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HARVESTING OF A PREDATOR-PREY MODEL WITH TWO EFFORT FUNCTIONS AND HOLLING TYPE IV RESPONSE FUNCTION

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Abstract. This study presents a mathematical model describing a three-species interaction in a marine ecosystem, involving two prey populations distributed across protected and exploited zones and a single predator species. The model is grounded in the Holling type IV functional response and incorporates two dynamic fishing effort functions governed by their own evolution equations. Unlike traditional static-effort frameworks, our approach reflects adaptive economic behavior over time. We investigate system dynamics through equilibrium analysis, local and global stability assessment using Lyapunov techniques, and derive an optimal harvesting strategy using Pontryagin's Maximum Principle. Numerical simulations illustrate how spatial management and effort adaptation jointly influence sustainability outcomes, offering insights for marine resource governance under complex ecological and economic feedbacks.

Keywords: predator-prey system, equilibria, stability, functional response, optimal harvesting policy.

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1. INTRODUCTION

Understanding the interplay between predator and prey has long captivated ecologists and applied mathematicians alike. It's a relationship as intricate as it is foundational-serving as a

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blueprint for countless population models over the years. As ecological challenges have become more complex, so too have the mathematical frameworks developed to study them. In recent decades, researchers have refined these models to reflect the nuanced dynamics between interacting species [5, 10, 25], often incorporating important ecological elements such as species toxicity [8, 25], competition across species [22], and strategies for sustainable harvesting [3]. These enhancements not only add biological realism but also offer valuable tools for managing living resources effectively.

One recurrent finding across ecological studies is that species-particularly prey-can undergo explosive growth when unchecked. While this might sound beneficial at first glance, it can quickly spiral into overpopulation or collapse, especially in ecosystems under human pressure. To mitigate such outcomes, marine policymakers have increasingly turned to spatial zoning: the division of ecosystems into fishing zones and no-take reserves. These protected areas function as ecological ”safe havens,” enabling juvenile organisms to mature and later repopulate exploited waters. In practice, this approach aims to balance ecological health with economic viability, but achieving that balance remains a persistent challenge. Adaptive management strategies, especially those that adjust fishing intensity in response to biological conditions, are therefore essential.

Within this context, we treat the fishing efforts E_1 and E_2 as time-dependent variables rather than fixed parameters. This reflects a more realistic approach where effort fluctuates based on profitability, resource availability, and management rules. As proposed in [12], these efforts are governed by their own differential equations, allowing the model to account for real-time feedback loops between ecological and economic forces.

Given these intricacies, our objective in this paper is to explore how interspecies competition and toxic effects [8, 19] shape predator-prey interactions when combined with dynamic harvesting policies. By modeling fishing effort as a function of system state, we open the door to more flexible and adaptive management strategies-ones that better align with the complex realities faced by fisheries managers.

Our work builds on the classical predator-prey frameworks established by Verhulst, Lotka, and Volterra [23, 16, 24], but introduces several important innovations. Among them is the inclusion of two distinct prey populations occupying reserved and unreserved zones, along with a predator species subject to a Holling type IV response. This functional form captures saturation and switching behavior more accurately than its simpler counterparts and is particularly relevant in systems where prey availability varies spatially.

The analysis that follows covers both the theoretical and applied aspects of the model. We explore equilibrium behavior, assess local and global stability using Lyapunov techniques, and derive optimal harvesting policies using Pontryagin's Maximum Principle. To validate our findings, we complement the theoretical work with simulations that illustrate how zoning and adaptive effort shape long-term ecological and economic outcomes. In doing so, we aim to contribute not just to the theory of bioeconomic modeling, but also to the practical toolkit available for sustainable fisheries governance.

2. The Mathematical Model

Based on the assumptions outlined earlier, the dynamics of the system are modeled by the following set of ordinary differential equations:

$$
\begin{cases}
\dfrac{dx}{dt} = r_1 x\left(1-\dfrac{x}{k}\right) - \sigma_1 x + \sigma_2 y - ux^2 - \dfrac{axz}{b+x^2} - q_1 E_1 x, \\
\dfrac{dy}{dt} = (r_2-\sigma_2)y + \sigma_1 x - \nu y^2, \\
\dfrac{dz}{dt} = \beta\dfrac{axz}{b+x^2} - dz - wz - q_2 E_2 z, \\
\dfrac{dE_1}{dt} = \lambda_1(q_1 x(m_1-\tau_1) - c_1)E_1, \\
\dfrac{dE_2}{dt} = \lambda_2(q_2 z(m_2-\tau_2) - c_2)E_2.
\end{cases}
\tag{1}
$$

The interpretation and values of the model parameters are summarized in Tables 1 and 2.

