_2 A(t) + c_2 A(t)J(t).
\end{cases}
\tag{3.2}
$$

We notice that the delay τ is in the integration part of A'. To make the model simpler to analyze, let $P(t) = e^{-\int_{t-\tau}^{t} d_1 + c_1 A(s) ds}$ be a helper function which stands for the possibility rate for survival. We can derive $\frac{dP(t)}{dt} = -C_1 P(t)\left(A(t) - A(t-\tau)\right)$ by fundamental theorem of calculus.

Hence, we can simplify the system of equation (3.2) by adding a new helper variable $P(t)$.

$$
\begin{cases}
\frac{dJ(t)}{dt} = rA(t)e^{-qA(t)} - d_1 J(t) - c_1 A(t)J(t) - rA(t-\tau)e^{-qA(t-\tau)}P(t) \\
\frac{dA(t)}{dt} = rA(t-\tau)e^{-qA(t-\tau)}P(t) - d_2 A(t) + c_2 A(t)J(t) \\
\frac{dP(t)}{dt} = -c_1 P(t)\left(A(t) - A(t-\tau)\right).
\end{cases}
\tag{3.3}
$$

Systems (3.2) and (3.3) are equivalent because $P(t)$ is simply just a helper function to reduce the exponential term in the system (3.2).

Coefficients Table	
Coefficients	Value
r	natural birth rate
q	birth capacity ratio
d_1	natural death rate of juveniles
d_2	natural death rate of adults
c_1	cannibalism rate
c_2	cannibalism growth rate
τ	recruitment delay

One thing needs to be noted is that c_1 is always larger than c_2. We can consider c_1 as the rate of how much juveniles are consumed by adults as prey and c_2 as the reduction of adult population death contributed by such cannibalism consumption. Hence, the rate of reduction should be smaller than the rate of consumption.

3.3 Well-posedness

In this section, the positivity and the boundedness of solutions are investigated to ensure the model is well-posed. For delay differential equations, the initial functions for the unknowns have to be given in the delay interval $[\tau, 0]$ to ensure the solution exists.

Let $X = C\left([-\tau, 0]; \mathbb{R}^2\right)$ be the Banach space of continuous function from $[-\tau, 0]$ to $\mathbb{R}$ equipped with supreme norm. By the fundamental theory of FDEs[6], for any given $(J(0), A(0)) \in X$, there exists a unique solution $(J(t), A(t))$ to the system (3.2). Biologically speaking, we need all the initial functions to be non-negative.

$$J(\theta) \geq 0, \ A(\theta) \geq 0, \ \text{for } \theta \in [-\tau, 0].$$

Additionally, for J, there is also a compatibility issue. We can use the theorem from Smith

[16]. By integrating the equation for of J in (3.2), we can obtain

$$J(t) = \int_{t-\tau}^{t} b\left(A(\xi)\right) \exp\left(-\int_{\xi}^{t} d_1 + c_1 A(s) ds\right) d\xi. \tag{3.4}$$

At $t = 0$, the above equation gives a constraint for the initial condition on J:

$$J(0) = \int_{-\tau}^{0} b\left(A(\xi)\right) \exp\left(-\int_{\xi}^{0} d_1 + c_1 A(s) ds\right) d\xi. \tag{3.5}$$

The compatibility condition also has its biological interpretation. The total juvenile population at $t = 0$ is the newborns during the time interval $[-\tau, 0]$ who have survived this period. It is also explained in the article of Kuang [10].

3.3.1 Positivity

For biological models, only positive solutions are feasible. With the initial functions satisfying (3.4) and (3.5), we can establish the following theorem for positivity.

Theorem 3.3.1 (Positivity) *Let $A(\theta)$, $J(\theta) \geq 0$ on $-\tau \leq \theta < 0$, $A(0) > 0$, and assume that $J(0)$ satisfies (3.5). Then, the solution of (3.2) remains positive.*

Proof Since we assume $A(\theta)$, $J(\theta) \geq 0$ on $-\tau \leq \theta < 0$, $A(0) > 0$, from the equation of $A(t)$ in (3.2), we obtain

$$\frac{dA(t)}{dt} = rA(t-\tau)e^{-qA(t-\tau)}P(t) - d_2 A(t) + c_2 A(t) J(t) \geq -d_2 A(t), \qquad t \in [0, \tau]$$

We can obtain the following by comparison argument

$$A(t) \geq A(0)e^{-d_2}, \qquad t \in [0, \tau]$$

We can conclude that $A(t) > 0$ if $A(0) > 0$ for $t \in [0, \tau]$. Repeating the argument, we can obtain the positivity in the following interval $[\tau, 2\tau]$, $[2\tau, 3\tau]$,..., and hence for $t \geq 0$

The positivity of $J(t)$ can be explained as the combination of (3.4) and the positivity of $A(t)$.

3.3.2 Boundedness

It is also very critical that the population of a biological model has a upper bound, which means the population can not grow infinitely. Hence, the boundedness of the system has to be proved in order to establish the well-posedness.

Theorem 3.3.2 (Boundedness) *Let $A(\theta)$, $J(\theta) \geq 0$ on $-\tau \leq \theta < 0$, $A(0) > 0$, and assume that $J(0)$ satisfies (3.5). Then, the solution of (3.2) is bounded*

Proof Again, we can consider system (3.2) just for simplicity. For boundedness of the solution, we can define

$$G(t) = J(t) + A(t).$$

By substituting system (3.2) into $G(t)$, we can obtain the following

$$
\begin{aligned}
\frac{d}{dt}[G(t)] &= rA(t)e^{-qA(t)} - d_1 J(t) - c_1 A(t)J(t) - d_2 A(t) + c_2 A(t)J(t) \\
&= rA(t)e^{-qA(t)} - d_1 J(t) - d_2 A(t) - (c_1 - c_2)A(t)J(t) \\
&\leq \frac{r}{qe} - d_1 J(t) - d_2 A(t) \\
&\leq \frac{r}{qe} - \min\{d_1, d_2\}(J(t) + A(t)) \\
&\leq \frac{r}{qe} - \min\{d_1, d_2\}G(t).
\end{aligned}
$$

Therefore, we can obtain that

$$\limsup_{t \to \infty} (G(t)) \leq \frac{r}{qe \min\{d_1, d_2\}}.$$

This implies that $G(t)$ is bounded, and so are $J(t)$ and $A(t)$. This completes the proof of this theorem. ■

3.4 Equilibria

The existence of equilibria is discussed in this section. In delay differential equations, similar to ordinary differential equations, an equilibrium is a time-independent solution. For system (3.3), we can obtain the equilibrium by solving the following the system of equation:

$$rAe^{-qA} - d_1 J - c_1 AJ - rAe^{-qA}P = 0, \tag{3.6}$$

$$rAe^{-qA}P - d_2 A + c_2 AJ = 0, \tag{3.7}$$

$$-c_1 P(A - A) = 0. \tag{3.8}$$

It is clear that an extinction equilibrium E_0 exits, and $E_0 = (0, 0, P^*)$ where P^* is a constant in (0,1). (3.8) is naturally true since the equation is always 0 for any given constant $A = A^*$. By

the definition of $P(t)$, we obtain

$$P^* = e^{-(d_1+c_1A^*)\tau}. \tag{3.9}$$

Hence, the extinction equilibrium

$$E_0 = (0, 0, e^{-d_1\tau}). \tag{3.10}$$

To obtain a positive equilibrium E^*, we need to solve the system of equations (3.6-3.8) for non-zero solutions. Adding (3.6) and (3.7), we obtain the following

