OSCILLATIONS IN A SIZE-STRUCTURED PREY PREDATOR MODEL

By

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To my mother and father, whose constant support and inspiration has lead me to achieve my goal
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This dissertation introduces a predator-prey model with the prey structured by body size based on reports in the literature that predation rates are prey-size specific. The model is built on the foundation of the one-species physiologically structured models studied earlier. Three types of equilibria are found: extinction, multiple prey-only equilibria and possibly multiple predator-prey coexistence equilibria. The stabilities of the equilibria are investigated. Comparison is made with the underlying ODE Lotka-Volterra model. It turns out that the ODE model can exhibit sustain oscillations if there is an Allee effect in the net reproduction rate, that is the net reproduction rate grows for some range of the prey’s population size. In contrast, it is shown that the structured PDE model can exhibit sustain oscillations even if the net reproductive rate is strictly declining. Those occur, however, if reproduction is size specific and limited to individuals of large enough size. Simulations are presented to support our hypothesis that size-specific predation can destabilize the predator-prey equilibrium in the PDE model.
CHAPTER 1
INTRODUCTION

1.1 Background

In ecology predation describes a biological interaction where a predator (an organism that is hunting) feeds on its prey (the organism that is attacked) \[15\]. Predator-prey interactions have fascinated mathematical biologists for a long time. Several long-term data sets have been collected for predator and prey interactions in nature. Predator-prey interactions can be one part in the huge chain or network where every species is linked to the other species in one or more ways, comprising a global food chain.

1.1.1 Food-web Ecology

An important aspect of ecology is to study the food relations. Different animals living and persisting in the environment are subjected to the food relations. One is dependent on the other. It was as early as 1959 when Hutchinson explained this system in a coherent fashion. “Eat or be eaten”, as Hutchinson put it, was termed as the raw dictum of the environment. In \[18\] Hutchinson explained the links between food chain, natural selection, effect of size, effects of terrestrial plants and how the interrelation of food chain affects the system. He also explained how limitation of diversity and niche requirements play a huge role in it. One of the question he raised was whether higher level of diversity leads to more or less stability in community ecology. This issue was later addressed in \[19\] and \[20\]. It has been a long standing question in ecology to identify the interaction strength and stability of the interaction between predator and prey. Sala and Graham devised methods to estimate the distribution of predator prey interaction strengths within a subtidal herbivore community of 45 species \[14\]. In contrast to the theories presented earlier, the authors proved that intermediate size predators under realistic circumstances can prove themselves as the most effective consumers. Article \[21\] designed both observational and experimental approaches for
estimating the interaction strength among the species and discussed their ties to the theory. All these discussions prove that there is a huge bond among different organisms, a bond which is the cause for the species to exist in the natural environment.

One of the most well-known examples in food-chain ecology is the one of the dynamical interactions of Canadian lynx and snowshoe hare with the data collected by the Hudson bay Company in Canada during the period 1821-1940 (see Figure 1-1). This example is now discussed in many mathematical biology textbooks [1]. These data sets have suggested that the predator-prey interactions in nature often persist in the form of oscillations. The question what accounts for the periodicity in the predator-prey dynamics has been a central question in mathematical biology for many years leading to a multitude of articles discussing oscillations in ordinary differential equation models [11].

![Figure 1-1. Oscillations in lynx-hare system. The numbers are in thousands](image-url)
1.1.2 Predominance of Body-size in Food-chain Network

Body size plays a big role in determining the different factors involved in predator-prey dynamics. Predators prefer prey of certain range in size. It is a natural instinct of living beings to prevent themselves from becoming prey to others. Hence prey tries to escape predation by evolving at a larger size. The author in [24] has collected samples from 26 different sites to prove that there is a relationship which existed between the prey body size and predation. His observation reveals the presence of negative correlation of prey size with the largest predator length in the system where the experiment was performed. Over the years ecologists have performed different experiments to prove the relationship between body size and predation. In another case study the authors in [23] have shown that guppies evolve at a larger size in order to avoid predation at smaller sizes. Furthermore, Jennings and Warr [16] claimed that smaller mean body-size ratios are characteristic of more stable predator-prey environment. Warren and Lawton suggest that if the body sizes of predators are larger than the body sizes of their preys then a "trophic hierarchy (cascade model)" might exist based on body size. Holt [22] was successful in designing models based on community modules (such as a predator-prey module) which not only portray the ecological interplay of the species involved but also allow the integration of evolutionary perspective through model parameters.

The main question we address in this dissertation is: Are oscillations in an ecological system where size-dependent predation plays a huge role?

1.2 Related Mathematical Work

In this dissertation we set forth the hypothesis that predation and prey individuals' body size may be responsible for the oscillations observed in the predator-prey interactions in nature. The interactions between the predator and the prey are strongly influenced both by the size of the predator and the size of the prey [13]. Biological literature abounds with articles discussing the role of size in predator-prey interactions in a variety of natural systems [12]. Yet, the role of size, as a continuous variable, in
the context of predator-prey models, has rarely been discussed in the mathematical biology literature. De Roos at al. investigate the role of food availability on the size of the predator *Daphnia* and find that there is coexistence in a stable equilibrium, and stable cycles \[10\]. In this dissertation we take the opposite perspective: we look at the impact of the size of the prey on the predator-prey interaction. Our size-structured partial differential equation model is based on the non-linear single-population size structured model analyzed in \[2\]. Our investigation is motivated by reports in the biological literature that predators prefer prey of certain body size, while the body size of all preys may vary in a large range \[3\]. It has been suggested that predators tend to prefer medium-size prey as too large prey may be too difficult to handle, while too small prey may be too challenging to catch. However, if adequate refuge is available, then the predation rate declines with the size of the prey \[6\]. The question whether prey size may be a destabilizing factor in the predator-prey interactions seems an open and interesting question that we address in this dissertation.

Mathematically, our results parallel most closely the investigation of a predator-prey model which accounts for prey age-structure \[4\]. Li finds, just as we do, three types of equilibria: an extinction equilibrium, a prey-only equilibrium, and a coexistence equilibrium, and performs partial analysis of their stabilities. A more general model in which both the predator and the prey are physiologically structured is introduced by Logan et al. \[8\] (see also \[7\]). However, such a model is rather complex, and the authors consider a number of more tractable special cases. In contrast with their model, which includes a Holling II functional response, our model only includes a linear size-dependent functional response. Our reason for accounting only for linear functional response is to eliminate the possibility that the Holling functional response, well known to destabilize predator-prey interactions, had destabilized the coexistence equilibrium. With linear functional response, and monotone decreasing recruitment rate, the underlying ODE model of our PDE system will not exhibit oscillations.
CHAPTER 2
THE MODEL AND INVESTIGATION OF THE EQUILIBRIA

2.1 The ODE Model and its Analysis

We first introduce an ODE Lotka-Volterra model. Let $N(t)$ be the population size, $P(t)$ be the population size of the predator. The Ordinary Differential Equation is given as follows.

\[ N' = (\beta(N) - \mu(N))N - \gamma PN \]
\[ P' = \alpha \gamma PN - dP \]
(2–1)

\[ N(0) = N_0, P(0) = P_0 \]

where $\beta(N)$ is the birth rate of prey, $\mu(N)$ is the death rate of the prey. The parameter $\gamma$ gives the predation rate, $\alpha$ is the predator conversion efficiency. Finally, the death rate of the predator is given by $d$. This system has an extinction equilibrium $E_0 = (0, 0)$ in which both the predator and the prey populations go extinct. The extinction equilibrium is locally stable if $\beta(0) < \mu(0)$, and unstable otherwise. For the remainder of this section we will assume that $\beta(0) > \mu(0)$ so that at least the prey population is viable.

In the absence of the predator, the prey-only equilibria are obtained as solutions to the equation

\[ \beta(N) = \mu(N). \]
(2–2)

Assume $\beta(N) \to 0$ as $N \to \infty$ and $\mu(N)$ is nondecreasing in $N$. These assumptions and the fact that $\beta(0) > \mu(0)$ imply that this equation has at least one positive solution $N^*$. However, equation (2–2) may have solutions even if $\beta(0) < \mu(0)$. Assume the equation has $k$ solutions $N_1^*, \ldots, N_k^*$, all of which are simple solutions and ordered in increasing order (see Figure 2-1).
Each of these solutions gives a prey-only equilibrium $E_j = (N_j^*, 0)$. Each of these equilibria is locally stable if

$$\beta'(N_j^*) < \mu'(N_j^*) \quad \text{and} \quad \alpha \gamma N_j^* - d < 0 \quad (2-3)$$

and unstable otherwise. The second inequality says that the predator cannot invade the $E_j$th equilibrium of the prey. Define the threshold quantity

$$\hat{N} = \frac{d}{\alpha \gamma}, \quad (2-4)$$

Clearly all prey-only equilibria $E_j$ satisfying $N_j^* > \hat{N}$ are unstable. In other words, if the prey-only population is large enough, it will support the predator to exist. We call the quantity $\hat{N}$ minimum threshold prey population size for existence of the predator. Since equilibria are all simple, the inequality between the derivatives of $\beta$ and $\mu$ changes with each equilibrium. For instance, on Figure 2-1, there are five solutions: $N_1^*, \ldots, N_5^*$. We have $\beta'(N_1^*) < \mu'(N_1^*), \beta'(N_2^*) > \mu'(N_2^*)$, etc. If the minimum threshold prey population size for existence of predator is large enough, then prey-only equilibria $N_1^*, N_3^*, N_5^*$ in Figure 2-1 will be locally stable.
System (2–1) has a unique coexistence equilibrium of the predator and the prey \( E^* = (\hat{N}, \hat{P}) \) where \( \hat{N} \) is given in (2–4), and \( \hat{P} = (\beta(\hat{N}) - \mu(\hat{N}))/\gamma \).

**Theorem 2.1.** The coexistence equilibrium is locally stable if and only if

\[
\beta'(\hat{N}) < \mu'('\hat{N}). \tag{2–5}
\]

**Proof.** The Jacobian of the system at the coexistence equilibrium point is given by the following matrix,

\[
J = \begin{pmatrix}
(\beta'(\hat{N}) - \mu'(\hat{N}))\hat{N} & -\gamma\hat{N} \\
\alpha\gamma\hat{P} & 0
\end{pmatrix}
\]

We observe that the determinant of the matrix \( J \) is positive. We now focus on the trace of the matrix. The two roots of the jacobian are negative or have negative real parts if and only if \( \beta'(\hat{N}) < \mu'(\hat{N}) \). This proves the condition for stability. If the condition is not satisfied then the trace of the matrix is positive and hence has two positive roots or roots with positive real parts. In either case it is unstable.

\[ \square \]

Note that the two roots of the Jacobian are given by the following equation,

\[
\lambda_{1,2} = \frac{(\beta'(\hat{N}) - \mu'(\hat{N}))\hat{N} \pm \sqrt{(\beta'(\hat{N}) - \mu'(\hat{N}))^2 \hat{N}^2 - 4\alpha\gamma^2 \hat{N} \hat{P}^2}}{2} \tag{2–6}
\]

The system will have a imaginary root only in the case when

\[ \beta'(\frac{d}{\alpha\gamma}) = \mu'(\frac{d}{\alpha\gamma}). \]

We show below that the derivative of the real part of the root with respect to \( d \) is given by

\[
\frac{(\beta''(\hat{N}) - \mu''(\hat{N}))\hat{N}}{2\alpha\gamma}
\]
which is not equal to zero unless \((\beta''(\hat{N}) = \mu''(\hat{N}))\). We can certainly choose a function like that. Hence the condition for Hopf Bifurcation is satisfied and we have oscillation in the ODE model.

If (2–5) fails, the coexistence equilibrium may become destabilized and sustained oscillations are possible (see Figure 2-2). Hence, the simple predator-prey model in (2–1) is capable of complex behavior.

![Figure 2-2. A graph of the functions \(N(t)\) and \(P(t)\). The graph shows oscillations in the numbers of the predator and the prey.](image)

### 2.2 The PDE Model

In this section we consider a size-structured population model introduced in the paper by Calsina and Saldaña [2]. The model is a non-linear first order partial differential equation, equipped with nonlocal boundary conditions. As we are interested in the size specific predation effects of a specialist predator we are going to extend that model to incorporate a predator population. The resulting extended model is a size-structured version of the well-known Lotka-Volterra predation model. The model, as introduced in [2], describes the dynamics of the size-structured prey. It is presented below in notation consistent with our extended size-structured predator-prey model:

\[
\begin{align*}
    u_t + (g(x, N(t))u(x, t))_x + \mu(x, N(t))u &= 0, x \in [0, \infty) \\
    g(0, N(t))u(0, t) &= \int_{0}^{\infty} \beta(x, N)u(x, t)dx, t > 0 \\
    u(x, 0) &= \phi(x), x \in [0, \infty)
\end{align*}
\]
where the total population size $N(t)$ at time $t$ is given by:

$$N(t) = \int_0^\infty u(x, t) \, dx.$$ 

The function $u(x, t)$ represents the density of the prey population of size $x$ and at time $t$. In particular that means that $\int_a^b u(x, t) \, dx$ represents the number of prey from size $a$ to size $b$ where both $a$ and $b$ are positive numbers. Here $\mu(x, N)$ represents the natural per capita size-dependent death rate. Furthermore, $\beta(x, N)$ gives the per capita size-dependent birth rate. The model assumes that all births occur to the same initial size which we have shifted to be zero. Both $\mu$ and $\beta$ are nonnegative, Lipschitz continuous with respect to $x$ and $N$ functions. Furthermore, the birth and death rates satisfy:

**Assumption 1.** The birth and death rate satisfy

- $\lim_{N \to \infty} \beta(x, N) = 0$
- $\beta$ is a bounded function with respect to both $x$ and $N$, that is,
  $$\sup_{x, N} \beta(x, N) = \bar{\beta}.$$ 
- $\beta(X, N)$ is positive as a function of $x$ on a set of positive measure.
- $\lim_{N \to \infty} \mu(x, N) = \infty$.
- $\mu$ is bounded from below:
  $$\mu(x, N) \geq \underline{\mu}.$$ 

The function $g(x, N)$ is the growth rate. We assume it is a continuously differentiable function with respect to $x$ and bounded by $g(0)$. For the remainder of this work we will assume that $g(x, N)$ is, in fact, independent of $N$, that is $g(x, N) = g(x)$. Furthermore, $g > 0$ for all $x \in [0, \infty)$. The initial condition $\phi(x)$ is a non-negative and integrable function, which is positive on a set of positive measure.

In the present dissertation we include the effect of a specialist predator. The inclusion of a specialist predator introduces an additional variable and also an additional
equation in the system. We assume the predator feeds on prey of specific size and denote the size-specific per capita predation rate as \( \gamma(x) \). The predation rate \( \gamma(x) \) is a bounded, Lipschitz continuous function with compact support. We assume that \( \gamma(x) > 0 \) on a set of positive measure. Denote by

\[
\Upsilon = \sup_x \gamma(x).
\]

We incorporate the effect of predation as predator-introduced additional mortality on the prey which is size-dependent. The resulting model is given as follows. This is the main model that we consider in this dissertation.

\[
\begin{align*}
    u_t + (g(x)u(x, t))_x &= -\mu(x, N)u - \gamma(x)Pu \\
    g(0)u(0, t) &= \int_{0}^{\infty} \beta(x, N)u(x, t)dx \\
    u(x, 0) &= \phi(x), \quad P(0) = P_0 \\
    P' &= P \int_{0}^{\infty} \alpha(x)\gamma(x)u(x, t)dx - dP
\end{align*}
\] (2–10)

The time-dependent function \( P(t) \) represents the total number of predators at time \( t \). The parameter \( \alpha(x) \) is the prey-size dependent predators metabolic efficiency by which the biomass of consumed prey is transformed into predator’s biomass. Finally, \( d \) is the death rate of predators. The total number of predators \( P \) is a nonnegative function. Predators death rate \( d \) and metabolic efficiency \( \alpha(x) \) are also nonnegative. The number of predators at time \( t = 0 \) is given by the nonnegative number \( P_0 \).