TABLE 1. Interpretation of the parameters

Parameter	Description
x	Biomass density of prey in the unreserved area
y	Biomass density of prey in the reserved area
z	Biomass density of the predator species
E_1	Harvesting effort applied in the unreserved area
E_2	Harvesting effort applied to the predator species
r_1, r_2	Intrinsic growth rates in the unreserved and reserved areas, respectively
q_1, q_2	Catchability coefficients for the prey and predator populations
σ_1, σ_2	Migration rates between reserved and unreserved zones
m_1, m_2	Selling prices per unit biomass for prey and predator
c_1, c_2	Costs per unit effort for harvesting prey and predator

TABLE 2. Interpretation of the parameters

Parameter	Description
τ_1, τ_2	Imposed taxes per unit harvested for prey and predator
λ_1, λ_2	Capital conversion coefficients
ux^2, νy^2	Toxicity-induced reduction terms in unreserved and reserved zones, respectively
wz	Reduction term for predator biomass
d	Natural death rate of the predator species
β	Conversion efficiency of predator from prey consumption
$\frac{axz}{b+x^2}$	Holling type IV functional response

3. System Solution Boundedness

In this section, we establish that the solutions of the proposed model are non-negative and bounded.

Lemma 1. *The set*

$$\Omega=\left\{(x,y,z)\in\mathbb{R}^3_+ :\ x+y+\frac{1}{\beta}z\le \frac{H}{d+w+(1-\beta)q_2E_2}+\frac{E_1}{\lambda_1(m_1-\tau_1)}+\frac{E_2}{\lambda_2(m_2-\tau_2)}\right\}$$

is an attracting region for solutions originating in the positive octant, where

$$H=\frac{k\left(r_1+d+w+(1-\beta)q_2E_2\right)^2}{4(r_1+u)}+\frac{k\left(r_2+d+w+(1-\beta)q_2E_2\right)^2}{4\nu}.$$

Proof. Define the function

$$Y(t)=x(t)+y(t)+\frac{1}{\beta}z(t)+\frac{E_1}{\lambda_1(m_1-\tau_1)}+\frac{E_2}{\lambda_2(m_2-\tau_2)}.$$

Differentiating and simplifying yields:

$$\begin{aligned}\frac{dY}{dt}+(d+w+(1-\beta)q_2E_2)Y(t)&=x\left(r_1+d+w+(1-\beta)q_2E_2\right)-x^2\left(\frac{r_1}{k}+u\right)\\&\quad+y\left(r_2+d+w+(1-\beta)q_2E_2\right)-\nu y^2\\&\quad+\left(d+w+(1-\beta)q_2E_2-\lambda_1c_1\right)\frac{E_1}{m_1-\tau_1}\\&\quad+\left(d+w+(1-\beta)q_2E_2-\lambda_2c_2\right)\frac{E_2}{m_2-\tau_2}.\end{aligned}$$

Applying the inequality

$$ax-bx^2\le\frac{a^2}{4b},\quad \text{for } a,b>0,$$

we obtain:

$$\frac{dY}{dt}+(d+w+(1-\beta)q_2E_2)Y(t)\le H.$$

By the differential inequality theorem [17], we conclude:

$$Y(t)\le\frac{H}{d+w+(1-\beta)q_2E_2}-\left(\frac{H}{d+w+(1-\beta)q_2E_2}-Y(0)\right)e^{-(d+w+(1-\beta)q_2E_2)t}.$$

Taking the limit as $t\to\infty$, we obtain:

$$0<Y(t)<\frac{H}{d+w+(1-\beta)q_2E_2},$$

which proves the lemma. □

4. Existence of Equilibria

Equilibrium points of the system 1 are found by setting the right-hand side of each differential equation to zero. The model admits six equilibrium points, one of which is the trivial equilibrium

$$P_0 = (0,0,0,0,0).$$

We now demonstrate the existence of five additional positive equilibria.