$$(d_1 + c_1A^* - c_2A^*)J^* = rA^*e^{-qA^*} - d_2A^*. \tag{3.11}$$

From (3.7), we obtain another equation of J^*,

$$c_2A^*J^* = d_2A^* - rA^*e^{-qA^*}P^*. \tag{3.12}$$

Combining (3.11) and (3.12), we can get an equation involving A^* only:

$$\begin{aligned}
\frac{rA^*e^{-qA^*} - d_2A^*}{d_1 + c_1A^* - c_2A^*} &= \frac{d_2A^* - rA^*e^{-qA^*}P^*}{c_2A^*}, \\
\implies \frac{c_2A^*}{d_1 + c_1A^* - c_2A^*} &= -\frac{d_2A^* - rA^*e^{-qA^*}P^*}{d_2A^* - rA^*e^{-qA^*}}, \\
\implies \frac{c_2A^*}{d_1 + (c_1 - c_2)A^*} &= -\frac{d_2 - re^{-qA^*}P^*}{d_2 - re^{-qA^*}} \\
&= -\frac{d_2 - re^{-d_1\tau}e^{-(q+c_1\tau)A^*}}{d_2 - re^{-qA^*}},
\end{aligned} \tag{3.13}$$

Let

$$g(A) = \frac{c_2A}{d_1 + (c_1 - c_2)A},$$

$$f(A) = -\frac{d_2 - re^{-d_1\tau}e^{-(q+c_1\tau)A}}{d_2 - re^{-qA}}.$$

We can begin the analysis by sketching the graphs of $g(A)$ and $f(A)$

Figure 3.1: Sketch of $g(A)$ and $f(A)$
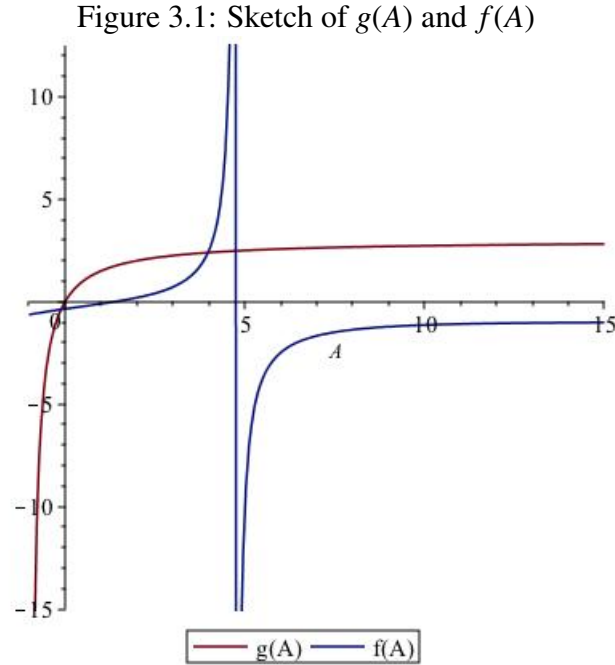
We are only interested in the first quadrant. For $g(A)$, it is simply a monotonically increasing function with respect to $A > 0$ since

$$g'(A) = \frac{c_2 d_1}{(d_1 + (c_1 - c_2)A)^2} \geq 0. \tag{3.14}$$

We can see that $g(0) = 0$ and $\lim_{A \to \infty} g(A) = \frac{c_2}{c_1 - c_2} > 0$. We also notice that for $f(A)$ has a vertical asymptote caused by the denominator $d_2 - re^{-qA}$, where $A_v = \frac{\ln(r/d_2)}{q}$ for the vertical asymptote. On the right hand side of the asymptote, $d_2 > re^{-qA}$, then $d_2 > re^{-d_1\tau}e^{-(q+c_1\tau)A^*}$ as well. Hence, $g(A) < 0$ on the right hand side of $A_v = \frac{\ln(r/d_2)}{q}$.

Now, we only have to consider the left hand side of this asymptote. First, we want to check if $g(A)$ is monotonically increasing on the left of the asymptote. We need to calculate the derivate of $f(A)$.

$$f'(A) = \frac{r\left(qd_2 e^{-qA} + rc_1\tau e^{-(c_1A+d_1)\tau - 2qA} - d_2(c_1\tau + q)e^{-(c_1A+d_1)\tau - qA}\right)}{(d_2 - re^{-qA})^2} \tag{3.15}$$

From (3.15), we know that both r and $(d_2 - re^{-qA})^2$ are non-negative. We only need to investigate the positivity of the following term

$$\omega(A) = qd_2 e^{-qA} + r\tau c_1 e^{-(c_1A+d_1)\tau - 2qA} - d_2(c_1\tau + q)e^{-(c_1A+d_1)\tau - qA}.$$

On the left of the asymptote (i.e. $d_2 < re^{-qA}$), we derive $e^{-qA} > \frac{d_2}{r}$. And hence,

$$
\begin{aligned}
\omega(A) &\geq qd_2\frac{d_2}{r} + r\tau c_1 e^{-(c_1A+d_1)\tau-qA}\frac{d_2}{r} - d_2\left(c_1\tau + q\right)e^{-(c_1A+d_1)\tau-qA} \\
&= qd_2 e^{-qA} + d_2\tau c_1 e^{-(c_1A+d_1)\tau-qA} - d_2\left(c_1\tau + q\right)e^{-(c_1A+d_1)\tau-qA} \\
&= qd_2 e^{-qA} - d_2 q e^{-(c_1A+d_1)\tau-qA} \\
&= qd_2 e^{-qA}\left(1 - e^{-(c_1A+d_1)\tau}\right) > 0.
\end{aligned}
$$

Now, we can conclude that $f(A)$ is monotonically increasing on the left hand side of the asymptote. However, there is still a scenario that there is no positive equilibrium illustrated in the following diagram.

Figure 3.2: Non-Existence of a Positive Equilibrium
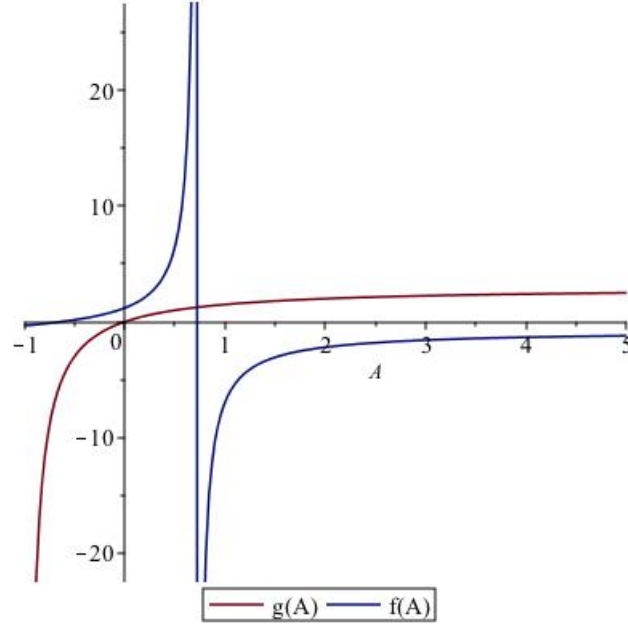
Hence, in order to guarantee a positive equilibrium, we need to have the following two conditions satisfied.

Firstly, the vertical asymptote of $f(A)$ has to be on the right half plane (i.e. $A_v = \frac{\ln(r/d_2)}{q} > 0$), which is equivalent to $r > d_2$.