**2.2.1 Equilibria of the Size-structured Predator-prey Model**

Existence and uniqueness of solutions to model (4–1) can be proved similarly as in [2]. In this section we are interested in time-independent solutions (equilibria) of the
model (4–1). The system for the equilibria is

\[(g(x)u(x))_x = -\mu(x, N)u - \gamma(x)Pu\]  \hspace{1cm} (2–11)

\[g(0)u(0) = \int_0^\infty \beta(x, N)u(x)\,dx\]  \hspace{1cm} (2–12)

\[0 = Pu(0)g(0)\int_0^\infty \alpha(x)\gamma(x)\pi(x, P, N)\,dx - dP\]  \hspace{1cm} (2–13)

where \(P\) is the total predator size at the equilibrium. The constant \(N\) represents the total prey size at the equilibrium and is given by:

\[N = \int_0^\infty u(x)\,dx.\]

Assuming that \(N\) and \(P\) are given constants, the differential equation for \(u\) (2–11) can be integrated

\[u(x) = u(0)\frac{g(0)}{g(x)}e^{-\int_0^x \left(\frac{\mu(x, N)}{\alpha(x)} + \frac{\gamma(x)P}{\alpha(x)}\right)ds} = u(0)g(0)\pi(x, P, N)\]  \hspace{1cm} (2–14)

where for a fixed \(P\) and \(N\) we have introduced the following notation

\[\pi(x, P, N) = \frac{1}{g(x)}e^{-\int_0^x \left(\frac{\mu(x, N)}{\alpha(x)}\right)ds - \int_0^x \frac{\gamma(x)}{\alpha(x)}Pds}.\]

The function \(\pi\) can be interpreted as the probability of the prey to survive till size \(x\). To find \(u(0), P\) and \(N\) we place the formula for \(u(x)\) into the renewal equation, the equation for the predator, and the equation of the total prey size. We obtain the following nonlinear system of three equations in the unknowns \(u(0), P\) and \(N\).

\[g(0)u(0) = u(0)g(0)\int_0^\infty \beta(x, N)\pi(x, P, N)\,dx\]

\[0 = Pu(0)g(0)\int_0^\infty \alpha(x)\gamma(x)\pi(x, P, N)\,dx - dP\]  \hspace{1cm} (2–15)

\[N = u(0)g(0)\int_0^\infty \pi(x, P, N)\,dx\]
An equilibrium solution of the system (4–1) is given by the triple \((u(0), P^*, N^*)\), where \(u(0), P^*, \text{ and } N^* \) are a solution of the system (2–15). System (2–15) always has the trivial solution where \(u(0) = 0, P^* = 0, \text{ and } N^* = 0\). The triple \(E_0 = (0, 0, 0)\) gives the extinction equilibrium. Besides the extinction equilibrium, we have two types of other equilibria. The first type are predator-free equilibria, where the predator goes extinct but the prey population size persists. The second type of equilibria are coexistence equilibria where both predator and prey are present. We consider the following two cases.

### 2.2.2 Prey-only Equilibria

In this case we have \(P^* = 0\). Hence the equilibria here would be of the form \((u(0), 0, N^*)\). We have to find the values of \(u(0)\) and \(N^*\). With \(P^* = 0\) system (2–15) takes the form

\[
\begin{align*}
1 &= \int_0^\infty \frac{\beta(x, N)}{g(x)} e^{-\int_0^x \frac{\mu(s, N)}{g(s)} ds} dx, \\
N &= \int_0^\infty u(0) \frac{g(0)}{g(x)} e^{-\int_0^x \frac{\mu(s, N)}{g(s)} ds} dx
\end{align*}
\]  

(2–16)

where

\[
\begin{align*}
u^*(x) &= u(0) \frac{g(0)}{g(x)} e^{-\int_0^x \frac{\mu(s, N)}{g(s)} ds}.
\end{align*}
\]  

(2–17)

The first equation in the system (2–16) is independent of the second equation and depends on \(N\) but not on \(u(0)\). We can first solve the first equation in system (2–16) for \(N\). Then we obtain \(u(0)\) from the second equation in system (2–16). Hence, given that we know \(N^*\), we get

\[
u(0) = \frac{N^*}{\int_0^\infty \frac{g(0)}{g(x)} e^{-\int_0^x \frac{\mu(s, N)}{g(s)} ds} dx}.
\]

Therefore, system (2–16) is essentially a decoupled non-linear system. We note that since \(g(0) > 0\) the denominator in the formula for \(u(0)\) is nonzero. We now focus on the number of solutions of the first equation in (2–16).
We define the net reproduction rate as a function of the prey population size:

\[ R(N) = \int_{0}^{\infty} \frac{\beta(x, N)}{g(x)} e^{-\int_{0}^{x} \frac{\mu(s, N)}{g(s)} ds} dx. \]  

(2–18)

The behavior of this function of \( N \) determines the mechanisms of growth of the prey population. To understand better the solutions of the equation \( R(N) = 1 \) we assume some typical types of birth and death rate functions and then try to explore the existence of equilibria.

**Assumption 2.** Assume the birth and death rates have the following properties:

- \( \beta(x, N) = R_0 \beta_0(N) \Phi(x) \).
- \( \mu(x, N) = \mu_0(N) + m(N) \Psi(x) \).
- \( [\beta_0(0)]^{-1} = \int_{0}^{\infty} \frac{\Phi(x)}{g(x)} e^{-\int_{0}^{x} \frac{\mu(s, 0)}{g(s)} ds} dx. \)
- All functions and constants are nonnegative (positive).

The equation for the total population size \( R(N) = 1 \) takes the form

\[ 1 = \int_{0}^{\infty} R_0 \beta_0(N) \Phi(x) e^{-\int_{0}^{x} \frac{\mu_0(N)+m(N)\Psi(x)}{g(x)} ds} dx \]  

(2–19)

We have to prove that there exists such \( N \) which satisfies equation (2–19). For \( N = 0 \) we have by the Assumptions 2 above

\[ \mathcal{R}(0) = R_0. \]

We call \( R_0 \) intrinsic reproduction number of the prey population. In what follows we consider specific examples.

**Case 1:** Suppose \( \mu(s, N) \) does not depend on \( N \) and we assume specific values for \( \mu_0 \) and \( m \). In particular, let \( \mu_0(N) = 0, m(N) = 1 \). Then, by Assumption 2 the net reproduction rate of the prey population takes the form

\[ \mathcal{R}(N) = R_0 \frac{\beta_0(N)}{\beta_0(0)} \]  

(2–20)
Figure 2-3. Alee effect in the case when $R_0 > 1$. The equation $R(N) = 1$ has a unique solution.

We will assume a particular form of the function $\beta_0(N)$, or more precisely, a particular form of the net reproduction rate, and then we will show that there exists $N^*$ such that $R(N^*) = 1$. We consider the following specific form of the net reproduction rate:

$$R(N) = R_0 \frac{e^{-(N-a)^2}}{e^{-a^2}} = R_0 e^{a^2-(N-a)^2} \quad (2-21)$$

where $a$ is a positive parameter. Since $R'(N) = R_0 e^{a^2-(N-a)^2} (-2(N - a))$, the derivative $R'(N) = 0$ at $N = a$ only. Also we observe that $N = a$ is a local maximum for the graph and $R(N) \to 0$ as $N \to \infty$. We consider two cases

1. **If** $R_0 > 1$. In this case there exists only one $N^*$ such that $R(N^*) = 1$. Figure 2-3 illustrates this scenario.

2. **If** $R_0 < 1$. In this case the graph either does not cross the line $y = 1$ or crosses twice. Thus, there exist either 0 or two $N^*$ such that $R(N^*) = 1$. The graph in Figure 2-4 shows that.

In the case $R_0 < 1$ the critical value of the parameter $a$ such that the equation $R(N) = 1$ transitions from having two solutions to having no solutions is denoted by $a_{cr}$. This critical value occurs when, through manipulations on $a$, the graph of $R(N) = R_0 e^{a^2-(N-a)^2}$ touches the line $y = 1$. In this case we have that $R'(N) = 0$ at $N = a$. 


Hence the critical value of $a = a_{cr}$ is given by the solution of the following equation

$$R(a_{cr}) = 1$$

Thus, the critical value of the parameter $a$ is

$$a_{cr} = \sqrt{\ln\frac{1}{R_0}}$$

The corresponding value of $N^*$ obtained when $a = a_{cr}$ is $N^*_{cr}$ and it is a double root of the equation $R(N) = 1$. All other roots of the equation $R(N) = 1$, when $a \neq a_{cr}$ are simple roots. We note that $R_0 < 1$, we have $\frac{1}{R_0} > 1$ and the square root is well defined and positive. The equilibria that are obtained in the case $R_0 < 1$ are called subthreshold equilibria.

The above example can be extended to allow for more than two equilibria. For instance, assume $a < b$ are two distinct parameters. Consider the following specific function

$$R(N) = R_0 e^{-(N-a)^2(N-b)^2 + a^2b^2}.$$  

We have again that $R(0) = R_0$. It can be seen that $R'(N) = 0$ at $N = a, b, \frac{a+b}{2}$. Therefore, the curve has only 3 horizontal tangent lines and hence it bends three times. Also as $N \to \infty$ we have $R(N) \to 0$. Consequently, if $R(0) > 1$ there exists either one or three $N^*$ such that $R(N^*) = 1$. If $R(0) < 1$, the equation $R(N) = 1$ may have no
solutions, two solutions or four solutions, if all solutions are simple. We illustrate this last case in Figure 2-5. We conclude that even in the case when the mortality rate does not depend on $N$, we may have multiple super and subthreshold equilibria.

![Figure 2-5. Multiple subthreshold equilibria. We have $\mathcal{R}(0) < 1$.](image)

**Case 2:** In this case we, in fact, consider the general case where both the birth rate and the death rate may depend on $N$. We recall that the general net reproduction rate defined as a function of the total prey size is given by (2–18). Equilibria of the total prey population size are solutions of the equation $\mathcal{R}(N) = 1$. We define in analogy with the example above, the *intrinsic reproduction number of the prey population* as

$$
\mathcal{R}_0 = \mathcal{R}(0) = \int_0^\infty \frac{\beta(x,0)}{g(x)} e^{-\int_0^x \frac{\mu(s)}{g(s)} ds} dx \quad (2–24)
$$

The assumptions on the birth rate and death rate as functions of $N$ guarantee that

$$
\lim_{N \to \infty} \mathcal{R}(N) = 0
$$

which states that the net reproduction rate of the prey population approaches zero as the prey population size grows to infinity. Thus, in the case when $\mathcal{R}_0 > 1$, that is $\mathcal{R}(0) > 1$ the equation $\mathcal{R}(N) = 1$ has at least one positive solution $N^*$. In the case $\mathcal{R}_0 < 1$, as the examples above suggest, the equation $\mathcal{R}(N) = 1$ may or may not have solutions. We summarize the findings in the following Theorem.

**Theorem 2.2.** We consider the following two cases:
1. Let $R_0 > 1$. Then, there is at least one positive prey-only equilibrium $E_1 = (u_1(0), 0, N_1^*)$. If there are multiple solutions to the equation $R(N) = 1$ and they are all simple, then there is an odd number of them $N_1^* \ldots N_k^*$ where $k$ is odd. Each of these solutions gives a prey-only equilibrium $E_j = (u_j(0), 0, N_j^*)$ for $j = 1, \ldots, k$.

2. Let $R_0 < 1$. Then, there may be no positive prey-only equilibrium. If there are multiple solutions to the equation $R(N) = 1$ and they are all simple, then there is an even number of them $N_1^* \ldots N_k^*$ where $k$ is even. Each of these solutions gives a prey-only equilibrium $E_j = (u_j(0), 0, N_j^*)$ for $j = 1, \ldots, k$.

We note that the requirement that all equilibria are simple is very important.

The general case when some equilibria can have higher multiplicities is much more complex. However, this condition can fail, and some solutions of $R(N) = 1$ can have higher multiplicity. In this case the parameters of the model have to satisfy additional constrains. Consequently, for very few choices of the parameters, equilibria of higher multiplicity are possible. In the example, the parameter value for which the root $N^*$ has a higher multiplicity, is only $a_{cr}$.

2.2.3 Predator-prey Coexistence Equilibria.

In this case we are looking for equilibria $(u(0), P^*, N^*)$ where $P^* \neq 0$.

**Assumption 3. Assume**

- The reproduction number of the prey population in the absence of the predator satisfies: $R_0 > 1$.
- The equation $R(N) = 1$ has $k$ solutions $N_1^* \ldots N_k^*$, where $k$ is odd. We assume that all solutions are simple.

We define the predator reproduction number at the $N_j$ prey-only equilibrium

$$R_{p,j} = \frac{N_j^* \int_0^\infty \alpha(x) \gamma(x) \pi(x, 0, N_j^*)}{d \int_0^\infty \pi(x, 0, N_j^*) dx}. \quad (2–25)$$
The predator’s reproduction number gives the ability of the predator to invade the \( N^*_j \) equilibrium of the prey. In particular, if \( R_{p,j} > 1 \), then the predator can invade the \( j \)th prey-only equilibrium.

**Assumption 4.** Assume that there exists \( N^*_j > 0 \) such that:

- **The predator’s reproduction number at the previous prey-only equilibrium** \( R_{p,j-1} < 1 \), that is, the predator cannot invade the \( N^*_{j-1} \)th prey-only equilibrium;
- **The predator’s reproduction number** \( R_{p,j} > 1 \), that is, we assume that the predator can invade the \( j \)th prey-only equilibrium.
- **Assume also,** \( j \) is odd.

We note that if \( R_{p,1} > 1 \), then the above assumption would be trivially satisfied.