4.1 $P_1(x,y,0,0,0)$**.** To find P_1, we solve the following reduced system:

$$\begin{cases} r_1 x\left(1-\frac{x}{k}\right) - \sigma_1 x + \sigma_2 y - u x^2 = 0, \\ (r_2-\sigma_2)y + \sigma_1 x - \nu y^2 = 0. \end{cases} \tag{2}$$

Solving the first equation of system (2) for y yields:

$$y = \frac{1}{\sigma_2}\left(\frac{r_1}{k}+u\right)x^2 - \frac{r_1-\sigma_1}{\sigma_2}x. \tag{3}$$

Substituting (3) into the second equation of (2) results in a cubic equation of the form:

$$a_3 x^3 + a_2 x^2 + a_1 x + a_0 = 0, \tag{4}$$

where the coefficients are:

$$\begin{aligned} a_3 &= -\frac{\nu}{\sigma_2^2}\left(\frac{r_1}{k}+u\right)^2, \\ a_2 &= \frac{2\nu}{\sigma_2^2}\left(\frac{r_1}{k}+u\right)(r_1-\sigma_1), \\ a_1 &= \frac{\nu}{\sigma_2^2}(r_2-\sigma_2)(r_1-\sigma_1)^2 + \frac{\sigma_1}{\sigma_2}, \\ a_0 &= \sigma_1 - (r_2-\sigma_2)\frac{r_1-\sigma_1}{\sigma_2}. \end{aligned}$$

Since $a_3 < 0$, Descartes' Rule of Signs implies the possibility of a unique positive solution $x = x^*$. For the existence of such a solution, the following inequalities must be satisfied:

$$\begin{aligned} a_2 > 0 &\iff \left(\frac{r_1}{k}+u\right)(r_1-\sigma_1) > 0, \\ a_1 > 0 &\iff \sigma_2\left(\frac{r_1}{k}+u\right)(r_2-\sigma_2) > (r_1-\sigma_1)^2\nu, \\ a_0 > 0 &\iff (r_2-\sigma_2)(r_1-\sigma_1) < \sigma_1\sigma_2. \end{aligned}$$

Once x^* is determined, the corresponding y^* value can be computed using equation (3). For $y^* > 0$, we require:

$$x^* > \frac{(r_1 - \sigma_1)k}{r_1 + ku}. \tag{5}$$

4.2 $P_2(x, y, z, 0, 0)$**.** To find the equilibrium point P_2, we seek positive values x^*, y^*, z^* under the condition $E_1 = E_2 = 0$. Substituting these into the system 1, we analyze each equation accordingly.

From the predator equation:

$$\frac{dz}{dt} = 0 \quad \Rightarrow \quad \frac{axz}{b + x^2} - (d + w)z = 0.$$

Solving for x^*, we derive a quadratic equation:

$$(d + w)x^2 - \beta ax + (d + w)b = 0.$$

The roots of this equation are:

$$x_1^* = \frac{\beta a + \sqrt{(\beta a)^2 - 4(d + w)^2 b}}{2(d + w)},$$
$$x_2^* = \frac{\beta a - \sqrt{(\beta a)^2 - 4(d + w)^2 b}}{2(d + w)}.$$

Next, we compute y^* using the prey-in-reserve equation:

$$\frac{dy}{dt} = 0 \quad \Rightarrow \quad (r_2 - \sigma_2)y + \sigma_1 x - \nu y^2 = 0.$$

Solving for y^* with $x = x_i^*$, we get:

$$y_1^* = \frac{(r_2 - \sigma_2) + \sqrt{(r_2 - \sigma_2)^2 + 4\nu\sigma_1 x_1^*}}{2\nu} > 0,$$
$$y_2^* = \frac{(r_2 - \sigma_2) + \sqrt{(r_2 - \sigma_2)^2 + 4\nu\sigma_1 x_2^*}}{2\nu} > 0.$$

Finally, we determine z^* from the unreserved prey equation:

$$\frac{dx}{dt} = 0 \quad \Rightarrow \quad z_i^* = \frac{b + (x_i^*)^2}{a x_i^*}\left[(r_1 - \sigma_1)x_i^* - \left(\frac{r_1}{k} + u\right)(x_i^*)^2 + \sigma_2 y_i^*\right], \quad i = 1, 2.$$