Additionally, we need the intersection of $f(A)$ and y-axis to be negative (i.e. $f(0) < 0$). Hence, we obtain $f(0) = -\frac{d_2-re^{-d_1\tau}}{d_2-r} < 0$. With the first condition which is necessary, we conclude that the second condition is $re^{-d_1\tau} > d_2$. Note that $re^{-d_1\tau} > d_2$ implies $r > d$, we have proved the following theorem about the existence of a positive equilibrium

Theorem 3.4.1 (Existence of the Positive Equilibrium) *System (3.3) has a unique positive*

equilibrium E^* if $re^{-d_1\tau} > d_2$.

We point out that by the biological meaning of the reproduction number (or ratio), denoted by R_0, we can easily derive that $R_0 = \frac{re^{-d_1\tau}}{d_2}$. Clearly, the condition in the above theorem is equivalent to $R_0 > 1$.

3.5 Stability Analysis

In this section, we discuss some simple criteria to determine the stability of an equilibrium of a differential equation with a single delay. Now, consider the following delay differential equation:

$$x'(t) = f(x(t), x(t - \tau)). \tag{3.16}$$

Assume that there is an equilibrium point x_e of (3.16), i.e. $f(x_e, x_e) = 0$. To check the stability of x_e, let $y = x - x_e$. By this definition, we can derive

$$\begin{aligned} y'(t) = x'(t) &= f(x(t), x(t - \tau)) \\ &= f(x_e + y(t), x_e + y(t - \tau)). \end{aligned} \tag{3.17}$$

Obviously $y = 0$ is the trivial equilibrium of (3.17); moreover, the stability of the equilibrium x_e for (3.16) is equivalent to the stability of the $y = 0$ for (3.17). Rewriting (3.17) using Taylor's expansion, we can obtain the following series

$$y'(t) = f'_{x(t)}(x_e, x_e)y(t) + f'_{x(t-\tau)}(x_e, x_e)y(t - \tau) + O(y^2(t)) + O(y^2(t - \tau)), \tag{3.18}$$

where O is higher terms.

Using the technique of linearization, we can drop the higher terms. To obtain the the following linearized equation of (3.17) at $y = 0$, which is also the linearization of (3.16) at $x = x_e$:

$$y'(t) = f'_{x(t)}(x_e, x_e)y(t) + f'_{x(t-\tau)}(x_e, x_e)y(t - \tau). \tag{3.19}$$

Let $a = f'_{x(t)}(x_e, x_e)$ and $b = f'_{x(t-\tau)}(x_e, x_e)$, and assume $y(t)$ has the solution with the form of $y(t) = \alpha e^{\lambda t}$, where $\alpha \neq 0, \lambda \in C$. Hence, (3.19) becomes

$$\begin{aligned} y'(t) &= f'_{x(t)}(x_e, x_e)y(t) + f'_{x(t-\tau)}(x_e, x_e)y(t - \tau) \\ &\Longrightarrow y'(t) = ay(t) + by(t - \tau) \\ &\Longrightarrow \alpha\lambda e^{\lambda t} = a\alpha e^{\lambda t} + b\alpha e^{\lambda(t-\tau)} \\ &\Longrightarrow 0 = \alpha(\lambda - a - be^{-\lambda\tau}), \end{aligned} \tag{3.20}$$

which leads to $\alpha(\lambda - a - be^{-\lambda\tau}) = 0$, the characteristic equation.

Similarly, for a linear system of delay differential equations

$$X'(t) = AX(t) + BX(t - \tau),$$

where A and B are $n \times n$ matrices, the characteristic equation is

$$det\left(\lambda I - A - Be^{-\lambda\tau}\right) = 0. \tag{3.21}$$

The trivial equilibrium $X = 0$ if all roots of (3.21) have negative real parts (see, e.g. [6]).

3.5.1   Stability of Extinction Equilibrium E_0

To check the local stability of the extinction equilibrium, we can use the method of linearization. The linearized system at the point (J^*, A^*, P^*) of system (3.3) is given by

$$\begin{cases} J'(t) = b'(A^*)A(t) - d_1 J(t) - c_1 J^* A(t) - c_1 A^* J(t) - b'(A^*)P^* A(t - \tau) - b(A^*)P(t) \\ A'(t) = b'(A^*)P^* A(t - \tau) + b(A^*)P(t) - d_2 A(t) + c_2 J^* A(t) + c_2 A^* J(t) \\ P'(t) = -c_1 P^*(A(t) - A(t - \tau)), \end{cases} \tag{3.22}$$

or

$$\begin{pmatrix} J'(t) \\ A'(t) \\ P'(t) \end{pmatrix} = \begin{pmatrix} -d_1 - c_1 A^* & b'(A^*) - c_1 J^* & -b(A^*) \\ c_2 A^* & -d_2 + c_2 J^* & b(A^*) \\ 0 & -c_1 P^* & 0 \end{pmatrix} \begin{pmatrix} J(t) \\ A(t) \\ P(t) \end{pmatrix}$$
$$+ \begin{pmatrix} 0 & -b'(A^*)P^* & 0 \\ 0 & b'(A^*)P^* & 0 \\ 0 & c_1 P^* & 0 \end{pmatrix} \begin{pmatrix} J(t - \tau) \\ A(t - \tau) \\ P(t - \tau) \end{pmatrix}. \tag{3.23}$$

In order to check the stability of the extinction equilibrium, we can substitute $(J^*, A^*, P^*) = (0, 0, e^{-d_1\tau})$ into (3.23) to obtain

$$\begin{pmatrix} J'(t) \\ A'(t) \\ P'(t) \end{pmatrix} = \begin{pmatrix} -d_1 & r & 0 \\ 0 & -d_2 & 0 \\ 0 & -c_1 e^{-d_1\tau} & 0 \end{pmatrix} \begin{pmatrix} J(t) \\ A(t) \\ P(t) \end{pmatrix} + \begin{pmatrix} 0 & -re^{-d_1\tau} & 0 \\ 0 & re^{-d_1\tau} & 0 \\ 0 & c_1 e^{-d_1\tau} & 0 \end{pmatrix} \begin{pmatrix} J(t - \tau) \\ A(t - \tau) \\ P(t - \tau) \end{pmatrix}$$

Note that both $J'(t)$ and $A'(t)$ equations are decoupled from $P(t)$ and $P(t - \tau)$, the linearization at E_0 can be reduced to the following system of two equations only:

$$\begin{pmatrix} J'(t) \\ A'(t) \end{pmatrix} = \begin{pmatrix} -d_1 & r \\ 0 & -d_2 \end{pmatrix} \begin{pmatrix} J(t) \\ A(t) \end{pmatrix} + \begin{pmatrix} 0 & -re^{-d_1\tau} \\ 0 & re^{-d_1\tau} \end{pmatrix} \begin{pmatrix} J(t - \tau) \\ A(t - \tau) \end{pmatrix}. \tag{3.24}$$

Based on (3.21), the characteristic equation for system (3.24) is the following

$$\begin{aligned} 0 &= \det\left(\begin{pmatrix} \lambda & 0 \\ 0 & \lambda \end{pmatrix} - \begin{pmatrix} -d_1 & r \\ 0 & -d_2 \end{pmatrix} - \begin{pmatrix} 0 & -re^{-(d_1+\lambda)\tau} \\ 0 & re^{-(d_1+\lambda)\tau} \end{pmatrix} \right) \\ &= \begin{vmatrix} \lambda + d_1 & -r + re^{-(d_1+\lambda)\tau} \\ 0 & \lambda + d_2 - re^{-(d_1+\lambda)\tau} \end{vmatrix} \\ &= (\lambda + d_1)\left(\lambda + d_2 - re^{-(\lambda+d_1)\tau}\right). \end{aligned} \tag{3.25}$$