In the case of predator-prey coexistence equilibria, the non-linear system for the equilibria (2–15) does not decouple. From the second equation we may express \( u(0) \) and eliminate it from the system. We have:

\[
 u(0)g(0) = \frac{d}{\int_0^\infty \frac{\alpha(x)\gamma(x)}{g(x)} e^{-\int_0^x \frac{\mu(s,N)}{\pi(s)}} ds - \int_0^x \frac{\mu(s)}{\pi(s)} ds} dx. \tag{2–26}
\]

Replacing \( u(0)g(0) \) in the equation for the total prey population size we obtain the following equation in \( P \) and \( N \):

\[
 N = \frac{\int_0^\infty \frac{d}{g(x)} e^{-\int_0^x \frac{u(s,N)}{g(x)}} ds - \int_0^x \frac{\mu(s)}{\pi(s)} ds} {\int_0^\infty \frac{\alpha(x)\gamma(x)}{g(x)} e^{-\int_0^x \frac{\mu(s,N)}{\pi(s)}} ds - \int_0^x \frac{\mu(s)}{\pi(s)} ds} dx.
\]

This equation coupled with the renewal equation leads to the following non-linear system for the variables \( N \) and \( P \).

\[
 \int_0^\infty \beta(x, N)\pi(x, P, N) dx = 1
\]

\[
 N = \frac{\int_0^\infty d\pi(x, P, N) dx} {\int_0^\infty \frac{\alpha(x)\gamma(x)}{g(x)} \pi(x, P, N) dx}. \tag{2–27}
\]

This is a non-linear system in \( N, P \). It does not decouple. We are looking for conditions that give a non-zero positive solution of that system. Each positive solution of the
system (2–27) gives one coexistence equilibrium \( E^* = (u^*(0), P^*, N^*) \). The first equation in system (2–27) prompts us to define the net reproduction rate of the prey in the presence of the predator. Denote the net reproduction rate of the prey in the presence of the predator by

\[
R(N, P) = \int_0^\infty \beta(x, N)\pi(x, P, N)dx. \tag{2–28}
\]

The first equation in system (2–27) gives \( R(N, P) = 1 \). We use the implicit function theorem to solve for \( P \) as a function of \( N \). For each arbitrary but fixed \( N \), the equation \( R(N, P) = 1 \) as an equation of \( P \) only has a unique solution, which, however, may be positive or negative. This defines \( P = f(N) \) as a continuous function for all \( N \geq 0 \). Moreover,

\[
\frac{\partial R(N, f(N))}{\partial P} = -\int_0^\infty \beta(x, N) \left( \int_0^x \frac{\gamma(s)}{g(s)} ds \right) \pi(x, f(N), N)dx < 0
\]

since \( \gamma(x) > 0 \) on a set of positive measure. The function \( P = f(N) \) has the following properties:

- \( f(N^*_1) = 0 \), that is the predator equilibrium size at the prey-only equilibria is zero.
- Since all prey-only equilibria are simple, \( f(N) \) has an alternating sign in the consecutive intervals. Since, \( R_0 > 1 \) the signs are the following:

\[
\begin{cases}
  f(N) > 0 & \text{on} & (0, N^*_1) \\
  f(N) < 0 & \text{on} & (N^*_1, N^*_2) \\
  \vdots & & \\
  f(N) > 0 & \text{on} & (N^*_{k-1}, N^*_k) \\
\end{cases} \tag{2–29}
\]

Now we replace \( P = f(N) \) in the second equation of (2–27). After replacing \( P \) the second equation in (2–27), we obtain an equation in \( N \) only. We can rearrange the terms in that equation to get the following form.

\[
\int_0^\infty (N\alpha(x)\gamma(x) - d) \frac{1}{g(x)} e^{-\int_0^x \frac{\mu(s, x)}{g(s)} ds - \int_0^x \frac{f(N^*_k)}{g(s)} ds} dx = 0 \tag{2–30}
\]
We recall that we assume that there exists a prey-only equilibrium, $N^*_j$ such that the predator can invade this equilibrium, that is $R_{p,j} > 1$. We introduce the following notation. Let the left hand side of the equation (2–30) be denoted by $F(N)$:

$$F(N) := \int_0^\infty (N\alpha(x)\gamma(x) - d)\frac{1}{g(x)}e^{-\int_0^x \frac{\alpha(s,N)}{g(s)} ds - \int_0^x \frac{\gamma(s)}{g(s)} ds} dx$$ (2–31)

Clearly we can see that $F(0) < 0$. Thus, if $R_{p,1} > 1$, we have $F(N^*_1) > 0$. Therefore, there exists $\hat{N} \in (0, N^*_1)$ such that $F(\hat{N}) = 0$. Then, the corresponding value of the predator population size is given by $\hat{P} = f(\hat{N})$, and since $R_0 > 1$, this value of the predator size is positive.

In the general case since $R_{p,j-1} < 1$, that implies that $F(N^*_j) < 0$. On the other hand, since $R_{p,j} > 1$, we have $F(N^*_j) > 0$. Therefore, there exist an $\hat{N} \in (N^*_{j-1}, N^*_j)$ such that $F(\hat{N}) = 0$. At the same time we have that $\hat{P} = F(\hat{N})$ and $\hat{P} > 0$. One can express the corresponding $\hat{u}(0)$ from equation (2–26). We summarize the findings in the following theorem.

**Theorem 2.3.** Let Assumption 3 and Assumption 4 hold. Then there is at least one coexistence equilibrium of the predator and the prey $E^* = (\hat{u}(0), \hat{P}, \hat{N})$.

Several remarks are in order.

- Conditions in Assumption 3 and Assumption 4 are sufficient conditions for a coexistence equilibrium to exist. A coexistence equilibrium may exist if one or more conditions fail. For instance, even if prey’s intrinsic reproduction number $R_0 < 1$, coexistence may still occur.

- In the size-structured case, unlike ODE case, the coexistence equilibrium may not be unique. Intuitively, that may be the case since size-specific predation may affect some (say more abundant) sizes of a prey-only equilibrium, and lead to coexistence. Since more than one prey-only equilibrium exists, each of them can be potentially perturbed this way to a coexistence equilibrium, leading to multiple coexistence equilibria.

**2.2.4 Stability Analysis**

In this section we consider the local stability of the equilibria of the model (4–1) around an equilibrium point. We linearize the model around a general equilibrium...
E = (u(0), P^*, N^*) where u(0) corresponds to \( u^*(x) = u(0)g(0)\pi(x, P^*, N^*) \). We introduce the following perturbations

\[
\begin{align*}
u(x, t) &= u^*(x) + \xi(x, t) \\
P(t) &= P^* + \eta(t) \\
N(t) &= N^* + n(t).
\end{align*}
\]

The last equality holds since

\[
N(t) = \int_{0}^{\infty} u(x, t) dx = \int_{0}^{\infty} (u^*(x) + \xi(x, t)) dx = N^* + n(t).
\]

It is clear from the above computations that

\[
n(t) = \int_{0}^{\infty} \xi(x, t) dx.
\]

Since the birth rate \( \beta(x, N) \) and the death rate \( \mu(x, N) \) are non-linear functions of the total population size, we expand them around the equilibrium point as

\[
\begin{align*}
\beta(x, N) &= \beta(x, N^* + n(t)) \\
&= \beta(x, N^*) + n(t)\beta'(x, N^*) + h.o.t \tag{2–34}
\end{align*}
\]

\[
\begin{align*}
\mu(x, N) &= \mu(x, N^* + n(t)) \\
&= \mu(x, N^*) + n(t)\mu'(x, N^*) + h.o.t \tag{2–36}
\end{align*}
\]

where,'h.o.t' in the equation above represents the higher order terms i.e the terms that involve products of perturbations. Since we consider the local stability around the equilibrium point we neglect the higher order terms. Hence the linearized equations of
the model \( (4-1) \) reduce to the following system:

\[
\begin{align*}
\xi_t + (g(x)\xi(x, t))_x &= -\mu(x, N^*)\xi - \mu'(x, N^*)u^*(x)\eta + \gamma(x)P^*\xi - \gamma(x)u^*(x)\eta \\
g(0)\xi(0, t) &= \int_0^\infty \beta(x, N^*)\xi(0, t)\,dx + n(t)\int_0^\infty \beta'(x, N^*)u^*(x)\,dx \\
\eta' &= P^*\int_0^\infty \alpha(x)\gamma(x)\xi(x, t)\,dx + \eta\int_0^\infty \alpha(x)\gamma(x)u^*(x)\,dx - d\eta
\end{align*}
\]

(2–38)

where \( n(t) \) is given by \((2–33)\). We use the linearizations above to investigate the stability of each type of equilibria: extinction, prey-only, and coexistence equilibria.

2.2.5 Extinction Equilibrium \( (u = 0, P = 0) \)

Here we consider the equilibrium where there is no predator or prey in the model. We perturb the extinction equilibrium with a small value and then observe the behavior in the long run. The system for the perturbations above takes the form

\[
\begin{align*}
\xi_t + (g(x)\xi(x, t))_x &= -\mu_0(x)\xi(x, t) \\
g(0)\xi(0, t) &= \int_0^\infty \beta_0(x)\xi(0, t)\,dx \\
\eta' &= -d\eta
\end{align*}
\]

(2–39)

where we have used the following notation: \( \beta_0(x) = \beta(x, 0) \) and \( \mu_0(x) = \mu(x, 0) \).

To find the stability of the equilibrium point we investigate the eigenvalues of the linearized operator by setting \( \xi(x, t) = e^{\lambda t}\bar{\xi}(x) \) and \( \eta(t) = e^{\lambda t}\bar{\eta} \). Hence we have the following eigenvalue problem for the stability of the extinction equilibrium:

\[
\begin{align*}
\lambda\bar{\xi}(x) + (g(x)\bar{\xi}(x))_x &= -\mu_0(x)\bar{\xi}(x) \\
g(0)\bar{\xi}(0) &= \int_0^\infty \beta_0(x)\bar{\xi}(x)\,dx \\
\lambda\bar{\eta} &= -d\bar{\eta}
\end{align*}
\]

(2–40)

Clearly, \( \lambda = -d \) is one of the eigenvalues which is negative. Further, we assume \( \lambda \neq -d \) so that \( \bar{\eta} = 0 \). To find the remaining eigenvalues we look for nonzero solution of the first two equations. In particular, we solve the first equation:

\[
\bar{\xi}(x) = \frac{g(0)\bar{\xi}(0)}{g(x)} e^{-\int_0^x \frac{\mu_0(\sigma)+\lambda}{\beta_0(\sigma)}\,d\sigma}
\]

(2–41)
and replace it in the second equation, obtaining the following characteristic equation

\[
\int_0^\infty \frac{\beta_0(x)}{g(x)} e^{-\int_0^x \frac{\mu_0(s)+\lambda}{g(s)} ds} dx = 1.
\]  

(2–42)

We denote by

\[G(\lambda) = \int_0^\infty \frac{\beta_0(x)}{g(x)} e^{-\int_0^x \frac{\mu_0(s)+\lambda}{g(s)} ds}.\]

Hence, the characteristic equation becomes \(G(\lambda) = 1\). For \(\lambda\) real, \(G(\lambda)\) is decreasing. Furthermore, it is clear from the definition of \(G(\lambda)\) that as \(\lambda \to \infty\), \(G(\lambda) \to 0\).

Furthermore,

\[G(0) = R_0.\]

We have the following two cases:

1. If \(R_0 > 1\): In this case \(G(0) > 1\). Therefore, then there exists positive real solution \(\lambda^* > 0\) to the equation \(G(\lambda) = 1\). Hence, the extinction equilibrium is unstable.

2. If \(R_0 < 1\): In this case \(G(0) < 1\), then because of the monotonicity of \(G(\lambda)\), the equation \(G(\lambda) = 1\) has a unique real solution \(\lambda^* < 0\). We now show that all other solutions to the characteristic equation \(G(\lambda) = 1\), which are complex, have negative real part. Indeed, for \(\lambda\) complex with \(\Re \lambda \geq 0\) we have

\[|G(\lambda)| \leq G(\Re \lambda) \leq R_0 < 1.\]

Hence, there do not exist any non-negative real solutions, or solutions with non-negative real part of \(\lambda\) for the characteristic equation \(G(\lambda) = 1\). We may conclude that the extinction equilibrium is locally asymptotically stable.

We summarize these findings in the following Theorem.

**Theorem 2.4.** If the intrinsic reproduction number of the prey population \(R_0 < 1\), then the extinction equilibrium \(E_0 = (0, 0, 0)\) is locally asymptotically stable. If the intrinsic reproduction number of the prey \(R_0 > 1\), then the extinction equilibrium is unstable.

We note that we cannot establish global stability of the extinction equilibrium in the case \(R_0 < 1\) because of the presence of subthreshold equilibria (see Figure 2-4).
2.2.6 Prey-only Equilibria

The equilibria in this case are given by $E_j = (u^*_j(x), 0, N^*_j)$ where $N^*_j = \int_0^\infty u^*_j(x)dx$.

For arbitrary prey-only equilibrium $E = (u^*(x), 0, N^*)$ the linearization of the original size-structured model (4–1) is obtained from the linearized system (2–38).

\[
\begin{align*}
\xi_t + (g(x)\xi(x, t))_x &= -\mu(x, N^*)\xi(x, t) - \mu'(x, N^*)u^*n(t) \\
g(0)\xi(x, t) &= \int_0^\infty (\beta(x, N^*)\xi(x, t) + \beta'(x, N^*)u^*n(t))dx \\
\eta'(t) &= \eta(t) \int_0^{\infty} \alpha(x)\gamma(x)u^*dx - d\eta
\end{align*}
\]

where $u^*(x)$ if given by (2–17). We can integrate the last equation in this system to obtain

\[\eta(t) = \eta_0 e^{(A-d)t}\] (2–44)

where $A = \int_0^{\infty} \alpha(x)\gamma(x)u^*(x)dx$. We recall that for the $j$th prey-only equilibrium the predator invasion number is given by

\[R_{p,j} = \frac{N^*_j \int_0^{\infty} \alpha(x)\gamma(x)\pi(x, 0, N^*_j)dx}{d \int_0^{\infty} \pi(x, 0, N^*_j)dx}\]

We note that the definition for $A$ and formula for $u(0)$ given by (2–26) imply that $R_{p,j} = A/d$. Therefore, if the predator can invade the prey-only equilibrium $R_{p,j} > 1$, then $A > d$, and the $j$th prey-only equilibrium is unstable. We summarize that in following theorem.

**Theorem 2.5.** The $j$th prey-only equilibrium $E_j = (u_j(0), 0, N_j^*)$ is unstable if $R_{p,j} > 1$.

**Proof.** If $R_{p,j} > 1$ then that implies $A > d$ and as a result from the solution $\eta(t)$ given in equation (2–44) we have that $\eta(t) \to \infty$ as $t \to \infty$. Hence the equilibrium is unstable. \qed

In the remainder of this section we consider prey-only equilibria $E_j$ which cannot be invaded by the predator, that is $R_{p,j} < 1$. We will again drop the subscript $j$. To
obtain the eigenvalue problem for the linearized operator, we are looking for a solution of (2–43) that has the form \( \xi(x, t) = e^{\lambda t} z(x) \) and \( \eta(t) = \eta e^{\lambda t} \). From the definition of \( n(t) \) we can get that

\[
n(t) = \int_0^\infty \xi(x, t) dx = e^{\lambda t} \int_0^\infty z(x) dx = n_0 e^{\lambda t}
\]

If we substitute the above quantities in the equations (2–43) then we can obtain the following eigenvalue problem:

\[
\lambda z(x) + (g(x)z(x))_x = -\mu(x, N^*) z(x) - \mu'(x, N^*) n_0 u^*(x) - \gamma(x) u^*(x)
\]

\[
g(0)z(0) = \int_0^\infty \beta(x, N^*) z(x) dx + n_0 \int_0^\infty \beta'(x, N^*) dx
\]

(2–45)

In the above system we are looking for a non-trivial solution \((z(x), \eta)\).

**Option 1:** Let \( \lambda = A - d \). Then \( \lambda < 0 \). Furthermore, the last equation is satisfied for every \( \eta \) where \( \eta \neq 0 \). We may choose as a non zero solution of equations (2–45) \((z(x), \eta)\), where \( z(x) \) is the solution of the first two equations with the given, chosen \( \eta \).

Such a solution \( z(x) \) exists if \( \lambda = A - d \) is not an eigenvalue of the first two equations of the system (2–45) with \( \eta = 0 \).

**Option 2:** \( \lambda \neq A - d \). We need to have \( \eta = 0 \). Then \( \lambda \eta = (A - d) \eta \). We may have a non-zero eigenvector, if the remaining two equations have a non-zero solution \( z(x) \). The remaining eigenvalues are solutions of the following system.

\[
\lambda z(x) + (g(x)z(x))_x = -\mu(x, N^*) z(x) - \mu'(x, N^*) u^* n_0
\]

(2–46)

\[
g(0)z(0) = \int_0^\infty \beta(x, N^*) z(x) dx + n_0 \int_0^\infty \beta'(x, N^*) dx
\]

(2–47)

Here \( z(x) \) can be positive or negative. We call \( \omega(x) = \mu'(x, N^*) u^* n_0 \).