To ensure $z_i^* > 0$, the following inequality must be satisfied:

$$0 < x_i^* < \frac{(r_1 - \sigma_1) + \sqrt{(r_1 - \sigma_1)^2 + \frac{4\sigma_2\left(\frac{r_1}{k} + u\right)y_i^*}{k}}}{2\left(\frac{r_1}{k} + u\right)}.$$

4.3 $P_3(x,y,0,E_1,0)$**.** To find the equilibrium point P_3, we begin by solving the fourth equation of system 1 under the condition $\frac{dE_1}{dt}=0$:

$$\lambda_1\left(q_1x^*(m_1-\tau_1)-c_1\right)E_1=0.$$

Assuming $E_1>0$, we obtain:

$$x^*=\frac{c_1}{q_1(m_1-\tau_1)}. \tag{6}$$

Next, to compute y^*, we consider the equation for $\frac{dy}{dt}=0$:

$$(r_2-\sigma_2)y+\sigma_1x-\nu y^2=0.$$

Substituting x^* from (6), we solve the resulting quadratic in y:

$$y^*=\frac{(r_2-\sigma_2)+\sqrt{(r_2-\sigma_2)^2+4\nu\sigma_1x^*}}{2\nu}.$$

Finally, substituting into the first equation of the system, $\frac{dx}{dt}=0$, we solve for E_1^*:

$$r_1x^*\left(1-\frac{x^*}{k}\right)-\sigma_1x^*+\sigma_2y^*-u(x^*)^2-\frac{ax^*z}{b+(x^*)^2}-q_1E_1^*x^*=0,$$

yielding:

$$E_1^*=\frac{(r_1-\sigma_1)x^*-\left(\frac{r_1}{k}+u\right)(x^*)^2+\sigma_2y^*}{q_1x^*}. \tag{7}$$

To ensure $E_1^*>0$, the following inequality must be satisfied:

$$(r_1-\sigma_1)x^*-\left(\frac{r_1}{k}+u\right)(x^*)^2+\sigma_2y^*>0, \tag{8}$$

which implies:

$$\sigma_2y^*>\frac{c_1}{q_1(m_1-\tau_1)}\left((r_1-\sigma_1)-\left(\frac{r_1}{k}+u\right)\frac{c_1}{q_1(m_1-\tau_1)}\right). \tag{9}$$

4.4 $P_4(x,y,z,0,E_2)$**.** To find the equilibrium point P_4, we begin by setting the fifth equation in the system to zero:

$$\frac{dE_2}{dt}=0 \quad\Rightarrow\quad \lambda_2(q_2z^*(m_2-\tau_2)-c_2)E_2=0.$$

Assuming $E_2>0$, we obtain:

$$z^*=\frac{c_2}{q_2(m_2-\tau_2)}. \tag{10}$$

The pair (x^*, y^*) must satisfy the following system:

$$\begin{cases} r_1 x^* \left(1 - \frac{x^*}{k}\right) - \sigma_1 x^* + \sigma_2 y^* - u(x^*)^2 - \frac{a x^* z^*}{b + (x^*)^2} = 0, \\ (r_2 - \sigma_2) y^* + \sigma_1 x^* - \nu (y^*)^2 = 0. \end{cases} \tag{11}$$

Solving the first equation in (11) for y^*, we get:

$$y^* = \frac{1}{\sigma_2}\left(\frac{a x^* z^*}{b + (x^*)^2} + \left(\frac{r_1}{k} + u\right)(x^*)^2 - (r_1 - \sigma_1) x^*\right).$$

Substituting this into the second equation of (11) yields a seventh-degree polynomial in x^*:

$$a_7 x^7 + a_6 x^6 + a_5 x^5 + a_4 x^4 + a_3 x^3 + a_2 x^2 + a_1 x + a_0 = 0, \tag{12}$$

with coefficients:

$$a_7 = -\frac{d^2 \nu}{\sigma_2^2}, \quad a_6 = \frac{2 d \nu c}{\sigma_2^2}, \quad a_5 = -\frac{2 d^2 \nu b}{\sigma_2^2} - \frac{\nu c^2}{\sigma_2^2} + \frac{ed}{\sigma_2},$$

$$a_4 = \frac{4 dbc\nu}{\sigma_2^2} + \frac{2adz\nu}{\sigma_2^2} - \frac{ec}{\sigma_2} + \sigma_1,$$