We know that E_0 is locally asymptotically stable if both all roots of (3.25) have negative real parts. Note that the factor $(\lambda + d_1)$ gives a root $\lambda = -d_1$, which is always negative. Then, the stability of E_0 is determined by the distribution of the roots of the equation

$$\lambda + d_2 - re^{-(\lambda+d_1)\tau} = 0. \tag{3.26}$$

There have been a lot of articles discussing how to analyze the root distribution of the equation (3.26) (see, e.g. [3, 6, 17]). Similar to the approach in Zhu and Zou [17], when $\tau = 0$, the equation (3.26) becomes

$$\lambda + d_2 - r = 0. \tag{3.27}$$

In this case, $R_0 = \frac{re^{-d_1\tau}}{d_2} < 1$ reduces to $\frac{r}{d_2} < 1$. Clearly, if $\frac{r}{d_2} < 1$, $d_2 - r > 0$, and (3.27) has a negative root which makes the system stable. Because the root of (3.26) depends on τ continuously, as delay τ increases, the root of (3.26) can only enter the right-half of complex plane by crossing the imaginary axis. Let $\lambda = iw$ with $w > 0$ be a purely imaginary root of (3.26), then,

$$iw + d_2 = re^{-d_1\tau}e^{-iw\tau}. \tag{3.28}$$

Taking moduli in both sides of the above equation gives

$$w^2 + d_2^2 = \left(re^{-d_1\tau}\right)^2. \tag{3.29}$$

If $R_0 = \frac{re^{-d_1\tau}}{d_2} < 1$, (3.29) has no non-negative real root. Therefore, there is no root of the form $\lambda = iw$ with $w > 0$ for (3.26), implying that the root of (3.26) can never cross the imaginary axis. Hence all roots of (3.26) have negative real parts when $R_0 < 1$. On the other hand, (3.26)

has a real positive root if $R_0 > 1$. Now, we can conclude that for system (3.3), extinction equilibrium E_0 is locally asymptotically stable if $re^{-\tau d_1} < d_2$, or equivalently $R_0 < 1$. On the other hand, when $re^{-\tau d_1} > d_2$, it is obvious that (3.27) has a real positive root. Hence, when $R_0 > 1$, E_0 becomes unstable.

Theorem 3.5.1 (Stability of E_0) *For system (3.3), the extinction equilibrium E_0 is locally asymptotically stable if $re^{-\tau d_1} < d_2$ (i.e. $R_0 < 1$), and it becomes unstable when $R_0 > 1$.*

We remark that if $re^{-\tau d_1} < d_2$ is replaced by a stronger condition $r < d_2$, we can actually obtain the global asymptotical stability of E_0.

Theorem 3.5.2 (Global Stability of E_0) *For system (3.3), the extinction equilibrium E_0 is globally asymptotically stable if $r < d_2$.*

Proof let $V = J + A$. Noted that $V(x) > 0$ if and only if $x \neq 0$, and $V(x) = 0$ if and only if $x = 0$. Then,

$$
\begin{aligned}
V' &= rA(t)e^{-qA(t)} - d_1 J(t) - d_2 A(t) - (c_1 - c_2)A(t)J(t) \\
&\leq rA(t)e^{-qA(t)} - d_2 A(t) \\
&\leq rA(t) - d_2 A(t) \\
&= (r - d_2)A(t).
\end{aligned}
$$

If $r < d_2$, $V' < 0$ because of the positivity of A(t) from Theorem (3.3.1)-(3.3.2). By LaSalle's invariance principle and the above inequality, we can conclude that the extinction equilibrium E_0 is globally asymptotically stable. ■

Interestingly, when there is no cannibalism present (i.e. $c_1 = c_2 = 0$), the extinction equilibrium is globally asymptotically stable when $R_0 < 1$, as stated in the following theorem.

Theorem 3.5.3 (Global Stability of E_0 without Cannibalism) *Assume that $c_1 = c_2 = 0$, if $R_0 < 1$, then the extinction equilibrium E_0 is globally asymptotically stable for system (3.3).*

Proof The system without cannibalism is show as the following.

$$
\begin{cases}
\frac{d\bar{J}(t)}{dt} = r\bar{A}(t)e^{-q\bar{A}(t)} - d_1\bar{J}(t) - r\bar{A}(t-\tau)e^{-q\bar{A}(t-\tau)}e^{-d_1\tau} \\
\frac{d\bar{A}(t)}{dt} = r\bar{A}(t-\tau)e^{-q\bar{A}(t-\tau)}e^{-d_1\tau} - d_2\bar{A}(t)
\end{cases}
\tag{3.30}
$$

For system (3.30), we can also conclude the positivity and boundedness of $\bar{J}(t)$ and $\bar{A}(t)$ similar to (3.2).

Since we know that both $\bar{J}(t)$ and $\bar{A}(t)$ are positively bounded. We can let $\bar{V} = \bar{A}(t) + \int_{t-\tau}^{t} r\bar{A}(t)e^{-q\bar{A}(t)}e^{-d_1\tau}dt$. Noted that $\bar{V}(x) > 0$ if and only if $x \neq 0$, and $\bar{V}(x) = 0$ if and only if $x = 0$. Then,

$$
\begin{aligned}
\bar{V}' &= r\bar{A}(t-\tau)e^{-q\bar{A}(t-\tau)}e^{-d_1\tau} - d_2\bar{A}(t) + r\bar{A}(t)e^{-q\bar{A}(t)}e^{-d_1\tau} - r\bar{A}(t-\tau)e^{-q\bar{A}(t-\tau)}e^{-d_1\tau} \\
&= r\bar{A}(t)e^{-q\bar{A}(t)}e^{-d_1\tau} - d_2\bar{A}(t) \\
&\leq r\bar{A}(t)e^{-d_1\tau} - d_2\bar{A}(t) \\
&= (re^{-d_1\tau} - d_2)\bar{A}(t).
\end{aligned}
$$

Now, we can conclude that $\lim_{t\to\infty} \bar{A}(t) = 0$ if $re^{-d_1\tau} < d_2$. By the definition of $\bar{J}(t)$ of (3.30), we can conclude that $\lim_{t\to\infty} \bar{J}(t) = 0$. Hence, we can conclude that without cannibalism, extinction equilibrium E_0 is globally asymptotically stable when $R_0 < 1$ ∎

It also reflects the definition of the basic reproduction number R_0. If R_0 is less than 1, the extinction equilibrium is locally asymptotically stable. Further more, when $r < d_2$, the extinction equilibrium is globally asymptotically stable. If R_0 is greater than 1, the extinction equilibrium is unstable, and there occurs a positive equilibrium E^*. Because the solution to system (3.3) is bounded and positive, if $R_0 > 1$, the solution will possibly be attracted to the positive equilibrium E^*.