**Subcase 1:** Here we assume \( \mu(x, N) = \mu(x) \) that is \( \mu \) does not depend on \( N \) so that we have \( \mu'(x, N^*) = 0 \) and as a result \( \omega(x) = 0 \). This reduces the system to the following
set of equations.

\[ \lambda z(x) + (g(x)z(x))_x = -\mu(x)z(x) \tag{2-48} \]

\[ g(0)z(0) = \int_0^\infty \beta(x, N^*)z(x)\,dx + n_0 \int_0^\infty \beta'(x, N^*)u^*\,dx \tag{2-49} \]

which can be easily solved to obtain \( g(x)z(x) = g(0)z(0)e^{-\int_0^x \frac{\lambda + \mu(s)}{g(s)}\,ds} \). Substituting this in the second equation above we have the following characteristic equation

\[ 1 = \int_0^\infty \frac{\beta(x, N^*)}{g(x)} e^{-\int_0^x \frac{\lambda + \mu(s)}{g(s)}\,ds} \,dx + \int_0^\infty \beta'(x, N^*)u^* \,dx \int_0^\infty \frac{1}{g(x)} e^{-\int_0^x \frac{\lambda + \mu(s)}{g(s)}\,ds} \,dx \tag{2-50} \]

We define

\[ G(\lambda) = \int_0^\infty \frac{\beta(x, N^*)}{g(x)} e^{-\int_0^x \frac{\lambda + \mu(s)}{g(s)}\,ds} \,dx + F \int_0^\infty \frac{1}{g(x)} e^{-\int_0^x \frac{\lambda + \mu(s)}{g(s)}\,ds} \,dx \tag{2-51} \]

where the constant \( F \) is given by

\[ F = \int_0^\infty \beta'(x, N^*)u^* \,dx. \]

Furthermore, we denote by

\[ K(\lambda) = \int_0^\infty \frac{\beta(x, N^*)}{g(x)} e^{-\int_0^x \frac{\lambda + \mu(s)}{g(s)}\,ds} \,dx, \]

\[ L(\lambda) = \int_0^\infty \frac{1}{g(x)} e^{-\int_0^x \frac{\lambda + \mu(s)}{g(s)}\,ds} \,dx. \tag{2-52} \]

Hence, the function \( G(\lambda) \) takes the form \( G(\lambda) = K(\lambda) + FL(\lambda) \). Clearly for \( \lambda = 0 \) we have

\[ G(0) = K(0) + FL(0) = \mathcal{R}(N^*) + FL(0) = 1 + FL(0) \tag{2-53} \]

since \( N^* \) is an equilibrium total population and is a solution to the equation \( \mathcal{R}(N) = 1 \).

It is clear from the form of \( G(\lambda) \) that for \( \lambda \) real, as \( \lambda \to \infty, G(\lambda) \to 0 \). Hence the characteristic equation \( G(\lambda) = 1 \) has a positive real solution if \( G(0) > 1 \). A positive real solution to the characteristics equation implies that the prey-only equilibrium \( E_j \) is unstable. Since \( G(0) > 1 \) if and only if \( F > 0 \), then \( F > 0 \) is a condition that implies
instability of the system, even if \( \lambda = A - d < 0 \). We summarize this result in the following lemma.

**Lemma 1.** Assume \( \mu(x, N) = \mu(x) \). If \( F > 0 \), then the \( j \)th prey-only equilibrium \( E_j \) is unstable. 

Concerning stability of the prey-only equilibria we have the following lemma.

**Lemma 2.** Assume \( F < 0 \), the birth rate \( \beta(x, N) = \beta(N) \). Furthermore, assume that for the prey-only equilibrium with total population size \( N^* \) the following inequality holds: 

\[-F < 2\beta(N^*) \]

Then the characteristic equation \( G(\lambda) = 1 \) has only roots with negative real part.

**Proof.** We consider the characteristic equation \( G(\lambda) = 1 \), where \( G(\lambda) \) is given by (2–51). The assumption that \( F < 0 \) implies that \( G(0) < 1 \). Assume there exists a root \( \lambda = a + ib \) of \( G(\lambda) = 1 \) where \( a \geq 0 \). That implies \( |(G(\lambda)| = 1 \). We have

\[
G(\lambda) = \int_0^\infty \frac{\beta(N^*)}{g(x)} e^{-\int_0^x \frac{\lambda + \mu(s)}{g(s)} ds} dx + F \int_0^\infty \frac{1}{g(x)} e^{-\int_0^x \frac{\lambda + \mu(s)}{g(s)} ds} dx \\
= (\beta(N^*) + F) \int_0^\infty \frac{1}{g(x)} e^{-\int_0^x \frac{\lambda + \mu(s)}{g(s)} ds} dx
\]

Taking absolute values and using the fact that \( G(\lambda) = 1 \), we have

\[
1 = |G(\lambda)| = |(\beta(N^*) + F) \int_0^\infty \frac{1}{g(x)} e^{-\int_0^x \frac{\lambda + \mu(s)}{g(s)} ds} dx| \\
\leq |(\beta(N^*) + F)| \int_0^\infty \frac{1}{g(x)} e^{-\int_0^x \frac{\Re(\lambda) + \mu(s)}{g(s)} ds} dx \\
< \int_0^\infty \frac{1}{g(x)} \beta(N^*) e^{-\int_0^x \frac{\mu(s)}{g(s)} ds} dx = 1
\]

We note that our assumption on \(-F < 2\beta(N^*)\) implies that we have \(|\beta(N^*) + F| < |\beta(N^*)| = \beta(N^*)\). The last sequence of inequalities leads to \(1 < 1\) which is a contradiction.
Thus there cannot exists a root $\lambda$ which has a non-negative real part when $G(0) < 1$. Thus, our claim is proved.

A couple of remarks are in order.

- The condition on the sign of $F$ is related to the net reproduction rate $R(N)$. In particular, in the case when $\mu$ is not a function of $N$, the rate of change of the prey populations net reproduction rate at the equilibrium total prey population size $N^*$ is given by

$$R'(N^*) = \int_0^\infty \frac{\beta'(x, N^*)}{g(x)} e^{-\int_0^x \frac{\mu(s)}{g(s)} ds} dx.$$ 

Hence, $F = u(0)g(0)R'(N^*)$, that is $F$ has the sign of the rate of change of the net reproductive rate at the prey-only equilibrium. So we established that if the net reproduction rate is increasing at the equilibrium, the equilibrium is unstable. If the net reproduction rate is decreasing, the equilibrium may be stable subject to additional assumptions.

- As we show below, if $\mu$ is constant, and $F < 0$, equilibrium is locally asymptotically stable with general birth rate $\beta(x, N)$.

- In the case when $F < 0$, if the birth and the death rate depend on $x$, then oscillations may be possible.

Subcase 2: Now we assume $\mu(x, N) = \mu(N)$, that is, $\mu$ depends on $N$ only. Further, assume that $\mu'(N) \geq 0$. System (2–46)-(2–47) takes the form

$$\begin{align*}
\lambda z(x) + (g(x)z(x))_x &= -\mu(N^*) z(x) - \mu'(N^*) u^* n_0 \\
g(0)z(0) &= \int_0^\infty \beta(x, N^*)z(x)dx + \int_0^\infty \beta'(x, N^*)u^* dnx_0
\end{align*}$$

(2–54)

We recall that $u^*(x) = \frac{u(0)g(0)}{g(x)} e^{-\int_0^x \frac{\mu(N^*)}{g(x)} ds}$. We solve the differential equation for $z(x)$ treating $n_0$ as given to obtain

$$z(x) = \frac{g(0)z(0)}{g(x)} e^{-\int_0^x \frac{\mu(N^*)+\lambda}{g(x)} ds} - \frac{\mu'(N^*) u(0) g(0) n_0}{\lambda} \left[ \frac{e^{-\int_0^x \frac{\mu(N^*)}{g(x)} ds}}{g(x)} - \frac{e^{-\int_0^x \frac{\mu(N^*)+\lambda}{g(x)} ds}}{g(x)} \right].$$

(2–55)

From definition of $n_0 = \int_0^\infty z(x) dx$ and using the formula for $z(x)$ we can express $n_0$ in terms of $g(0)z(0)$:

$$n_0 = \frac{g(0)z(0)}{\lambda + \mu(N^*) + \frac{\mu'(N^*) u(0) g(0)}{\mu(N^*)}}.$$ 

(2–56)
We substitute \( z(x) \) and \( n_0 \) back in the second equation of (2–54). We obtain the following characteristic equation:

\[
1 = \int_0^\infty \frac{\beta(x, N^*)}{g(x)} e^{-\int_0^x \frac{\mu(N^*)}{g(s)} ds} dx \left[ 1 + \frac{\mu'(N^*) u(0) g(0)}{\lambda + \mu(N^*) + \frac{\mu'(N^*) g(0) u(0)}{\mu(N^*)}} \right]
\]

(2–57)

\[
-\frac{\mu'(N^*) u(0) g(0)}{\lambda + \mu(N^*) + \frac{\mu'(N^*) g(0) u(0)}{\mu(N^*)}} + \frac{F}{\lambda + \mu(N^*) + \frac{\mu'(N^*) g(0) u(0)}{\mu(N^*)}}
\]

(2–58)

where \( F = \int_0^\infty \beta'(x, N^*) u^*(x) dx \). Denoting by \( G(\lambda) \) the expression on the right hand side of the above equation, we can write the characteristic equation as \( G(\lambda) = 1 \). The eigenvalues of the system (2–54) are the real and complex solutions of that equation. As before, it can be seen that for \( \lambda \) real \( G(\lambda) \to 0 \) as \( \lambda \to \infty \). \( G(0) \) is defined as the limit of the function \( G(\lambda) \) as \( \lambda \to 0 \). Hence,

\[
G(0) = 1 + \frac{F}{\mu(N^*) + \frac{\mu'(N^*) g(0) u(0)}{\mu(N^*)}} - \frac{\mu'(N^*) u(0) g(0)}{\mu(N^*) + \frac{\mu'(N^*) g(0) u(0)}{\mu(N^*)}} \int_0^\infty \frac{\beta(x, N^*)}{g(x)} \left( \int_0^x \frac{1}{g(s)} ds \right) e^{-\int_0^x \mu(N^*) ds} dx
\]

The relationship of \( G(0) \) with one is determined by the sign of the expression \( F - \mu'(N^*) g(0) u(0) \int_0^\infty \beta(x, N^*) e^{-\int_0^x \frac{\mu(N^*)}{g(s)} ds} \left( \int_0^x \frac{ds}{g(s)} \right) dx \). We have that \( G(0) > 1 \) if and only if

\[
F - \mu'(N^*) g(0) u(0) \int_0^\infty \beta(x, N^*) e^{-\int_0^x \frac{\mu(N^*)}{g(s)} ds} \left( \int_0^x \frac{ds}{g(s)} \right) dx > 0.
\]

(2–59)

In this case by the similar argument as before we can say that the equilibrium is unstable. We now show that the sign of the expression above is determined by the rate of change of the net reproduction rate at the equilibrium total prey population size \( N^* \). In particular, we have

\[
\mathcal{R}'(N^*) = \int_0^\infty \beta'(x, N^*) e^{-\mu(N^*) \int_0^x \frac{1}{g(s)} ds} dx
\]

\[
-\mu'(N^*) \int_0^\infty \frac{\beta(x, N^*)}{g(x)} \left( \int_0^x \frac{1}{g(s)} ds \right) e^{-\mu(N^*) \int_0^x \frac{1}{g(s)} ds} dx
\]
Thus, we find again that if the net reproduction rate of the prey population is increasing through the equilibrium, the prey-only equilibrium is unstable. We summarize that in the following lemma:

**Lemma 3.** Assume $\mu(x, N) = \mu(N)$ and $\mu'(N) \geq 0$. If $R'(N^*_j) > 0$, then the prey-only equilibrium $E_j$ is unstable.

Stability of an equilibrium in this case is given by the following lemma.

**Lemma 4.** Assume $\mu(x, N) = \mu(N)$ and $\mu'(N) \geq 0$. If $F < 0$ there cannot exist any root $\lambda$ of the characteristic equation $G(\lambda) = 1$ with $\Re(\lambda) \geq 0$.

**Proof.** Assume $\Re(\lambda) \geq 0$. We rewrite the characteristics equation $G(\lambda) = 1$ in the following form.

\[
\int_0^{\infty} \beta(x, N^*_j) e^{-\int_0^x \frac{\mu(N^*_j) + \lambda}{g(0)} ds} dx = 1 - \frac{F \lambda}{\lambda + \mu(N^*_j) + \mu'(N) g(0) u(0)}
\]

Simplifying the expression we have

\[
\int_0^{\infty} \beta(x, N^*_j) e^{-\int_0^x \frac{\mu(N^*_j) + \lambda}{g(0)} ds} dx = 1 - \frac{k\lambda}{\lambda^2 + r\lambda + s}
\]

The absolute value of left side of the previous equation is less or equal to one. We can show that the absolute value of right side of the equation is greater than one. We can treat the right side of the equation as $1 + \frac{k\lambda}{\lambda^2 + r\lambda + s}$. It can be shown that the real part of this expression is strictly greater than one. Hence absolute value is greater than one, which leads to a contradiction. This shows that there do not exist any roots with non-negative real part for the characteristic equation $G(\lambda) = 1$ when $F$ is negative. 

\[\square\]
2.2.7 Stability of a Coexistence Equilibrium

The equilibrium in this case is represented by \((u^*(x), P^*, N^*)\), where \(N^* = \int_0^\infty u^*(x)dx\). We will investigate the local stability of the coexistence equilibrium starting from the linearized system (2–38). First we notice that from the equation for the equilibrium we have

\[
\int_0^\infty \alpha(x)\gamma(x)u^*(x)dx = d.
\]

That simplifies the third equation in (2–38). We are looking for a solution of the form \(\xi(x, t) = e^{\lambda t}\xi(x), \eta(t) = \eta e^{\lambda t}, n(t) = ne^{\lambda t}\). We substitute this form of solution into equations (2–38) to get,

\[
\begin{align*}
(g(x)\xi(x))_x &= -\lambda \xi(x) - \mu \xi(x) - \mu' u^*(x)n - \gamma(x)P^*\xi(x) - \gamma(x)u^*\eta \\
g(0)\xi(0) &= \int_0^\infty \beta(x, N^*)\xi(x)dx + n\int_0^\infty \beta'(x, N^*)u^*dx
\end{align*}
\tag{2–62}
\]

where

\[
n = \int_0^\infty \xi(x)dx.
\]

In what follows in this subsection we consider two cases: constant predation and size-specific predation.

**Case 1: Constant predation:** We make the following simplifying assumptions

**Assumption 5.** Assume

- \(\mu\) is a function of \(N^*\) only, that is, \(\mu(x, N^*) = \mu(N^*)\);
- \(\gamma(x)\) is constant: \(\gamma(x) = \gamma\);
- \(\alpha(x)\) is constant: \(\alpha(x) = \alpha\).