$$a_3 = \frac{\nu d^2 b^2}{\sigma_2^2} - \frac{2\nu c^2 b}{\sigma_2^2} - \frac{2azbc\nu}{\sigma_2^2} + \frac{2ebd}{\sigma_2},$$

$$a_2 = \frac{2dcb^2 \nu}{\sigma_2^2} + \frac{2adzb\nu}{\sigma_2^2} - \frac{2ecb}{\sigma_2} - \frac{aze}{\sigma_2} + 2b\sigma_1,$$

$$a_1 = \frac{\nu c^2 b^2}{\sigma_2^2} - \frac{2acbz\nu}{\sigma_2^2} + \frac{edb^2}{\sigma_2} - \nu a^2 z^2,$$

$$a_0 = -\frac{ecb^2}{\sigma_2} + \frac{azbe}{\sigma_2} + \sigma_1 b^2.$$

Since $(a_7 < 0)$, for uniqueness and positivity of a solution, all coefficients must be positive.

To ensure $(y^* > 0)$, we require:

$$[z > \frac{(r_1 - \sigma_1)}{a} b.]$$

4.5 $P_5(x, y, z, E_1, E_2)$**.** To find the full positive equilibrium (P_5), we solve system with all components non-zero. From the fourth and fifth equations:

$$[x = \frac{c_1}{q_1(m_1 - \tau_1)}, z = \frac{c_2}{q_2(m_2 - \tau_2)}.]$$

Substituting (x) into the second equation yields:

$$[y = \frac{(r_2-\sigma_2)+\sqrt{(r_2-\sigma_2)^2+4\nu\sigma_1 x}}{2\nu}.]$$

We then compute (E_1) and (E_2) using:

$$E_1 = \frac{1}{q_1 x}\left(r_1 x\left(1-\frac{x}{k}\right)-\sigma_1 x+\sigma_2 y-ux^2-\frac{axz}{b+x^2}\right) > 0,$$
$$E_2 = \frac{1}{q_2}\left(\frac{\beta ax}{b+x^2}-d-w\right) > 0.$$

5. Dynamic Behavior of Equilibria

5.1 Local Stability of Equilibria. The goal in this section is to study the local stability of all equilibrium points by finding the eigenvalues of the Jacobian matrix $J(x,y,z,E_1,E_2)$.

The Jacobian matrix is:

$$J(x,y,z,E_1,E_2) = \begin{pmatrix} J_{11} & J_{12} & J_{13} & J_{14} & 0 \\ J_{21} & J_{22} & 0 & 0 & 0 \\ J_{31} & 0 & J_{33} & J_{34} & J_{35} \\ J_{41} & 0 & 0 & J_{44} & 0 \\ 0 & 0 & J_{53} & 0 & J_{55} \end{pmatrix}$$

$$J_{11} = r_1-\sigma_1-q_1E_1-\left(\frac{2r_1}{k}+2u\right)x-\frac{az(b-x^2)}{(b+x^2)^2}, \quad J_{12} = \sigma_2,$$

$$J_{13} = -\frac{ax}{b+x^2}, \qquad J_{14} = -q_1 x, \quad J_{15} = 0,$$

$$J_{21} = \sigma_1, \qquad J_{22} = r_2-\sigma_2-2\nu y,$$

$$J_{23} = 0, \qquad J_{24} = 0, \quad J_{25} = 0,$$

$$J_{31} = \frac{\beta az(b-x^2)}{(b+x^2)^2}, \qquad J_{32} = 0,$$

$$J_{33} = \frac{\beta ax}{b+x^2}-d-w, \qquad J_{34} = 0, \quad J_{35} = -q_2 z,$$

$$J_{41} = \lambda_1 E_1 q_1(m_1-\tau_1), \qquad J_{42} = 0,$$

$$J_{43} = 0, \qquad J_{44} = \lambda_1(q_1 x(m_1-\tau_1)-c_1), \quad J_{45} = 0,$$

$$J_{51} = 0, \qquad J_{52} = 0,$$

$J_{53} = \lambda_2 E_2 q_2 (m_2 - \tau_2),$ $\quad J_{54} = 0, \quad J_{55} = \lambda_2 (q_2 z (m_2 - \tau_2) - c_2).$

Theorem 5.1.1. The equilibrium point $P_0(0,0,0,0,0)$ of system (1) is unstable.