3.5.2   Stability of Positive Equilibrium E^*

When $R_0 > 1$, the extinction equilibrium E_0 becomes unstable, and by Theorem 3.4.1., we know that there exists a unique positive equilibrium E^*. Because we cannot explicitly solve the system of equation (3.11)-(3.12), we denote the positive equilibrium by

$$
E^* = (\frac{rA^*e^{-qA^*} - d_2A^*}{(d_1 + c_1A^* - c_2A^*)}, A^*, e^{-(d_1+c_1A^*)\tau}). \tag{3.31}
$$

We substitute the positive equilibrium E^* into the linearized system (3.22). By (3.21), we obtain the characteristic equation using Maple

$$
\begin{aligned}
&(Ac_1 + d_1)\lambda^3 + \Big((qA - 1)(Ac_1 + d_1)re^{(-Ac_1 - \lambda - d_1)\tau - qA} - Ac_1re^{-qA} + (Ac_1 + d_1)^2 + (Ac_1 + d_1)d_2\Big)\lambda^2 \\
&+ \Big[(-Ac_1 + (qA - 1)((c_1 - c_2)A + d_1))(Ac_1 + d_1)re^{(-Ac_1 - \lambda - d_1)\tau - qA} + A(Ac_1 + d_1)rc_1e^{(-Ac_1 - d_1)\tau - qA} + \\
&\quad A\Big(A^2qc_1c_2 + \big(qc_2d_1 - c_1{}^2\big)A - d_1(c_1 + c_2)\Big)re^{-qA} + (Ac_1 + d_1)^2 d_2\Big]\lambda \\
&- Ac_1((c_1 - c_2)A + d_1)(Ac_1 + d_1)re^{(-Ac_1 - \lambda - d_1)\tau - qA} + Ac_1((c_1 - c_2)A + d_1)(Ac_1 + d_1)re^{(-Ac_1 - d_1)\tau - qA} \\
&= 0,
\end{aligned}
$$

$$(3.32)$$

where A is equivalent at A^*. The stability of E^* is determined by the distribution of roots of (3.32). Unfortunately, it is very difficult to solve this characteristic equation because it is a transcendental equation of degree three. Even the discussion of the distribution of its roots becomes extremely difficult with six variables. Then, we try to explore if linearization at E^* for the original system (3.2) would be easier since the characteristic equation is only of degree two.

Let

$$
\begin{cases}
J(t) = J^* + u(t) \\
A(t) = A^* + v(t)
\end{cases}
$$

The linearized system at point (J^*, A^*) of system (3.2) is given by

$$
\begin{cases}
u'(t) = b'(A^*)v(t) - d_1u(t) - c_1J^*v(t) - c_1A^*u(t) \\
\quad -b'(A^*)e^{-(d_1 + c_1A^*)\tau}v(t - \tau) + c_1b(A^*)e^{-(d_1 + c_1A^*)\tau}\int_{t-\tau}^{t} v(s)ds \\
v'(t) = b'(A^*)e^{-(d_1 + c_1A^*)\tau}v(t - \tau) - c_1b(A^*)e^{-(d_1 + c_1A^*)\tau}\int_{t-\tau}^{t} v(s)ds \\
\quad -d_2v(t) + c_2J^*v(t) + c_2A^*u(t).
\end{cases}
$$

$$(3.33)$$

In the linearized system, there is a integration $\int_{t-\tau}^{t} v(s)ds$. Assuming the solution of $v(t)$ is $v_0e^{\lambda t}$, $\int_{t-\tau}^{t} v(s)ds = \frac{1}{\lambda}(v(t) - v(t - \tau))$. Then, (3.33) can be rewritten as

$$
\begin{cases}
u'(t) = b'(A^*)v(t) - d_1u(t) - c_1J^*v(t) - c_1A^*u(t) \\
\quad -b'(A^*)e^{-(d_1 + c_1A^*)\tau}v(t - \tau) + c_1b(A^*)e^{-(d_1 + c_1A^*)\tau}\frac{1}{\lambda}\Big(v(t) - v(t - \tau)\Big) \\
v'(t) = b'(A^*)e^{-(d_1 + c_1A^*)\tau}v(t - \tau) - c_1b(A^*)e^{-(d_1 + c_1A^*)\tau}\frac{1}{\lambda}\Big(v(t) - v(t - \tau)\Big) \\
\quad -d_2v(t) + c_2J^*v(t) + c_2A^*u(t),
\end{cases}
$$

$$(3.34)$$

or

$$\begin{pmatrix} u'(t) \\ v'(t) \end{pmatrix} = \begin{pmatrix} -d_1 - c_1A^* & b'(A^*) - c_1J^* + \frac{1}{\lambda}c_1b(A^*)e^{-(d_1+c_1A^*)\tau} \\ c_2A^* & -d_2 + c_2J^* - \frac{1}{\lambda}c_1b(A^*)e^{-(d_1+c_1A^*)\tau} \end{pmatrix} \begin{pmatrix} u(t) \\ v(t) \end{pmatrix}$$
$$+ \begin{pmatrix} 0 & -b'(A^*)e^{-(d_1+c_1A^*)\tau} - \frac{1}{\lambda}c_1b(A^*)e^{-(d_1+c_1A^*)\tau} \\ 0 & b'(A^*)e^{-(d_1+c_1A^*)\tau} + \frac{1}{\lambda}c_1b(A^*)e^{-(d_1+c_1A^*)\tau} \end{pmatrix} \begin{pmatrix} u(t-\tau) \\ v(t-\tau) \end{pmatrix}.$$

(3.35)

By (3.21), we obtain the characteristic equation

$$\frac{1}{\lambda}\Bigg[(Ac_1 + d_1)\lambda^3 + \Big((qA-1)(Ac_1+d_1)re^{(-Ac_1-\lambda-d_1)\tau-qA} - Ac_1re^{-qA} + (Ac_1+d_1)^2 + (Ac_1+d_1)d_2\Big)\lambda^2$$
$$+ \Big[(-Ac_1 + (qA-1)((c_1-c_2)A+d_1))(Ac_1+d_1)re^{(-Ac_1-\lambda-d_1)\tau-qA} + A(Ac_1+d_1)rc_1e^{(-Ac_1-d_1)\tau-qA}+$$
$$A\Big(A^2qc_1c_2 + \big(qc_2d_1 - c_1{}^2\big)A - d_1(c_1+c_2)\Big)re^{-qA} + (Ac_1+d_1)^2 d_2\Big]\lambda$$
$$- Ac_1((c_1-c_2)A+d_1)(Ac_1+d_1)re^{(-Ac_1-\lambda-d_1)\tau-qA} + Ac_1((c_1-c_2)A+d_1)(Ac_1+d_1)re^{(-Ac_1-d_1)\tau-qA}\Bigg]$$
$$= 0,$$

(3.36)

where A is equivalent at A^*. We notice that the only difference between (3.36) and (3.32) is that there is a $\frac{1}{\lambda}$ term. For (3.32), there is a trivial eigenvalue $\lambda = 0$, and for (3.36), $\lambda = 0$ is not an eigenvalue. It reflects that the eigenvalue $\lambda = 0$ is corresponding to $P(t)$. Solving (3.36) is still very difficult.

Although the analytical discussion of the stability of positive equilibrium is challenging, we can still explore the stability using numerical simulations, which will be introduced in the next section.

3.6   Numerical Simulation

In this section, we are going to simulate the solution of system (3.3) using DDE23 of MAT-LAB. In particular, we are changing the natural birth rate r and the cannibalism rate c_1. For cannibalism growth rate, we set c_2 to be proportional to c_1. As mentioned in the first section, c_2 is always less than c_1. For simplicity, we set $c_2 = 0.8c_1$ First, we give some values to the

coefficients and the initial solution

Coefficients Table	
Coefficients	Value
q	0.01
d_1	0.4
d_2	0.3
c_2	$0.8c_1$
τ	2

And the initial solution is given as

$$A(\gamma) = A_i = 5, \ P(\gamma) = e^{(-5c_1 - d_1)2}, \ \text{for } \gamma \in [-2, 0]$$

By definition of $P(t) = e^{-\int_{t-\tau}^{t} d_1 + c_1 A(s) ds}$. Since we set $A(\gamma) = A_i = 5$, $P(\gamma) = e^{(-5c_1 - d_1)2}$. Also, in each case, we need to calculate corresponding $J(\gamma)$ to fit the compatibility criterion (3.5). We are going to change the natural birth rate r in each case with and without cannibalism, and to see the effect of cannibalism on population dynamics.