In the previous section we showed that with the above assumption on \(\mu\), and any function \(\beta\), the prey-only equilibrium is locally asymptotically stable. In this section we will see that, even if predation is constant with respect to size, it has the ability to destabilize the predator-prey coexistence equilibrium.
With the above assumptions, from equations (2–62) we have:

\[(g(x)\xi(x))_x + \left(\frac{\lambda + \mu + P^*}{g(x)}\right) g(x)\xi(x) = -(\mu'(N)n + \gamma\eta)u^*(x)\]

\[g(0)\xi(0) = \int_0^\infty \beta(x, N^*)\xi(x)dx + Fn\]  

\[\lambda = \frac{P^*\alpha\gamma n}{\eta}\]  

(2–63)

Integrating the first equation in the system above we obtain the following formula:

\[g(x)\xi(x) = g(0)\xi(0)e^{-\int_0^x \frac{\lambda + \mu + \gamma P^*}{g(s)}ds} \]

\[-u(0)g(0)(\mu'n + \gamma\eta)e^{-\int_0^x \frac{\lambda + \mu + \gamma P^*}{g(s)}ds} \int_0^x \frac{\lambda}{g(s)}d\sigma ds\]  

(2–64)

(2–65)

This leads to the following form of the equations

\[\xi(x) = g(0)\xi(0)\frac{e^{-\int_0^x \frac{\lambda + \mu + \gamma P^*}{g(s)}ds}}{g(x)} - \frac{u(0)g(0)(\mu'n + \gamma\eta)}{\lambda}e^{-\int_0^x \frac{\lambda + \mu + \gamma P^*}{g(s)}ds} \left[ e^{\int_0^x \frac{\lambda}{g(s)}ds} - 1 \right] \]

\[= g(0)\xi(0)\frac{e^{-\int_0^x \frac{\lambda + \mu + \gamma P^*}{g(s)}ds}}{g(x)} - \frac{u(0)g(0)(\mu'n + \gamma\eta)}{\lambda} \left[ \frac{e^{-\int_0^x \frac{\lambda + \mu + \gamma P^*}{g(s)}ds}}{g(x)} - \frac{e^{-\int_0^x \frac{\lambda + \mu + \gamma P^*}{g(s)}ds}}{g(x)} \right] \]

We know that \(n = \int_0^\infty \xi(x)dx\). Integrating \(\xi(x)\) we have

\[n = \frac{g(0)\xi(0)}{\lambda + \mu + \gamma P^*} - \frac{u(0)g(0)(\mu'n + \gamma\eta)}{(\mu + \gamma P^*)(\lambda + \mu + \gamma P^*)}\]  

(2–66)

Solving for \(n\) from (2–66) we have

\[n = \frac{g(0)\xi(0)\lambda}{\lambda^2 + L\lambda + K} \quad \eta = \frac{g(0)\xi(0)P^*\alpha\gamma}{\lambda^2 + L\lambda + K}\]

where we have introduced the following notation:

\[K = \frac{u(0)g(0)\gamma^2 P^*\alpha}{\mu + \gamma P^*} \quad L = \mu + \gamma P^* + \frac{u(0)g(0)\mu'}{\mu + \gamma P^*}\]
Substituting the value of $\eta$ and $n$ we have the following form of $\xi(x)$.

$$\xi(x) = g(0)\xi(0)\frac{e^{-\int_0^x \frac{\lambda + \mu + \gamma P^*}{g(s)} ds}}{g(x)} - \frac{u(0)g(0)\xi(0)}{(\lambda^2 + \lambda L + K)} \left[ \mu' + \frac{\gamma P^* \alpha}{\lambda} \right] \left[ \frac{e^{-\int_0^x \frac{\lambda + \mu + \gamma P^*}{g(s)} ds}}{g(x)} - \frac{e^{-\int_0^x \frac{\lambda + \mu + \gamma P^*}{g(s)} ds}}{g(x)} \right]$$ (2–67)

Substituting this in the second equation of (2–63) we obtain the characteristic equation

$$G(\lambda) = 1$$

where we have the following form of $G(\lambda)$:

$$G(\lambda) = \int_0^\infty \frac{\beta(x, N^*)}{g(x)} e^{-\int_0^x \frac{\lambda + \mu + \gamma P^*}{g(s)} ds} \left[ 1 + \frac{u(0)g(0)}{\lambda^2 + \lambda L + K} \left( \mu' + \frac{\gamma^2 P^* \alpha}{\lambda} \right) \right] - \frac{u(0)g(0)}{\lambda^2 + \lambda L + K} \left( \mu' + \frac{\gamma^2 P^* \alpha}{\lambda} \right) + \frac{F\lambda}{\lambda^2 + \lambda L + K}$$ (2–68)

We observe here that $G(0)$ has the following form:

$$G(0) = 1 - \frac{u(0)g(0)\gamma^2 P^* \alpha}{K} \int_0^\infty \frac{\beta(x, N^*)}{g(x)} e^{-\int_0^x \frac{\lambda + \mu + \gamma P^*}{g(s)} ds} \int_0^x \frac{ds}{g(s)} dx$$ (2–69)

This shows that we always have: $G(0) < 1$. We can rewrite the characteristic equation in the following form:

$$1 - \frac{F\lambda^2}{\lambda^3 + \lambda L^2 + (K + u(0)g(0)\mu')\lambda + \gamma^2 P^* \alpha u(0)g(0)} = \int_0^\infty \frac{\beta(x, N^*)}{g(x)} e^{-\int_0^x \frac{\lambda + \mu + \gamma P^*}{g(s)} ds} dx$$ (2–70)

Stability of the coexistence equilibrium can be established in the following special case:

**Lemma 5.** Assume $F < 0$, and the size-specific birth rate has the form

$$\beta(x, N^*) = \beta(N^*) e^{-\int_0^x \frac{\rho}{g(s)} ds}$$

where $\rho$ is a given non-negative parameter. Then the predator-prey coexistence equilibrium is locally asymptotically stable.
Proof. The denominator of the left-hand side in the characteristic equation can be
rewritten in the form:

\[ \lambda^3 + L\lambda^2 + (K + u(0)g(0)\mu')\lambda + \gamma^2P^*\alpha u(0)g(0) = (\lambda + \mu + \gamma P^*)[\lambda^2 + Q\lambda + R] \quad (2–72) \]

where

\[ Q = \frac{u(0)g(0)\mu'}{\mu + \gamma P^*}, \quad R = \frac{u(0)g(0)\gamma^2P^*\alpha}{\mu + \gamma P^*} \]

We rewrite the characteristic equation in the form

\[ \frac{F\lambda^2}{\lambda^3 + L\lambda^2 + (K + u(0)g(0)\mu')\lambda + \gamma^2P^*\alpha u(0)g(0)} = 1 - \frac{\beta(N^*)}{\lambda + \rho + \mu + \gamma P^*} \]

The equations for the equilibrium imply

\[ \rho + \mu + \gamma P^* = \beta(N^*) \]

Hence, the characteristic equation simplifies to

\[ \frac{F\lambda}{\lambda^3 + L\lambda^2 + (K + u(0)g(0)\mu')\lambda + \gamma^2P^*\alpha u(0)g(0)} = \frac{1}{\lambda + \rho + \mu + \gamma P^*} \]

which rewritten as a cubic equation becomes

\[ \lambda^3 + A\lambda^2 + B\lambda + C = 0 \]

where the coefficients are given by

\[ A = Q + (\mu + \gamma P^*) - F \quad (2–73) \]
\[ B = (\mu + \gamma P^*)Q + R - F(\rho + \mu + \gamma P^*) \quad (2–74) \]
\[ C = (\mu + \gamma P^*)R \quad (2–75) \]

Since, \( F < 0 \), it follows that \( A > 0, B > 0, \) and \( C > 0 \). Furthermore, it is not hard to
see that \( AB > C \). Thus, Routh-Hurwitz criteria imply that the roots are negative or have
negative real parts. Oscillations in this case do not occur. \( \Box \)
CHAPTER 3
HOPF BIFURCATION AND OSCILLATIONS

3.1 $\beta$-step Function, Everything Else is Constant.

**Theorem 3.1.** Assume $F < 0$, $\mu$ is a constant that does not depend on $N^*$, and the size-specific birth rate has the following form

$$\beta(x, N^*) = \beta(N^*) \chi_{[A, \infty)}(x)$$

where $\chi_{[A, \infty)}$ is the characteristic function of the interval $[A, \infty)$, that is $\chi(x) = 1$, if $x > A$ and zero elsewhere. Assume further that the following inequality holds:

$$\frac{u(0)g(0)\gamma^2P^*\alpha}{\mu + \gamma P^*} < 2(\mu + \gamma P^*)(-F).$$

$$\text{(3–1)}$$

Then, Hopf bifurcation occurs for some value of $A$, and the system exhibits sustained oscillations.

**Note:** We note that inequality (3–1) can be rewritten in the form

$$\frac{1}{2} \frac{\gamma^2 P^* \alpha}{\mu + \gamma P^*} e^{(\mu + \gamma P^*) A} < -\beta'(N^*)$$

which can be obtained from writing $F$ in terms of the parameters. This inequality implies that the oscillations occur if the predator size $P^*$ at equilibrium and predator predation rate $\gamma P^*$ are sufficiently small relative to the growth rate of the prey at the equilibrium $-\beta'(N^*)$. In other words, for an equilibrium for which prey’s net reproductive rate is decreasing ($\beta'(N^*) < 0$), predator’s abundance should be low for oscillations to occur.

**Proof.** Throughout this proof we will consider the special case when $g(x) = 1$. With this form of the birth rate, we can integrate the integral in the right-hand side of the characteristic equation (2–70). With the assumption that $\mu' = 0$, and the denominator in the form (2–72), the characteristic equation becomes:

$$1 - \frac{F \lambda^2}{(\lambda + \mu + \gamma P^*)(\lambda^2 + R)} = \frac{\beta(N^*)}{\lambda + \mu + \gamma P^*} e^{-(\lambda + \mu + \gamma P^*) A}$$

$$\text{(3–2)}$$
We note that the equation for the equilibria implies that
\[
\mu + \gamma P^* = \beta(N^*)e^{-(\mu + \gamma P^*)A}.
\]

Hence, the characteristic equation simplifies to
\[
\lambda + \eta - \frac{F\lambda^2}{\lambda^2 + R} = \eta e^{-\lambda A}
\]
where \( \eta = \mu + \gamma P^* \). Lemma 5 implies that for \( A = 0 \) (with \( \rho = 0 \)) the above equation has only roots with negative real parts and the coexistence equilibrium is locally stable. As a first step to establishing Hopf bifurcation for some \( A_0 > 0 \), we look for purely imaginary solutions of the simplified characteristic equation \( (3-3) \). Set \( \lambda = i\omega \). The equation \( (3-3) \) becomes
\[
i\omega + \eta + \frac{F\omega^2}{R - \omega^2} = \eta e^{-i\omega A}
\]
Separating the real and imaginary part in the above equation, we obtain that \( \omega \) should satisfy the following system:
\[
\eta + \frac{F\omega^2}{R - \omega^2} = \eta \cos(\omega A)
\]
\[
\omega = -\eta \sin(\omega A)
\]
We eliminate the trigonometric functions by squaring both sides of the each equation above, and adding the equations. Thus, \( \omega \) should satisfy the following equation
\[
\left( \eta + \frac{F\omega^2}{R - \omega^2} \right)^2 + \omega^2 = \eta^2.
\]
\[
(3-4)
\]
We set \( \omega^2 = z \) to obtain
\[
\left( \eta + \frac{Fz}{R - z} \right)^2 + z = \eta^2.
\]
\[
(3-5)
\]
Rewriting the above equation as a polynomial equation in \( z \) we obtain
\[
z[z^2 - (2\eta F - F^2 + 2R)z + (R^2 + 2\eta RF)] = 0.
\]
Assumption (3–1) guarantees that the above equation has three real roots: a negative one, zero, and a positive one. Let $z_0 = \omega_0^2$ be the positive root. Then $\omega_0 = \sqrt{z_0}$. To complete the bifurcation analysis, we choose the maturation size $A$ as a bifurcation parameter. We view the solutions of the characteristic equation (3–3) as functions of the parameter $A$, namely $\lambda(A) = \rho(A) + i\omega(A)$. For some value $A_0$ we have $\rho(A_0) = 0$, and $\omega(A_0) = \omega_0$. We need to show that the roots cross the imaginary axis with non-zero speed, that is we need to show that

$$\frac{d\Re(\lambda(A))}{dA}|_{A=A_0} > 0.$$ 

To see this last inequality, we differentiate the characteristic equation (3–3) with respect to the bifurcation parameter $A$ to obtain:

$$\left[1 + \eta A e^{-\lambda A} - \frac{2FR\lambda}{(\lambda^2 + R)^2}\right] \frac{d\lambda}{dA} = -\eta \lambda e^{-\lambda A}.$$

To simplify the computation, we look at the inverse of $\frac{d\lambda}{dA}$:

$$\left(\frac{d\lambda}{dA}\right)^{-1} = \frac{1 - \frac{2FR\lambda}{(\lambda^2 + R)^2}}{-\eta \lambda e^{-\lambda A}} - \frac{A}{\lambda} = \frac{1 - \frac{2FR\lambda}{(\lambda^2 + R)^2}}{-\lambda \left(\lambda + \eta - \frac{F\lambda^2}{\lambda^2 + R}\right)} - \frac{A}{\lambda}$$

(3–6)

(3–7)

We set $\lambda = i\omega_0$ and rationalize the denominator:

$$\left(\frac{d\lambda}{dA}\right)^{-1} \bigg|_{\lambda=i\omega_0} = \frac{1 - \frac{2FRi\omega_0}{(-\omega_0^2 + R)^2}}{-i\omega_0 \left(i\omega_0 + \eta + \frac{F\omega_0^2}{-\omega_0^2 + R}\right)} - \frac{A}{i\omega_0} = \frac{\left[1 - \frac{2FRi\omega_0}{(-\omega_0^2 + R)^2}\right] \left(-i\omega_0 + \eta + \frac{F\omega_0^2}{-\omega_0^2 + R}\right)^2 + Ai\omega_0}{\omega_0}$$

(3–8)

We take the real part of the expression in the right-hand side and using (3–4) we obtain:

$$\Re\left(\frac{d\lambda}{dA}\right)^{-1} = \frac{1}{\eta^2} \left[\frac{2FR}{(R - \omega_0^2)^2} \left(\eta + \frac{F\omega_0^2}{R - \omega_0^2}\right) + 1\right]$$

(3–9)
The expression on the right hand side is not automatically positive since $F < 0$. To see its positivity, we recall that $\omega_0^2 = z_0$, and $z_0$ is the rightmost solution of the equation $h(z) = \eta^2$ where

$$h(z) = \left( \eta + \frac{Fz}{R - z} \right)^2 + z.$$  

We observe that, since $z_0$ is the positive root of the equation,

$$z_0 = R + \frac{2\eta F - F^2 + \sqrt{(2\eta F - F^2)^2 - 4RF^2}}{2} < R.$$  

Hence this $z_0$ is on left of $R$. In addition $h(z)$ has only one asymptote at $z = R$. Hence the function is continuous between 0 and $R$. Furthermore, the first derivative of this function is given by

$$h'(z) = \frac{2FR}{(R - z)^2} \left( \eta + \frac{Fz}{R - z} \right) + 1 \quad (3-10)$$

Note that

$$h'(0) = \frac{R^2 + 2\eta RF}{R^2} < 0$$

by assumption and clearly $h(z) \to +\infty$ as $z \to R^-$. Since $h(z)$ cannot have more than one positive root other than $z_0$, we have that $h'(z_0) > 0$, that is

$$\frac{2FR}{(R - z_0)^2} \left( \eta + \frac{Fz_0}{R - z_0} \right) + 1 > 0. \quad (3-11)$$

The last inequality implies that

$$\left( \frac{d\Re\chi}{dA} \right)^{-1} |_{A=A_0} > 0.$$

This completes the proof.  