Proof. Consider the characteristic equation at the equilibrium $P_0(0,0,0,0,0)$:

$$(13)\quad (-\lambda_1 c_1 - \lambda)(-\lambda_2 c_2 - \lambda)(-d - w - \lambda) \times \left(\lambda^2 - \lambda(r_1 - \sigma_1 + r_2 - \sigma_2) + (r_1 - \sigma_1)(r_2 - \sigma_2) - \sigma_1 \sigma_2\right) = 0.$$

The eigenvalues are:

$$X_1 = -(d + w) < 0,$$

$$X_2 = -\lambda_1 c_1 < 0,$$

$$X_3 = -\lambda_2 c_2 < 0.$$

Let X_4 and X_5 be the remaining two eigenvalues. Their sum is:

$$X_4 + X_5 = r_1 - \sigma_1 + r_2 - \sigma_2 > 0,$$

which implies at least one of them is positive. Therefore, the equilibrium $P_0(0,0,0,0,0)$ is unstable. □

Theorem 5.1.2. The equilibrium point $P_1(x, y, 0, 0, 0)$ of system (1) is locally asymptotically stable.

Proof. Consider the characteristic equation at the equilibrium $P_1(x, y, 0, 0, 0)$:

$$(14)\quad (-\lambda_2 c_2 - X_1)\left[\lambda_1 (q_1 x (m_1 - \tau_1) - c_1 - X_2)\right]\left(\frac{\beta a x}{b + x^2} - d - w - X_3\right) \times \left[\left(r_1 - \sigma_1 - \left(\frac{2r_1}{k} + 2u\right)x - X_4\right)(r_2 - \sigma_2 - 2\nu y - X_5) - \sigma_1 \sigma_2\right] = 0.$$

The eigenvalues are:

$$X_1 = -\lambda_2 c_2 < 0,$$

$$X_2 = \lambda_1 \left(q_1 x (m_1 - \tau_1) - c_1\right) < 0, \quad \text{if} \quad x < \frac{c_1}{q_1 (m_1 - \tau_1)},$$

$$X_3 = \frac{\beta a x}{b+x^2} - d - w < 0, \quad \text{if} \quad x \notin [x_1^*, x_2^*].$$

Let X_4 and X_5 be the remaining two eigenvalues, which are solutions to the quadratic equation:

$$X^2 - nX + m = 0, \tag{15}$$

where:

$$n = \left(r_1 - \sigma_1 - \left(\frac{2r_1}{k} + 2u\right)x\right) + (r_2 - \sigma_2 - 2\nu y),$$

$$m = \left(r_1 - \sigma_1 - \left(\frac{2r_1}{k} + 2u\right)x\right)(r_2 - \sigma_2 - 2\nu y) - \sigma_1\sigma_2.$$

Since $X_4 + X_5 < 0$ and $X_4 X_5 > 0$, it follows that:

$$X_4, X_5 < 0.$$

Therefore, the equilibrium $P_1(x,y,0,0,0)$ is locally asymptotically stable. □

Theorem 5.1.3. The equilibrium point $P_2(x,y,z,0,0)$ of system (1) is locally asymptotically stable.

Proof. Consider the characteristic equation at the equilibrium $P_2(x,y,z,0,0)$:

(16)

$$(X - (q_2 z(m_2 - \tau_2) - c_2) - \lambda)(X - (q_1 x(m_1 - \tau_1) - c_1) - \lambda)\left(X^3 + d_2 X^2 + d_1 X + d_0\right) = 0,$$

where:

$$X = q_1 x(m_1 - \tau_1) - c_1 < 0, \quad \text{if} \quad x < \frac{c_1}{q_1(m_1 - \tau_1)},$$

$$X = q_2 z(m_2 - \tau_2) < 0, \quad \text{if} \quad z < \frac{c_2}{q_2(m_2 - \tau_2)}.$$