3.6.1 Case 1: $r < d_2$

Here, we get the initial solution using (3.5)

$$J(\gamma) = 1.102767026, \ A(\gamma) = 5, \ P(\gamma) = .1652988882, \ \text{for } \gamma \in [-\tau, 0]$$
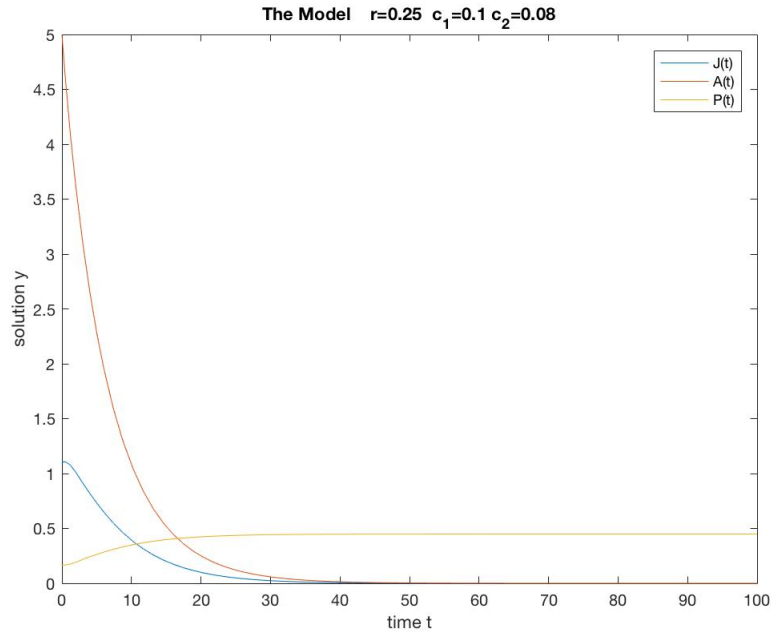
Figure 3.3: $r = 0.25$, $c_1 = 0.1$, $c_1 = 0.08$

In the first case, we set the natural birth rate $r = 0.25 < d_2$. By Theorem 3.5.1, the extinction equilibrium E_0 is globally asymptotically stable, which matches the numerical simulation. Biologically speaking, when the maximum natural birth rate is at a low level compared to the death rate, the fish population will decline, and soon go extinct. The solution of system (3.3) tends to the extinction equilibrium.

3.6.2   Case 2: $d_2 < r < d_2 e^{d_1 \tau}$ with Cannibalism

In case 2, we are trying to investigate whether extinction equilibrium is stable globally stable if $d_2 < r < d_2 e^{d_1 \tau}$ with cannibalism. We set the birth rate $r = 0.65$ and $c_1 = 0.15$, and the initial functions can be obtained as:

$$J(\gamma) = 2.418735524, \ A(\gamma) = 5, \ P(\gamma) = .1002588437, \ \text{for } \gamma \in [-\tau, 0]$$
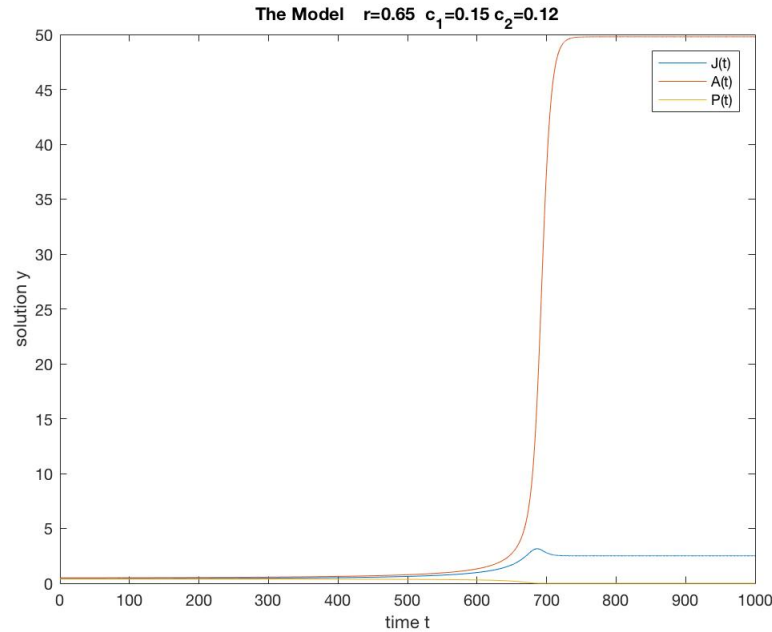
Figure 3.4: $r = 0.65$, $c_1 = 0.15$, $c_1 = 0.12$

From Figure 3.4, we conclude that the extinction equilibrium does not have global stability when $d_2 < r < d_2 e^{d_1 \tau}$ with cannibalism, which can be explained by Theorem 3.5.2 and Theorem 3.5.3. The solutions tend to the positive equilibrium when there is a cannibalism. Now, we are wondering whether the solutions will have the same trend when there is no cannibalism present.

3.6.3   Case 3: $d_2 < r < d_2 e^{d_1 \tau}$ without Cannibalism

In case 3, we only modify the cannibalism coefficients c_1 and c_2 from case 2. Here, $c_1 = c_2 = 0$.

$$J(\gamma) = 4.255992752, \ A(\gamma) = 5, \ P(\gamma) = .4493289641, \ \text{for } \gamma \in [-\tau, 0]$$
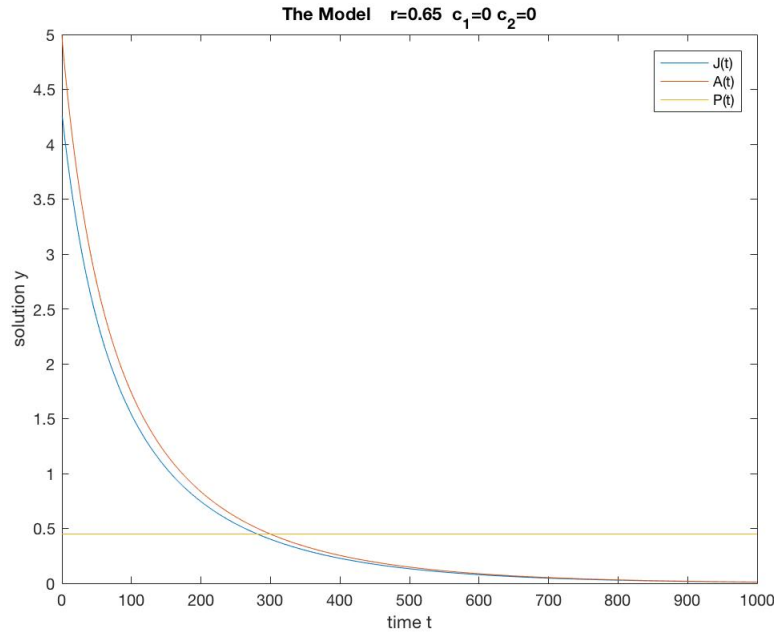
Figure 3.5: $r = 0.65$, $c_1 = 0$, $c_1 = 0$

Here, without cannibalism, we note that the populations go extinct. From Theorem 3.5.3, the extinction equilibrium is globally asymptotically stable if $r < d_2 e^{d_1 \tau}$ with no cannibalism. Compared to case 2, we see that cannibalism destabilize the extinction equilibrium. With cannibalism, we need a stronger condition (i.e. $r < d_2$) to obtain the global stability of the extinction equilibrium.