3.2 $\beta$-step Function & $\gamma$-step Function

For this section we make the following assumptions:

Assumption 6. Assume

- $\mu(x, N^*) = \mu$ is a constant;

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- \( \gamma(x) \) is given by
  \[
  \gamma(x) = \begin{cases} 
  0 & 0 \leq x < A \\
  \gamma & x > A
  \end{cases}
  \]

- \( \alpha(x) \) is constant: \( \alpha(x) = \alpha \).

**Theorem 3.2.** Suppose assumption 6 holds. Also we assume \( g(x) = 1 \) and \( \mu'(N^*) = 0 \). As before we take prey birth rate as a separable function \( \beta(x, N^*) = \beta(N^*)\beta_0(x) \) with \( \beta_0(x) = \chi_{[A, \infty)} \). This condition guarantees the presence of sustained oscillations in the present PDE model.

**Note:** The assumptions in the theorem, model a predator which feeds selectively only on larger reproductive prey sizes.

**Proof.** We start again from system (2–62). Solving the differential equation we obtain

\[
\xi(x) = \xi(0)\pi(\lambda; x, P^*) - \eta u(0)\pi(\lambda; x, P^*) \frac{1}{\lambda} [e^{\lambda x} - e^{\lambda A}]. \tag{3–12}
\]

Computing the integral of \( \xi \) we have

\[
\int_A^\infty \xi(x) dx = \xi(0)e^{-(\lambda+\mu)A} \frac{1}{\lambda + \mu + \gamma P^*} - \frac{\eta u(0)\gamma}{\lambda} e^{-\mu A} \left[ \frac{1}{\mu + \gamma P^*} - \frac{1}{\lambda + \mu + \gamma P^*} \right] - \frac{\eta d}{\alpha(\lambda + \mu + \gamma P^*)}
\]

where we have used the equilibrium equation \( \alpha\gamma u(0)e^{-\mu A} = d(\mu + \gamma P^*) \). Substituting in the equation for \( \eta \) in (2–62) we obtain the following formula for \( \eta \):

\[
\eta = \frac{\xi(0)\alpha \gamma P^* e^{-(\lambda+\mu)A}}{\lambda^2 + L\lambda + K} \tag{3–13}
\]

where \( L = \mu + \gamma P^* \) and \( K = \gamma P^*d \). The integrals of \( \xi \) are given by:

\[
\int_A^\infty \xi(x) dx = \xi(0)\frac{\lambda e^{-(\lambda+\mu)A}}{\lambda^2 + L\lambda + K} \quad \int_0^\infty \xi(x) dx = \frac{\xi(0)}{\lambda + \mu} (1 - e^{-(\lambda+\mu)A}) \tag{3–14}
\]
Substituting in the equation for $\xi(0)$, and canceling $\xi(0)$ we obtain the following characteristic equation:

$$1 = \beta(N^*) \frac{\lambda e^{-(\lambda+\mu)A}}{\lambda^2 + L\lambda + K} + F \left[ \frac{1}{\lambda+\mu} (1 - e^{-(\lambda+\mu)A}) + \frac{\lambda e^{-(\lambda+\mu)A}}{\lambda^2 + L\lambda + K} \right]. \quad (3-15)$$

The above characteristic equation simplifies to

$$(\lambda + \mu - F)(\lambda^2 + L\lambda + K) = [\beta(N^*)\lambda(\lambda + \mu) - F\gamma P^*(\lambda + d)]e^{-(\lambda+\mu)A}. \quad (3-16)$$

Using the corresponding equation for the equilibria:

$$e^{-\mu A}\beta(N^*) = \mu + \gamma P^* \quad (3-16)$$

the characteristic equation takes the form:

$$(\lambda + \mu - F)(\lambda^2 + L\lambda + K) = L[\lambda(\lambda + \mu) - V\gamma P^*(\lambda + d)]e^{-\lambda A} \quad (3-17)$$

where $V = F/\beta(N^*)$. Furthermore, the characteristic equation can be rewritten as:

$$\lambda^3 + a_1\lambda^2 + a_2\lambda + a_3 = [T_1\lambda^2 + T_2\lambda + T_3]e^{-\lambda A} \quad (3-18)$$

where

$$a_1 = \mu - F + L \quad (3-19)$$
$$a_2 = L(\mu - F) + K \quad (3-20)$$
$$a_3 = (\mu - F)K \quad (3-21)$$

and

$$T_1 = L$$
$$T_2 = L(\mu - V\gamma P^*)$$
$$T_3 = L\nu K$$

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In order to derive the Hopf Bifurcation in this model we assume $\lambda = i \omega$ is a root of (3–18). This implies that $\omega$ has to satisfy the following equation.

\[-i \omega^3 - a_1 \omega^2 + a_2 \omega i + a_3 = iT_2 \omega \cos(\omega \tau) + (T_3 - T_1 \omega^2) \cos(\omega \tau) + T_2 \omega \sin(\omega \tau) - i(T_3 - T_1 \omega^2) \sin(\omega \tau)\]

(3–23)

(3–24)

We separate the real and imaginary parts to obtain the following sets of equations.

\[a_2 \omega - \omega^3 = T_2 \omega \cos(\omega A) - (T_3 - T_1 \omega^2) \sin(\omega A)\]

(3–25)

\[a_3 - a_1 \omega^2 = (T_3 - T_1 \omega^2) \cos(\omega \tau) + T_2 \omega \sin(\omega \tau)\]

(3–26)

From the above two equations we eliminate $\sin(\omega A)$ and $\cos(\omega A)$ by squaring and adding the function to obtain the following equation.

\[\omega^6 + (a_1^2 - 2a_2 - T_1^2)\omega^4 + (a_2^2 - 2a_1a_3 + 2T_1T_3 - T_2^2)\omega^2 + a_3^2 - T_3^2 = 0\]

(3–27)

Since this equation lacks any odd powers of $\omega$ we can use the substitution $z = \omega^2$. This reduces (3–27) to a third order equation in $z$ given as follows.

\[h(z) = z^3 + \alpha z^2 + \beta z + \vartheta = 0\]

(3–28)

where the coefficients are given as follows.

\[\alpha = a_1^2 - 2a_2 - T_1^2\]

(3–29)

\[\beta = a_2^2 - 2a_1a_3 + 2T_1T_3 - T_2^2\]

(3–30)

\[\vartheta = a_3^2 - T_3^2\]

(3–31)
If $\vartheta < 0$ i.e. $a_3^2 < T_3^2$ then we will show that there exists an oscillation in the system. Note that $h(z) \to \infty$ as $z \to \infty$. Also $h(0) = \vartheta < 0$. Thus (3–28) has one positive solution and this implies the existence of a real root of 3–27 given by $\omega_0 = \sqrt{z_0}$. Now we start observing the root $\lambda$ as a function of $A$. Let us assume $\lambda(A) = \eta(A) + i\omega(A)$ be the eigenvalue of (3–18) such that for some initial value of the bifurcation parameter $A_0$ we have $\eta(A_0) = 0$ and $\omega(A_0) = \omega_0$ (where we can assume that $\omega_0 > 0$ without loss of generality.) Thus from (3–27) and (3–25) we can infer that

$$
\tau_j = \frac{1}{\omega_0} \arccos \left( \frac{(a_1 T_1 - T_2)\omega_0^4 + (a_2 T_2 - a_3 T_1 - a_1 T_3)\omega_0^2 + a_3 T_3}{T_2^2\omega_0^2 + (T_3 - T_1\omega_0^2)^2} \right) + \frac{2j\pi}{\omega_0}, j = 0, 1, 2, ..., 
(3–32)
$$

In order to prove the Hopf Bifurcation we state the following Theorem and lemma.

**Theorem 3.3.** Let us assume $\omega_0$ is the largest positive root of (3–27). Then $i\omega(A_0) = i\omega_0$ is a simple root of (3–18) and $\eta(A) + i\omega(A)$ is differentiable with respect to $A$ in a neighborhood of $A = A_0$.

It is easy to observe that $i\omega_0$ is a simple root and is analytic. Using the analytic version of Implicit Function Theorem $\eta(A) + i\omega(A)$ is defined and analytic in a neighborhood of $A_0$.

**Lemma 6.** Let $x_1, x_2, x_3$ be the roots of the equation

$$
g(x) = x^3 + \alpha x^2 + \beta x + \vartheta = 0, (\beta < 0) \quad (3–33)
$$

and $x_3$ is the largest positive simple root, then $\frac{dg(x)}{dx} |_{x=x_3} > 0$.

To establish the Hopf Bifurcation at $A = A_0$ we need to show that $\frac{d\text{Re}\lambda(A)}{dA} |_{A=A_0} > 0$. Differentiating (3–18) with respect to $A$ we get the following equation,

$$
(3\lambda^2 + 2a_1 \lambda + a_2) \frac{d\lambda}{dA} = \left[ -\tau e^{-\lambda A}(T_1 \lambda^2 + T_2 \lambda + T_3) + e^{-\lambda A}(2T_1 \lambda + T_2) \right] \frac{d\lambda}{dA} - \lambda e^{-\lambda A}(T_1 \lambda^2 + T_2 \lambda + T_3) \quad (3–34)
$$

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This leads to

\[
\frac{d\lambda}{dA}^{-1} = \frac{3\lambda^2 + 2a_1\lambda + a_2 + Ae^{-\lambda A} (T_1 \lambda^2 + T_2 \lambda + T_3) - e^{-\lambda A} (2T_1 \lambda + T_2)}{-\lambda e^{-\lambda A} (T_1 \lambda^2 + T_2 \lambda + T_3)} 
\]

\[
= \frac{3\lambda^2 + 2a_1\lambda + a_2}{-\lambda e^{-\lambda A} (T_1 \lambda^2 + T_2 \lambda + T_3)} + \frac{2T_1 \lambda + T_2}{\lambda} - A
\]

\[
= \frac{2\lambda^3 + a_1\lambda^2 - a_3}{-\lambda^2 (\lambda^3 + a_1\lambda^2 + a_2\lambda + a_3)} + \frac{T_1 \lambda^2 - T_3}{\lambda^2 (T_1 \lambda^2 + T_2 \lambda + T_3)} - A 
\]

Thus we have,

\[
\text{Sign}\{\frac{\text{Re}\lambda}{dA}\}_{\lambda=\iota\omega_0} = \text{Sign}\{\text{Re}\left(\frac{d\lambda}{dA}\right)^{-1}\}_{\lambda=\iota\omega_0} \tag{3-39} 
\]

\[
= \text{Sign}\{\text{Re}\left[\frac{2\lambda^3 + a_1\lambda^2 - a_3}{\lambda^2 (\lambda^3 + a_1\lambda^2 + a_2\lambda + a_3)}\right]\}_{\lambda=\iota\omega_0} + \text{Re}\left[\frac{T_1 \lambda^2 - T_3}{\lambda^2 (T_1 \lambda^2 + T_2 \lambda + T_3)}\right] 
\]

\[
= \text{Sign}\{\text{Re}\left[\frac{-2\omega_0^3 i - a_1\omega_0^2 - a_3}{\omega_0^2(-\omega_0^3 i - a_1\omega_0^2 + a_2\omega_0 i + a_3)}\right]\} + \text{Re}\left[\frac{-\omega_0^2(-T_1\omega_0^2 - T_2\omega_0 i + T_3)}{\omega_0^2(T_3 - T_1\omega_0^2 + T_2\omega_0^2)}\right] \tag{3-40} 
\]

\[
= \text{Sign}\left\{\frac{2\omega_0^6 + (a_1^2 - 2a_2)\omega_0^4 - a_3^2}{\omega_0^2((a_1\omega_0^2 - a_3)^2 + (\omega_0^3 - a_2\omega_0)^2)} + \frac{T_1^2 - T_2^2}{\omega_0^2(T_3 - T_1\omega_0^2 + T_2\omega_0^2)}\right\} \tag{3-41} 
\]

\[
= \text{Sign}\left\{\frac{3\omega_0^4 + 2(a_1^2 - 2a_2 - T_1^2)\omega_0^2 + (a_2^2 - 2a_1a_3 - 2T_1 T_3 - T_2^2)}{(a_1\omega_0^2 - a_3)^2 + (\omega_0^3 - a_2\omega_0)^2}\right\} \tag{3-42} 
\]

Since \( h(z) = z^3 + \alpha Z^2 + \beta z + \vartheta \), We can conclude that,

\[
\frac{dh(z)}{dz} = 3z^2 + 2\alpha z + \beta = 3z^2 + 2(a_1^2 - 2a_2 - T_1^2)z + (a_2^2 - 2a_1a_3 - 2T_1 T_3 - T_2^2) \tag{3-43} 
\]

As \( \omega_0 \) is the largest positive simple root of (3–27) from the preceding Lemma we have, \( \frac{dh(z)}{dz} \bigg|_{z=\omega_0} > 0 \). Hence

\[
\frac{d\text{Re}(\lambda)}{dA} = \frac{\frac{dh(\omega_0)}{dz}}{(a_1\omega_0^2 - a_3)^2 + (\omega_0^3 - a_2\omega_0)^2} > 0 \tag{3-44} 
\]

This proves the existence of Hopf Bifurcation in the PDE model in this case when the predator feed preferentially on larger sizes.
CHAPTER 4
NUMERICAL ANALYSIS OF THE PDE MODEL

4.1 Numerical Scheme

Let us consider the model with $\alpha$ as constant.

$$u_t + (g(x)u(x, t))_x = -\mu(x, N)u - \gamma(x)Pu$$

$$g(0)u(0, t) = \int_0^\infty \beta(x, N)u(x, t)dx$$

$$u(x, 0) = \phi(x), P(0) = P_0$$

$$P' = P\alpha \int_0^\infty \gamma(x)u(x, t)dx - dP$$

The numerical scheme is given by

$$\frac{\hat{u}_j^{k+1} - \hat{u}_j^k}{\Delta t} + \frac{g_j \hat{u}_j^{k+1} - g_{j-1} \hat{u}_{j-1}^{k+1}}{\Delta x} + \mu_j^k \hat{u}_j^{k+1} + \gamma_j P^k \hat{u}_j^{k+1} = 0$$

We use the following notation in the analysis.

$$\epsilon_j^k = u(x_j, t_k) - \hat{u}_j^k, \eta^k = P^k - \hat{P}^k, \rho^k = N^k - \hat{N}^k$$

We take the maximal time to be $T$ and maximal size to be $A$. We discretize the $x$ variable with step $\Delta x$ as $x_j = x_0 + j\Delta x, j = 1, 2, ..., m$ and the time variable $t$ with step $\Delta t$ as $t^k = k\Delta t, k = 1, 2, ..., n$.

4.2 Numerical Analysis

**Theorem 4.1.** If the functions $\beta(x, N), \gamma(x), \alpha, \mu(x, N)$ are bounded and if the rate of change of $\beta$ and $\mu$ with respect to $N$ is also restricted within proper bounds, then the numerical scheme of the PDE model is converging of the order $\Delta t$.