The coefficients d_2, d_1, d_0 are given by:

$$d_2 = -(r_1 - \sigma_1 - (\frac{2r_1}{k} + 2u)x - \frac{az(b-x^2)}{(b+x^2)^2}) + (r_2 - \sigma_2) - 2\nu y + \frac{\beta a x}{b+x^2} - d - w,$$

$$d_1 = r_1 - \sigma_1 - q_1 E_1 - (\frac{2r_1}{k} + 2u)x - \frac{az(b-x^2)}{(b+x^2)^2} + \frac{\beta a x}{b+x^2} - d - w + (r_2 - \sigma_2) - 2\nu y$$
$$+ r_1 - \sigma_1 - q_1 E_1 - (\frac{2r_1}{k} + 2u)x - az(b-x^2)(r_2 - \sigma_2) - 2\nu y - \sigma_2\sigma_1$$

$$-\frac{\beta az(b-x^2)}{(b+x^2)^2}-\frac{ax}{b+x^2},$$

$$d_0=-\left((\frac{\beta ax}{b+x^2}-d-w)(r_1-\sigma_1-q_1E_1-(\frac{2r_1}{k}+2u)x-\frac{az(b-x^2)}{(b+x^2)^2})((r_2-\sigma_2)-2\nu y)\right)$$
$$+\left((\frac{\beta ax}{b+x^2}-d-w)\sigma_2\sigma_1\right)+\left(\frac{\beta az(b-x^2)}{(b+x^2)^2}\left(-\frac{ax}{b+x^2}\right)((r_2-\sigma_2)-2\nu y)\right).$$

Using the Horowitz criteria, the equilibrium $P_2(x,y,z,0,0)$ is locally asymptotically stable if:

$$x<\frac{c_1}{q_1(m_1-\tau_1)},\quad z<\frac{c_2}{q_2(m_2-\tau_2)},\quad d_0,d_1,d_2>0,\quad \text{and}\quad d_2d_1-d_0>0.$$

This completes the proof. □

Theorem 5.2.3. The equilibrium point $P_3(x,y,0,E_1,0)$ of system (1) is locally asymptotically stable.

Proof. Consider the characteristic equation at the equilibrium $P_3(x,y,0,E_1,0)$:

$$\lambda_1q_1^2(m_1-\tau_1)E_1x(-\lambda_2c_2-\lambda)$$
$$\left[\lambda^2-\lambda\left(\frac{\beta ax}{b+x^2}-d-w+r_2-\sigma_2-2\nu y\right)+\frac{\beta ax}{b+x^2}-d-w+r_2-\sigma_2-2\nu y\right]=0$$

From this characteristic equation, we immediately have one eigenvalue:

$$X_1=-\lambda_2c_2<0, \tag{17}$$

which suggests local asymptotic stability at P_3.

Let X_2 and X_3 be the remaining two eigenvalues, which are solutions to the quadratic equation:

$$\lambda^2-\lambda\left(\frac{\beta ax}{b+x^2}-d-w+r_2-\sigma_2-2\nu y\right)+\frac{\beta ax}{b+x^2}-d-w+r_2-\sigma_2-2\nu y=0. \tag{18}$$

We note that:

$$X_2+X_3<0,$$

$$X_2\cdot X_3>0.$$

Consequently, it follows that:

$$X_2<0\quad\text{and}\quad X_3<0.$$

Hence, all eigenvalues have negative real parts, confirming local asymptotic stability. □

Theorem 5.2.4. The equilibrium point $P_4(x,y,z,0,E_2)$ of system (1) is locally asymptotically stable.

Proof. Consider the characteristic equation at the equilibrium $P_4(x,y,z,0,E_2)$:

$$(A-\lambda)(-\lambda^3+\Phi_1\lambda^2++\Phi_2\lambda+\Phi_3)=0 \tag{19}$$

Where: $\Phi_1 = B+C+a+E-b$, $\Phi_2 = -Bc+(B+c)(a+E)-b(D+c)-c$, $\Phi_3 = aBc+EBc-bDc-cB$, $a = J_{41}J_{14}$, $b = J_{31}J_{13}$, $c = J_{12}J_{21}$, $B = J_{33}$
$C = J_{22}$, $D = J_{44}$, $E = J_{11}$

From this characteristic equation, we immediately have one eigenvalue:

$$X_1 = A = J_{55} = \lambda_2(q_2z(m_2-\tau_2)-c_2) < 0, \tag{20}$$

which suggests local asymptotic stability at P_4 if $z < \frac{c_2}{q_2(m_2-\tau_2)}$

For the remaining two eigenvalues, which are solutions to the equation:

$$\lambda^3+(-\Phi_1)\lambda^2+(-\Phi_2)\lambda+(-\Phi_3)=0 \tag{21}$$

Since: $\Phi_1,\Phi_2,\Phi_3 > 0$, we have local asymptotic stability at P_4 whenever: $\Phi_1\Phi_2+\Phi_3 > 0$ using the the Horowitz criteria. □

Theorem 5.2.5. The equilibrium point $P_5(x,y,z,E_1E_2)$ of system (1) is locally asymptotically stable.