Biologically speaking, when the birth rate is in a low stage (i.e. $r < d_2 e^{d_1 \tau}$), the population will decline because of the net reproduction number R_0 is less than 1. The fish population will not survive with out some decrease in the adult population. When there is cannibalism, adult death rate decreases. Hence, the population still might survive.

3.6.4 Case 4: $r > d_2 e^{d_1 \tau}$, Stable Positive Equilibrium

In case 4, we show that when the natural birth rate r is not too large, the positive equilibrium E^* is stable.

$$J(\gamma) = 31.36046672, \ A(\gamma) = 5, \ P(\gamma) = .4065696597, \text{ for } \gamma \in [-\tau, 0]$$
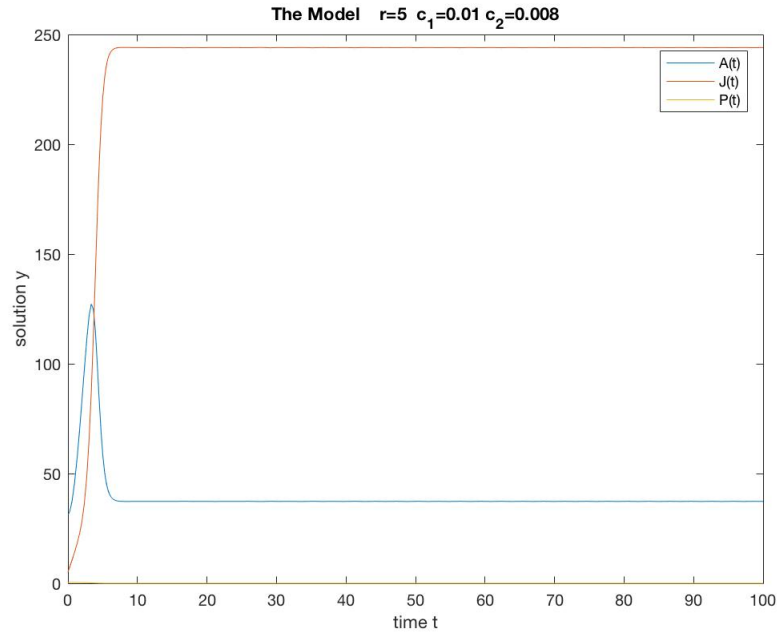
Figure 3.6: $r = 5$, $c_1 = 0.01$, $c_1 = 0.008$

From Figure 3.6, we see that the adult population is increasing until it hits to its equilibrium. For juveniles, the population increases first. However, with the increasing adult population, the juvenile population then decline because of the cannibalism. Then, both juvenile and adult population will tend to their equilibria.

3.6.5 Case 5: $r > d_2 e^{d_1 \tau}$, Periodic Solutions

In case 5, we investigate if periodic solutions exist when the natural birth rate r is relatively large. In this case, we set the natural birth rate $r = 200$ with a small cannibalism.

$$J(\gamma) = 1308.968025, \ A(\gamma) = 5, \ P(\gamma) = .4488798597, \ \text{for } \gamma \in [-\tau, 0]$$
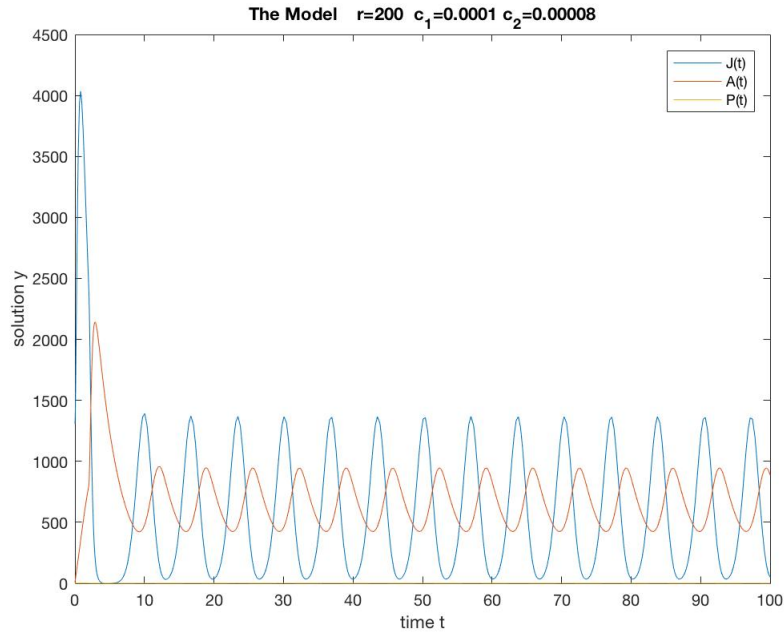
Figure 3.7: $r = 200$, $c_1 = 0.0001$, $c_1 = 0.00008$

In Figure 3.7, we notice that there exist periodic solutions when r is relatively large. The population of juveniles cycles around 0-1400. Then, we increase the cannibalism coefficients.
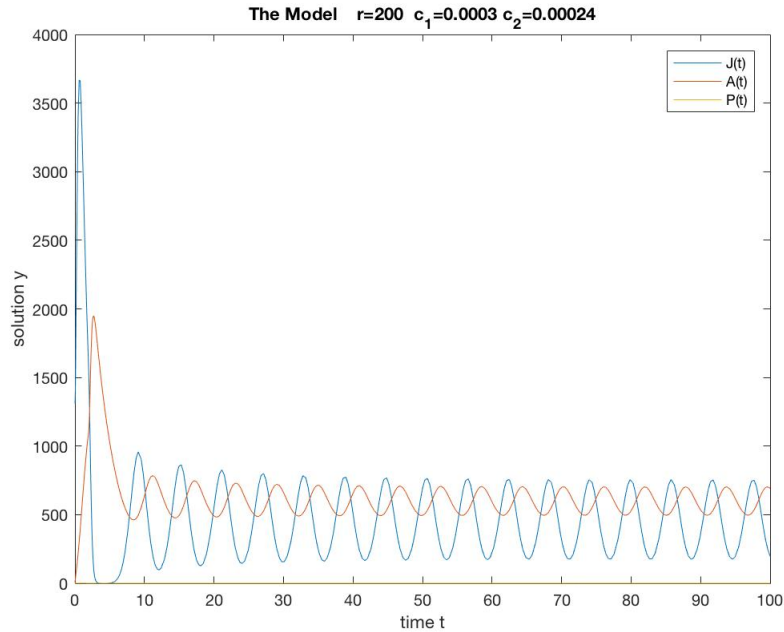