**Proof.** We consider model 4–1. To show the convergence of the numerical scheme, we introduce the following discretization of the model.
\[ u(x_{j-1}, t)g(x_{j-1}) = u(x_j - \Delta x, t)g(x_j - \Delta x) \]
\[ = u(x_j, t)g(x_j) - \frac{\partial}{\partial x} (g(x_j)u(x_j, t))\Delta x + \frac{\partial^2}{\partial x^2} (g(\xi)u(\xi, t))(\Delta x)^2/2 \]

where \( x_{j-1} \leq \xi \leq x_j \). Solving for \( \frac{\partial}{\partial x} (g(x_j)u(x_j, t)) \) gives the following form

\[ \frac{\partial}{\partial x} (g(x_j)u(x_j, t)) = \frac{u(x_j, t)g(x_j) - u(x_{j-1}, t)g(x_{j-1})}{\Delta x} + \frac{\partial^2}{\partial x^2} (g(\xi)u(\xi, t))(\Delta x)^2/2 \] (4–5)

We replace \( t \) in (4–5) by \( t_{k+1} \) to obtain the following equation.

\[ \frac{\partial}{\partial x} (g(x_j)u(x_j, t_{k+1})) = \frac{u(x_j, t_{k+1})g(x_j) - u(x_{j-1}, t_{k+1})g(x_{j-1})}{\Delta x} + \frac{\partial^2}{\partial x^2} (g(\xi)u(\xi, t_{k+1}))(\Delta x)^2/2 \] (4–7)

Now we expand \( u(x, t) \) in terms of the time variable.

\[ u(x, t_k) = u(x, t_{k+1} - \Delta t) \] (4–9)
\[ = u(x, t_{k+1}) - \frac{\partial}{\partial t} u(x, t_{k+1})\Delta t + \frac{\partial^2}{\partial t^2} u(x, \xi) (\Delta t)^2/2 \] (4–10)

where \( \xi \) is different from the one before and satisfies \( t_k < \xi < t_{k+1} \).

Solving for \( \frac{\partial}{\partial t} u(x, t_{k+1}) \) we obtain,

\[ \frac{\partial}{\partial t} u(x, t_{k+1}) = \frac{u(x, t_{k+1}) - u(x, t_k)}{\Delta t} + \frac{\partial^2}{\partial t^2} u(x, \xi) (\Delta t)^2/2 \] (4–11)

We replace \( x \) in (4–11) by \( x_j \) to obtain the following equation.
\[
\frac{\partial}{\partial t}u(x, t_{k+1}) = \frac{u(x, t_{k+1}) - u(x, t_k)}{\Delta t} + \frac{\partial^2}{\partial t^2}u(x, \xi)(\Delta t) + \frac{\partial^2}{\partial t^2}u(x, \xi)(\Delta t) + \frac{\partial^2}{\partial t^2}u(x, \xi)(\Delta t) + \frac{\partial^2}{\partial t^2}u(x, \xi)(\Delta t)
\] (4–12)

Combining (4–7) and (4–12) we have the following sets of equation.

\[
\frac{u(x, t_{k+1}) - u(x, t_k)}{\Delta t} + \frac{\partial}{\partial t}u(x, t_{k+1}) + \frac{\partial}{\partial x}(g(x_j)u(x_j, t_{k+1})) = \frac{u(x, t_{k+1}) - u(x, t_k)}{\Delta t} + \frac{\partial}{\partial x}(g(x_j)u(x_j, t_{k+1})) + \frac{\partial}{\partial x}(g(x_j)u(x_j, t_{k+1}))
\] (4–13)

\[
\frac{u(x, t_{k+1}) - u(x, t_k)}{\Delta t} + \frac{\partial}{\partial x}(g(x_j) - u(x_{j-1}, t_{k+1})g(x_{j-1})) + \frac{\partial}{\partial x}(g(x_j) - u(x_{j-1}, t_{k+1})g(x_{j-1})) + \frac{\partial}{\partial x}(g(x_j) - u(x_{j-1}, t_{k+1})g(x_{j-1}))
\] (4–14)

\[
\frac{\partial^2}{\partial t^2}u(x, \xi)(\Delta t) + \frac{\partial^2}{\partial t^2}u(x, \xi)(\Delta t) + \frac{\partial^2}{\partial t^2}u(x, \xi)(\Delta t) + \frac{\partial^2}{\partial t^2}u(x, \xi)(\Delta t)
\] (4–15)

\[
\frac{\partial^2}{\partial x^2}(g(x_j)u(x_j, t_{k+1}))(\Delta x) + \frac{\partial^2}{\partial x^2}(g(x_j)u(x_j, t_{k+1}))(\Delta x)
\] (4–16)

We now expand the terms containing \(\gamma(x)\) and \(\mu(x)\),

\[
\gamma(x_j)P(t_{k+1})u(x_j, t_{k+1}) = \gamma(x_j)u(x_j, t_{k+1})P(t_k + \Delta t)
\]

\[
= \gamma(x_j)u[x_j, t_{k+1}][P(t_k) + \Delta tP'(\xi)]
\]

\[
= \gamma(x_j)u(x_j, t_{k+1})P(t_k) + \gamma(x_j)u(x_j, t_{k+1})P'(\xi)\Delta t
\]

\[
\mu(x_j, N(t_{k+1}))u(x_j, t_{k+1}) = u(x_j, t_{k+1})\mu(x_j, N(t_k) + N'(\xi)\Delta t)
\]

\[
= u(x_j, t_{k+1})[\mu(x_j, N(t_k)) + N'(\xi)\frac{\partial\mu(x_j, \xi)}{\partial N}\Delta t]
\]

Substituting back all the derived terms above in the original equation we obtain the following equation.

\[
\frac{u(x, t_{k+1}) - u(x, t_k)}{\Delta t} + \frac{u(x, t_{k+1})g(x_j)u(x_{j-1}, t_{k+1})g(x_{j-1})}{\Delta x} + \mu(x_j, N(t_{k+1}))u(x_j, t_{k+1}) + \gamma(x_j)P(t_{k+1})u(x_j, t_{k+1}) = \]

\[
-u(x_j, t_{k+1})N'(\xi)\frac{\partial\mu(x_j, \xi)}{\partial N}\Delta t - \gamma(x_j)u(x_j, t_{k+1})P'(\xi)\Delta t - \frac{\partial^2}{\partial t^2}u(x, \xi)(\Delta t) + \frac{\partial^2}{\partial t^2}u(x, \xi)(\Delta t) + \frac{\partial^2}{\partial t^2}u(x, \xi)(\Delta t) + \frac{\partial^2}{\partial t^2}u(x, \xi)(\Delta t)
\] (4–17)

\[
(4–18)
\]

\[
(4–19)
\]

\[
(4–20)
\]
The numerical scheme is given by

\[
\frac{\hat{u}_j^{k+1} - \hat{u}_j^k}{\Delta t} + \frac{g_j \hat{u}_j^{k+1} - g_{j-1} \hat{u}_{j-1}^{k+1}}{\Delta x} + \mu_j^k \hat{u}_j^{k+1} + \gamma_j P^k \hat{u}_j^{k+1} = 0
\]  

(4–21)

Taking the difference between (4–17) and (4–21) we obtain

\[
\frac{u(x_j, t_{k+1}) - \hat{u}_j^{k+1} - (u(x_j, t_k) - \hat{u}_j^k)}{\Delta t} + \frac{g_j(u(x_j, t_{k+1}) - \hat{u}_j^{k+1}) - g_{j-1}(u(x_{j-1}, t_{k+1}) - \hat{u}_{j-1}^{k+1})}{\Delta x} + \mu(x_j, N(t_{k+1}))u(x_j, t_{k+1}) - \mu_j^k \hat{u}_j^{k+1} + (\gamma(x_j)P(t_{k+1})u(x_j, t_{k+1}) - \gamma_j P^k \hat{u}_j^{k+1})
\]

\[
= -u(x_j, t_{k+1}) N'(\xi) \frac{\partial \mu(x_j, \xi)}{\partial N} \Delta t - \gamma(x_j)u(x_j, t_{k+1}) P'(\xi) \Delta t - \frac{\partial^2}{\partial t^2} u(x, \xi) \frac{(\Delta t)}{2} + \frac{\partial^2}{\partial x^2} (g(\xi) u(\xi, t_{k+1})) \frac{(\Delta x)}{2}
\]

Now we observe that

\[
P(t_{k+1})u(x_j, t_{k+1}) - P^k \hat{u}_j^{k+1} = u(x_j, t_{k+1}) \eta_j^k + \hat{P}^k \epsilon_j^{k+1},
\]

\[
(\mu(x_j, N(t_{k+1}))u(x_j, t_{k+1}) - \mu_j^k \hat{u}_j^{k+1})
\]

\[
= \mu(x_j, N^k)[u(x_j, t_{k+1}) - \hat{u}_j^{k+1}] + [\mu(x_j, N^k) - \mu_j^k] u_j^{k+1}
\]

\[
= \mu(x_j, N^k) \epsilon_j^{k+1} + \mu'(x_j, \xi) \rho^k \epsilon_j^{k+1}
\]

Combining the above equation we can have the following form of the equation,

\[
\frac{\epsilon_j^{k+1} - \epsilon_j^k}{\Delta t} + \frac{g_j \epsilon_j^{k+1} - g_{j-1} \epsilon_{j-1}^{k+1}}{\Delta x} + \mu(x_j, N^k) \epsilon_j^{k+1} + \mu'(x_j, \xi) \rho^k \epsilon_j^{k+1} + \gamma u(x_j, t_{k+1}) \eta_j^k + \gamma_j \hat{P}^k \epsilon_j^{k+1} = 0
\]  

(4–22)

\[
\frac{\partial u(x, \xi)}{\partial N} \Delta t - \gamma(x_j)u(x_j, t_{k+1}) P'(\xi) \Delta t - \frac{\partial^2}{\partial t^2} u(x, \xi) \frac{(\Delta t)}{2} + \frac{\partial^2}{\partial x^2} (g(\xi) u(\xi, t_{k+1})) \frac{(\Delta x)}{2}
\]  

(4–23)
Multiplying by \( \Delta t \) on both sides we arrive at the following equation,

\[
\epsilon_j^{k+1} - \epsilon_j^k + \frac{\Delta t}{\Delta x} (g_j \epsilon_j^{k+1} - g_{j-1} \epsilon_{j-1}^{k+1}) + \Delta t \mu(x_j, N_k) \epsilon_j^{k+1} + \Delta t \gamma_j u(x_j, t_{k+1}) \eta^k + \Delta t \gamma_j \hat{P}_k \epsilon_j^{k+1}
\]

\( 4-26 \)

\[
= -u(x_j, t_{k+1}) N' (\xi) \frac{\partial \mu(x_j, \xi)}{\partial N} (\Delta t)^2 - \gamma(x_j) u(x_j, t_{k+1}) P'(\xi) (\Delta t)^2
\]

\( 4-27 \)

\[
c - \frac{\partial^2}{\partial t^2} u(x, \xi) \frac{(\Delta t)^2}{2} + \frac{\partial^2}{\partial x^2} (g(\xi) u(\xi, t_{k+1})) \frac{(\Delta x)(\Delta t)}{2}
\]

\( 4-28 \)

\[
\Delta t \mu(x_j, N_k) \epsilon_j^{k+1} + \Delta t \mu'(x_j, \xi) \rho^k u_j^{k+1} - \Delta t \gamma_j u(x_j, t_{k+1}) \eta^k + \mathcal{O}((\Delta t)^2)
\]

\( 4-29 \)

From the structure of the original model we have that the derivative of \( u \) along the characteristic lines is negative. Hence \( u(x, t) \) is bounded for all \( x \) and \( t \). This implies \( N(t) \) is also bounded, which is obtained by the integral of \( u(x, t) \).

Since \( u(x, t) \) is a positive function, the derivative of \( u(x, t) \) cannot be unbounded, since that will make \( u \) negative for some values of time \( t \). This leads to \( dN \) also bounded. We let \( \Delta x = \kappa \Delta t \), for some constant \( k \).

Solving for \( \epsilon_j^{k+1} \) leads to an equation of the form,

\[
m_j \epsilon_j^{k+1} = \epsilon_j^k + \frac{\Delta t}{\Delta x} g_{j-1} \epsilon_{j-1}^{k+1} - \Delta t \mu'(x_j, \xi) \rho^k u_j^{k+1} - \Delta t \gamma_j u(x_j, t_{k+1}) \eta^k + \mathcal{O}((\Delta t)^2)
\]

\( 4-30 \)

where we call \( m_j = 1 + g_j \frac{\Delta t}{\Delta x} + \Delta t \mu(x_j, N_k) + \Delta t \gamma_j \hat{P}_k \).

Note \( m_j \geq 0 \), hence taking absolute value on both sides we have the following form,

\[
m_j |\epsilon_j^{k+1}| \leq |\epsilon_j^k| + \frac{\Delta t}{\Delta x} g_{j-1} |\epsilon_{j-1}^{k+1}| + \Delta t |\mu'(x_j, \xi)||\rho^k| u_j^{k+1} - \Delta t \gamma_j u(x_j, t_{k+1}) |\eta^k| + \mathcal{O}((\Delta t)^2)
\]

\( 4-32 \)
From the behavior of the parameters we know that $\mu$ is bounded from below by $\mu$. Let $T$ be the maximum time and if $n$ is the number of steps in the numerical simulations we have,

$$m_j \geq 1 + g_j \frac{\Delta t}{\Delta x} + \Delta t \mu + \Delta t \gamma \hat{\rho}^k$$

This reduces (4–32) to the following form,

$$\begin{align*}
(1 + \Delta t(\mu))|\epsilon_j^{k+1}|\Delta x + \Delta t(g_j|\epsilon_j^{k+1} - g_{j-1}|\epsilon_{j-1}^{k+1}) & \\
\leq |\epsilon_j^k| + \frac{\Delta t}{\Delta x}g_{j-1}|\epsilon_{j-1}^{k+1}| + \Delta t|\mu'(x_j, \xi)||\rho^k|u_j^{k+1} + \\
\Delta t \gamma_j u(x_j, t_{k+1})|\eta^k| + \bigO((\Delta t)^2) & \quad (4–34)
\end{align*}$$

We note that $\gamma_j$ is a bounded function hence $\gamma_j \leq \tilde{\gamma}$. If $\mu'$ is unbounded, that implies the prey population dies at an infinite rate which will result in the extinction of the prey population at an exponential rate. Hence $\mu' \leq \bar{\mu}$ (constant). Summing over all $n$ we have,

$$\begin{align*}
(1 + \frac{T}{n\mu})||\epsilon^{k+1}|| + \Delta t(g_0|\epsilon_0^{k+1} - g_0|\epsilon_0^{k+1}) & \\
||\epsilon^k|| + C_1 \Delta t|\rho^k| + C_2 \Delta t|\eta^k| + \bigO((\Delta t)^2). & \quad (4–37)
\end{align*}$$

Solving for $||\epsilon^{k+1}||$ results in the following equation.

$$
||\epsilon^{k+1}|| \leq \frac{\Delta t}{(1 + \frac{T}{n\mu})}(g_0|\epsilon_0^{k+1} - g_0|\epsilon_0^{k+1}) + \\
\frac{1}{(1 + \frac{T}{n\mu})}((||\epsilon^k|| + C_1 \Delta t|\rho^k| + C_2 \Delta t|\eta^k|) + \bigO((\Delta t)^2)) & \quad (4–39)
$$

Now let us consider the boundary condition,

$$g_0 u(0, t) = \int_0^\infty \beta(x, N) u(x, t) dx$$

Writing the integral in discrete terms we have,
\[ g_0 u(0, t_{k+1}) = \sum_{j=1}^{n} \beta(x_j, N^{k+1}) u(x_j, t_{k+1}) \delta x \]  \hspace{1cm} (4-41)

The numerical scheme is given by

\[ g_0 \hat{u}_0^{k+1} = \sum_{j=1}^{n} \beta_j^{k+1} \hat{u}_j^k \Delta x \]  \hspace{1cm} (4-42)

Rewriting (4-41) and expressing the factors in terms of \( \beta_j^k \) we have the following structure,

\[
\beta(x_j, N^{k+1}) u(x_j, t_{k+1}) = \beta(x_j, N(t_k + \Delta t)) u(x_j, t_k + \Delta t) = [\beta(x_j, N(t_k)) + \beta'(x_j, N(t_k)) \Delta t N'() [u(x_j, t_k) + \Delta t u'(x_j, \xi)]]
\]

\[ = \beta(x_j, N(t_k)) u(x_j, t_k) + O(\Delta t) \]

Since \( \beta \) and \( \beta' \) are bounded functions.

\[ \sum_{j=1}^{n} \beta(x_j, N^{k+1}) u(x_j, t_k) \Delta x + O(\Delta t) = g_0 u(0, t_{k+1}) \]  \hspace{1cm} (4-43)

Taking the difference between (4-43) and (4-42) we have

\[ g_0 \epsilon_0^{k+1} = \sum_{j=1}^{n} \beta_j^{k+1} \epsilon_j^k \Delta x + O(\Delta t) \]  \hspace{1cm} (4-44)

Taking the absolute values on the above equation we have,

\[ g_0 |\epsilon_0^{k+1}| \leq \overline{\beta} \sum_{j=1}^{n} |\epsilon_j^k| \Delta x + O(\Delta t) = \overline{\beta} ||\epsilon^k|| + O(\Delta t) \]  \hspace{1cm} (4-45)

Substituting the above form in (4-39) we have
\[ ||e^{k+1}|| \leq \left( \frac{\Delta t}{1 + \frac{T_n}{\mu}} + \frac{1}{(1 + \frac{T_n}{\mu})} \right) ||e^{k}|| + C_1 \Delta t |\rho^k| + C_2 \Delta t |\eta^k| + (\Delta t)^2 \] (4–46)

Let's now focus on the predator equation,

\[ P' = P \int_0^\infty \alpha \gamma(x) u(x, t) dx - dP \]

We discretize the continuous equation to obtain

\[ P(t_k) = P(t_k + \Delta t) = P(t_k) + \Delta t P'(t_k) + \frac{(\Delta t)^2}{2} P''(\xi) \]

Using (4–47) version of the discrete form in the original equation we have,

\[ \frac{P(t_{k+1}) - P(t_k)}{\Delta t} - \frac{\Delta t}{2} P''(\xi) = P'(t_k) \] (4–47)

Hence we arrive at the following equation,

\[ \frac{P(t_{k+1}) - P(t_k)}{\Delta t} - \frac{\Delta t}{2} P''(\xi) = P(t_k) \alpha \sum_{j=1}^n \gamma(x_j) u(x_j, t_k) \Delta x - d(P(t_{k+1}) - \Delta t P'(\xi)) \] (4–49)

The numerical scheme corresponding to the above method is given by,
\[
\frac{\dot{P}_{k+1} - \dot{P}_k}{\Delta t} - \dot{P}_k \alpha \sum_{j=1}^{n} \gamma_j u_j^k + d \dot{P}_{k+1} = 0
\]  
(4–52)

We take the difference between (4–50) and (4–52) to obtain,

\[
\frac{\eta^k_{k+1} - \eta^k}{\Delta t} - \alpha \left( \sum_{j=1}^{n} \gamma_j \epsilon_j^k \Delta x \right) \dot{P}_k
\]  
(4–53)

\[-\alpha \sum_{j=1}^{n} \gamma_j u_j(x_j, t_k) \Delta x \eta^k + d \eta^k_{k+1}
\]  
(4–54)

\[=
\frac{\Delta t}{2} P''(\xi) + d \Delta t P'(\xi) + O(\Delta t)
\]  
(4–55)

We solve for \(\eta^k_{k+1}\),

\[(1 + d \Delta t)\eta^k_{k+1} - \eta^k + \alpha \left( \sum_{j=1}^{n} \gamma_j \epsilon_j^k \Delta x \right) \dot{P}_k
\]  
(4–56)

\[+ \alpha \sum_{j=1}^{n} \gamma_j u_j(x_j, t_k) \Delta x \eta^k \Delta t + O(\Delta t)
\]  
(4–57)

\[(1 + d \Delta t)\eta^k_{k+1} = \eta^k \left( 1 + \alpha \sum_{j=1}^{n} \gamma_j u_j(x_j, t_k) \Delta x \Delta t \right) +
\]  
(4–58)

\[\alpha \left( \sum_{j=1}^{n} \gamma_j \epsilon_j^k \Delta x \right) \dot{P}_k \Delta t + O((\Delta t)^2)
\]  
(4–59)

(4–60)

Taking the absolute value on both sides we have,

\[(1 + d \Delta t)\|\eta^k_{k+1}\| \leq \|\eta^k\| \left( 1 + \alpha \sum_{j=1}^{n} \gamma_j u_j(x_j, t_k) \Delta x \Delta t \right) +
\]  
(4–61)

\[\alpha \left( \sum_{j=1}^{n} \gamma_j |\epsilon_j^k| \Delta x \right) \dot{P}_k \Delta t + O((\Delta t)^2)
\]  
(4–62)

(4–63)

Since \(\dot{P}_k\) is bounded, \(\gamma_j \leq \gamma\) and \(\dot{P}_k \leq \dot{P}\),

59
\[ \alpha \sum_{j=1}^{N} \gamma_j u(x_j, t_k) \Delta x \leq \alpha \bar{\gamma} \hat{N}^k \leq \bar{N} \]

where \( \hat{N}^k \) is also bounded as proved before.

\[
\sum_{j=1}^{N} \gamma_j |\epsilon_j^k| \Delta x \leq \bar{\gamma} ||\epsilon^k||
\]

(4–64)

Therefore, \((1 + d\Delta t)||\eta^{k+1}|| \leq ||\eta^k|| + \Delta t \overline{P} \alpha \bar{\gamma} ||\epsilon^k|| + O(\Delta t)
\]

(4–65)

Hence, \(||\eta^{k+1}|| \leq \frac{1 + \overline{N}\Delta t}{1 + d\Delta t} ||\eta^k|| + \frac{\overline{P} \alpha \bar{\gamma} \Delta t}{1 + d\Delta t} ||\epsilon^k|| + O(\Delta t^2)\)

(4–66)

Note that,

\[
N(t_k) = \sum_{j=1}^{N} u(x_j, t_k) \Delta x
\]

(4–67)

\[
\hat{N}^k = \sum_{j=1}^{N} \hat{\epsilon}_j^k \Delta x
\]

(4–68)

\[
\Rightarrow \rho^k = \sum_{j=1}^{N} \epsilon_j^k \Delta x
\]

(4–69)

\[
\Rightarrow ||\rho^k|| \leq ||\epsilon^k||
\]

(4–70)

This shows that we only need to work with \( \epsilon^k \) and \( \eta^k \).

\[
||\epsilon^{k+1}|| + ||\eta^{k+1}|| \leq \left( \frac{\Delta t}{1 + \mu \Delta t} + \frac{1}{1 + \mu \Delta t} + C_1 \Delta t + \frac{\overline{P} \alpha \bar{\gamma} \Delta t}{1 + d\Delta t} \right) ||\epsilon^k||
\]

(4–71)

\[
+ \left( \frac{1 + \overline{N}\Delta t}{1 + d\Delta t} + C_2 \Delta t \right) ||\eta^k|| + O(\Delta t^2)
\]

(4–72)

(4–73)

(Since \(||\rho^k|| \leq ||\epsilon^k||\))

Note we can find \( C, d \) such that,
\[
\left( \frac{\Delta t}{1 + \mu \Delta t} + \frac{1}{1 + \mu \Delta t} + C_1 \Delta t + \frac{P_0 \alpha \gamma \Delta t}{1 + d \Delta t} \right) \leq \frac{1 + C \Delta t}{1 + d \Delta t}
\]

\[
||\epsilon^{k+1}|| + ||\eta^{k+1}|| \leq (1 + \frac{C \Delta t}{1 + d \Delta t})(||\eta^k|| + ||\epsilon^k||) + \mathcal{O}(\Delta t) \quad (4-74)
\]

\[
\leq (\mathcal{O}(\Delta t))(1 + p + p^2 + p^3 + \ldots + p^k) + p^{k+1}(||\epsilon^0|| + ||\eta^0||) \quad (4-75)
\]

\[
\leq \mathcal{O}(\Delta t) \left( \frac{p^k - 1}{p - 1} \right) + p^{k+1}(||\epsilon^0|| + ||\eta^0||) \quad (4-76)
\]

where \( p = \frac{1 + C \Delta t}{1 + d \Delta t} \).

Note that, using the initial conditions of the function we have,

\[
||\epsilon^0|| = \sum_{j=1}^{N} |\epsilon_j^0| \Delta x
\]

\[
= \sum_{j=1}^{N} |u(x_j, 0) - \hat{u}_j^0| \Delta x
\]

\[
= \sum_{j=1}^{N} |\phi(x_j) - \phi(x_j)| \Delta x
\]

\[= 0.\]

Similarly for the \( \eta \) function we have

\[
||\eta^0|| = |P^0 - \hat{P}^0| = |P_0 - P_0| = 0.
\]

This shows that,
\[
\|\epsilon^{k+1}\| + \|\eta^{k+1}\| \leq (4-79)
\]
\[
\bigcirc(\Delta t) \frac{p^k - 1}{p - 1} = \Delta t \leq \frac{T}{n} M \left( 1 + \frac{C}{1 + d T/N} \right)^k - 1 \leq \frac{T M}{|c - d| T} (1 + d T/N) (1 + \frac{|C - d| T}{N}) N \Delta t \leq \bar{C} \Delta t
\]

where \( \bigcirc(\Delta t) \leq M \), where \( \Delta t = T/n \)

Hence the convergence is of order \( \Delta t \).

\[\Box\]

4.3 Simulations using the Numerical Discretization

The finite difference method, defined above, can be used to simulate the PDE model. To find parameters that would produce oscillations, we let \( \lambda = \xi + wi \) and separate the real and imaginary part in (3–17). We let \( \xi = 0.001 \). We further assign values to some of the parameters. Thus, we assign \( \mu = 0.1, -F = 1, \) and \( A = 1 \). We also take \( \beta(x, N^*) = \bar{\beta} \chi(A, \infty) e^{-c N^*} \). For a given \( w \) the system for the real and the imaginary part becomes a linear system in \( \gamma P^* \), and \( d \gamma P^* \). We solve that linear system using Mathematica, and we obtain \( \gamma P^* = f_1(w) \) and \( d \gamma P^* = f_2(w) \) as functions of \( w \).

The parametric plot of these two functions in the \((\gamma P^*, d \gamma P^*)\) plane is given in Figure 4-1. For \( w = 3.96055 \) we obtain the following positive values for \( \gamma P^* = 0.35 \) and \( d \gamma P^* = 16.3689 \). That gives a value for \( d = 46.7682857 \). Using the equations for the equilibria, we determine that \( \bar{\beta} = 9.62023, c = 1, \) and \( \alpha = 23.2591 \). The parameter \( \gamma \) is determined so that predator's reproduction number is larger than one. In particular, we took, \( \gamma = 1 \). The resulting oscillations of the predator and the prey are presented in Figure 4-2.
Figure 4-1. Parametric plot in the \((\gamma P^*, d\gamma P^*)\).

Figure 4-2. The left figure shows the cycle in the \((N, P)\) plane with time as a parameter. The right figure shows the oscillations in the total number of prey and the predator as functions of time when those oscillations have stabilized.
In this article we introduce a non-linear predator-prey model where the prey is structured by size. The main question that we address is whether predation on a size-structured prey can be responsible for the sustained oscillations observed in the predator-prey dynamics in nature. We consider two main aspects:

1. We show that the presence of a predator which predates on a size-structured prey can destabilize an otherwise stable equilibrium of the prey, even if the predation of the predator is size non-specific.

2. We show that size-specific predation is capable of producing oscillations in the predator-prey dynamics. We find that can be the case by examining a scenario when the predator predates on the reproductive sizes of the prey only.

To address the main question we first examine the dynamics of the corresponding ODE model, where the prey is homogeneous with respect to size. We find that the ODE model has an extinction equilibrium, can potentially have multiple prey-only equilibria, and a unique predator-prey coexistence equilibrium. The coexistence equilibrium is locally asymptotically stable if the prey’s growth rate decreases with the increase of the prey population. If, however, prey growth rate exhibits Allee effect, then the predator-prey coexistence equilibrium can become destabilized and oscillations are possible. To rule out that this scenario is responsible for the oscillations in the size-structured model, we assume in most cases that the prey birth rate declines with the population size.

The size-structured model also has an extinction equilibrium and multiple prey-only equilibria. We could not rule out the possibility that multiple coexistence equilibria exist. To interpret conditions for existence of equilibria we define net reproduction rate of the prey population as a function of the prey population size \( R(N) \), and intrinsic reproduction number of the prey population \( R_0 \), defined as the value of the net reproduction rate when the prey population size is zero. We find that if \( R_0 > 1 \) there is always at least one prey-only equilibrium. If \( R_0 < 1 \) then there may be no
prey-only equilibria, or there may be an even number of prey-only equilibria, if they are all simple. Furthermore, we define predator reproduction at the $N_j^*$ prey-only equilibrium. Conditions on the predator reproduction number guarantee existence of a predator-prey coexistence equilibrium.

We find that the extinction equilibrium is locally stable if $R_0 < 1$ and unstable otherwise. The extinction equilibrium cannot be globally stable because of the presence of subthreshold equilibria. Furthermore, we find that the $j$th prey-only equilibrium $E_j$ is unstable if the reproduction number of the predator at the $j$th only equilibrium $R_{p,j} > 1$. Of the prey-only equilibria for which $R_{p,j} < 1$ holds, the ones for which the net reproduction rate of the prey satisfies $R'(N_j^*) > 0$ are also unstable. The key result on stability of prey-only equilibria says that if the death rate is size independent and increasing with prey population size, while the birth rate is decreasing with population but may depend on individuals' size in an arbitrary fashion, then the prey-only equilibrium is stable.

We investigated the stability of the coexistence equilibria in two cases. In the first case all rates are constant with respect to individuals' size, except the birth rate which may be arbitrary. For exponential in size birth rate we show that the coexistence equilibrium is locally asymptotically stable. However, if the predator predates uniformly on all sizes, but only mature individuals reproduce, then even if the prey's birth rate is decreasing with the prey's total population size, then the coexistence equilibrium may become unstable, and Hopf bifurcation occurs. We note that in these conditions, if all sizes of the prey reproduced uniformly, then oscillations would not have occurred. In the second case, all rates are constant with exception of the predation rate and prey birth rate. In this case we allow the predator to predate on individuals of reproductive size. We conclude that the predator-prey equilibrium can become unstable and oscillations are possible. Thus, the answer to our main question whether size-specific predation can destabilize the predator-prey dynamics is “yes”. The idea of size-specific predation
destabilizing the dynamics is somewhat paradoxal as size may permit size refuges for the prey from predation which may seem stabilizing. However, evolution of the prey to more advantageous sizes, not preyed on by the predator, happens on evolutionary scale which may be much slower than the time the predator needs to adapt to preying on different sizes. In a recent article Mougi and Iwasa [9] find that if the predator’s trait evolves faster than the prey’s, oscillations are possible and likely. In other words, size is only a temporary escape mechanism for the prey and as such may be responsible for the oscillatory dynamics [10].
REFERENCES


BIOGRAPHICAL SKETCH

Souvik Bhattacharya received his Bachelor of Science in mathematics from St. Xavier’s College, Kolkata (India) in 2003 and Master of Science in Mathematics from Indian Institute of Technology, Kanpur (India) in 2003. He joined the Department of Mathematics at University of Florida in August, 2006 to pursue a PhD in mathematics. He received his Ph.D from the University of Florida in the summer of 2011.