Figure 3.8: $r = 200$, $c_1 = 0.0003$, $c_1 = 0.00024$

In Figure 3.8, with a slightly stronger cannibalism effect, the solutions cycle within a smaller range. For juveniles, the population cycles within 100-800. Here, we conclude that the cannibalism has a stabilizing effect in population dynamics by lowering the equilibrium or oscillation. Next, we increase the cannibalism effect.
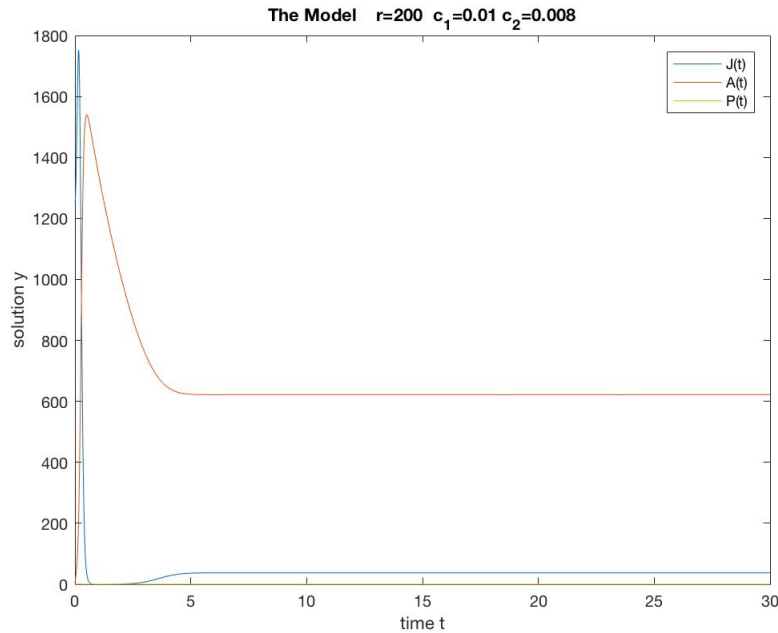

Figure 3.9: $r = 200$, $c_1 = 0.01$, $c_1 = 0.008$

Here in Figure 3.9, there is a stronger cannibalism effect than in Figure 3.8. Not surprisingly, we obtain a stable positive equilibrium. Based on Figures 3.7-3.9, we conclude that, with an increasing cannibalism effect, the periodic solutions will have a smaller oscillations, and eventually the positive equilibrium will become stable.

To sum up, we noticed a stabilizing effect of cannibalism. When the birth rate is in the range of $[d_2, d_2 e^{d_1 \tau}]$, cannibalism can make a life boat effect that makes the extinction equilibrium unstable. When $r > d_2 e^{d_1 \tau}$, cannibalism has a stabilizing effect including making the oscillations smaller and positive equilibrium stable.

Biologically speaking, the most interesting phenomenon is the life boat effect of cannibalism. When the birth rate r is slightly bigger than d_2 while smaller than $d_2 e^{d_1 \tau}$, adults fish can survive by consuming a small amount of juveniles. Without cannibalism, the whole population will decline, and eventually go extinct. However, with the presence of cannibalism, fish can still survive when the birth rate r is slightly higher than adult death rate d_2.

3.7 Conclusion

Cannibalism is a very common phenomenon in ecology. How cannibalism plays the role in population dynamics is still debating. In this section, we proposed a delay-differential equation model to study the effect of cannibalism in population dynamics. In the model, the population is divided into two stages, juveniles, and adults. Juveniles are not biologically mature and can be consumed by adults. Adults are biologically mature and can consume juveniles. Cannibalism increases the juvenile death rate and decreases the adult death rate. In terms of delay, it takes juveniles τ years to move into the adult stage. By the analysis of eigenvalues and constructing Lyapunov function, we have proved that the extinction equilibrium E_0 is globally asymptotically stable if the net reproduction rate $r < d_2$, and locally asymptotically stable if $R_0 < 1$. The stability of the positive equilibrium E^* is very difficult to prove analytically.

By numerical simulation, we ran 5 cases of simulations with different natural birth rate r with and without the presence of cannibalism. Firstly, we found that cannibalism has a destabilizing effect on extinction equilibrium when $d_2 < r < d_2 e^{d_1 \tau}$. When $r > d_2 e^{d_1 \tau}$, we found that the cannibalism is a stabilizing factor in population dynamics of walleye. Depending on how strong the cannibalism effect is, cannibalism stabilizes the population by either making the positive equilibrium stable or reducing the amplitude of the periodic solutions. In fact, this stabilizing effect has been studied in some previous works [2, 14, 1]. The analytical analysis of positive equilibrium is yet to be explored. However, using the numerical visualization, we are able to conclude that cannibalism does have a stabilizing effect on population dynamics.

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Chapter 4

Summary and Future Work

In this thesis, we have studied how to model the population dynamics of walleye incorporated with the cannibalism effect. We have concluded in both two models that cannibalism frankly stabilizes the population fluctuations. In Chapter 1, we discussed the life cycle and the food sources of walleye to better understand how to accurately model the population. Additionally, some previous mathematical models have been included.

In Chapter 2, we created a discreet matrix population model with cannibalism terms motivated by LPA model [2]. To study population dynamics, it is very natural to use the discreet model because population data is usually collected on an annual basis. Also, a lot of short-term factors can be ignored such as temperature fluctuations and mating seasons. In our matrix model, we divide the population into three age groups, making the assumption that the newborns and juveniles have the same life span. Also, the model includes the cannibalism terms as size-dependent cannibalism. Because the size of fish is dependent on the age of the fish, we also consider size-dependent cannibalism as age-dependent. The positivity and boundedness of the matrix model were proven first. Then, we defined the basic reproduction rate R_0, and found two equilibria which are an extinction equilibrium and a unique positive equilibrium. We found that when $R_0 < 1$, the extinction equilibrium is globally asymptotically stable. When $R_0 > 1$, there exists a positive equilibrium E^*. The stability of the positive equilibrium is unknown. However, if $R_0 > 1$ is sufficiently close to 1 and $\mu_a < 1$, the positive equilibrium is locally asymptotically stable. We also ran some numerical simulations to check the results. We found that bifurcation occurs when R_0 increases. There might also exist a periodic solution and then chaos. In terms of cannibalism, we found that cannibalism stabilizes the population dynamics.

In Chapter 3, we created a delay differential equation (DDE) model with cannibalism. Motived by Nicholson's blowflies equation [1, 3], we divided the walleye population into two groups, juveniles, and adults. By adding a compatibility condition to the initial functions, we

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proved the positivity and the boundedness of the system. We also define the net reproduction rate R_0 for the system. We found that when $R_0 < 1$, the extinction equilibrium is locally asymptotically stable. Without cannibalism, the extinction equilibrium is indeed globally asymptotically stable if $R_0 < 1$. Adding the cannibalism term affects the global stability of E_0, requiring $R_0 < e^{-d_1\tau}$. In another word, cannibalism might destabilize the extinction equilibrium when $e^{-d_1\tau} < R_0 < 1$. This could be the life boat effect of the fish population. When $R_0 > 1$, there exists a positive equilibrium E^*. The stability of the positive equilibrium is unknown since it is very challenging to find the eigenvalues of the characteristic equation. We did some numerical simulations with different natural birth rates and cannibalism rates. We found that when r increases, the net reproduction rate R_0 also increases. The extinction equilibrium will be stable when R_0 is small. When R_0 increases, the extinction equilibrium will lose its stability, and positive equilibrium will be stable. As r increases, there will be a periodic solution in present. For each natural birth rate, we increase the cannibalism rate. We found that the cannibalism is stabilizing the population cycles. In fact, the bigger the cannibalism rate is, the more stable the system will be. The result matches the result from Chapter 2.

In this thesis, there are still facing some challenging problems remaining open and worth studying in the future. In Chapter 2, the global stability of the positive equilibrium is still not known. From numerical simulations, we are guessing that there must be an interval of R_0 so that the positive equilibrium is globally asymptotically stable. In Chapter 3, the stability of the positive equilibrium is not known neither, which requires further studies.

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