Proof. Consider the characteristic equation at the equilibrium $P_5(x,y,z,E_1E_2)$:

$$\lambda^4-\Phi_1\lambda^3+\Phi_2\lambda^2+\Phi_3\lambda+\Phi_4=0 \tag{22}$$

Where: $\Phi_1 = E+B+F+G+e$, $\Phi_2 = -a-b+EB+FG-c+eB+eE+Cd$, $\Phi_3 = aB+aC+bD+bD-EFG-BFG-EBF-EBG+cF+cG-ad-eBE+eDB+eDE-ce$
$\Phi_4 = CeG+ADb-Cfg+Ebed-aBC-bBD$
Where: $a = J_{14}J_{41}$, $B = J_{22}$, $C = J_{55}$, $b = J_{13}J_{31}$, $D = J_{44}$, $E = J_{11}$, $F = J_{33}$, $G = J_{44}$
$c = J_{12}J_{21}$,$d = J_{35}J_{53}$, $e = J_{35}$.
Using the Horowitz criteria we have local asymptotic stability at P_5 whenever: $\Phi_1 < 0$, $\phi_1\Phi_2+\Phi_3 < 0$, $\Phi_4 > 0$, and -$\Phi_1\Phi_2-\Phi_3+\Phi_1^2\Phi_4 > 0$ □

5.2 Global Stability of Equilibria. We consider the following Lyapunov function:

$$\begin{aligned} V(x,y,z,E_1,E_2) = &\left(x - x^* - \ln\left(\frac{x}{x^*}\right)\right) + l_1\left(y - y^* - \ln\left(\frac{y}{y^*}\right)\right) \\ &+ l_2\left(z - z^* - \ln\left(\frac{z}{z^*}\right)\right) + l_3\left(E_1 - E_1^* - \ln\left(\frac{E_1}{E_1^*}\right)\right) \\ &+ l_4\left(E_2 - E_2^* - \ln\left(\frac{E_2}{E_2^*}\right)\right). \end{aligned}$$

Theorem 5.2.1. The equilibrium point $P(x^*, y^*, 0, 0, 0)$ *of system (1) is globally asymptotically stable.*

Proof. Set $z = E_1 = E_2 = 0$. The Lyapunov function simplifies to:

$$V(x,y) = \left(x - x^* - \ln\left(\frac{x}{x^*}\right)\right) + l_1\left(y - y^* - \ln\left(\frac{y}{y^*}\right)\right).$$

Differentiating V along the trajectories of the system:

$$\frac{dV}{dt} = \left(1 - \frac{x^*}{x}\right)\frac{dx}{dt} + l_1\left(1 - \frac{y^*}{y}\right)\frac{dy}{dt}.$$

From the reduced system (with $z = E_1 = E_2 = 0$), we have:

$$\begin{aligned} \frac{dx}{dt} &= r_1 x\left(1 - \frac{x}{k}\right) - \sigma_1 x + \sigma_2 y - u x^2, \\ \frac{dy}{dt} &= (r_2 - \sigma_2) y + \sigma_1 x - \nu y^2. \end{aligned} \tag{23}$$

At equilibrium:

$$\begin{aligned} r_1 x^*\left(1 - \frac{x^*}{k}\right) - \sigma_1 x^* + \sigma_2 y^* - u(x^*)^2 = 0, \\ (r_2 - \sigma_2) y^* + \sigma_1 x^* - \nu (y^*)^2 = 0. \end{aligned} \tag{24}$$

Choosing:

$$l_1 = \frac{\sigma_2 y^*}{\sigma_1 x^*},$$

we obtain:

$$\frac{dV}{dt} = -\left(\frac{r_1}{k} + u\right)(x - x^*)^2 - \nu \cdot \frac{\sigma_2 y^*}{\sigma_1 x^*}(y - y^*)^2 - \frac{\sigma_2}{x x^* y}(x^* y - x y^*)^2.$$

Each term is non-positive and vanishes only at $x = x^*, y = y^*$. Therefore:

$$\frac{dV}{dt} < 0 \quad \text{for all} \quad (x,y) \neq (x^*, y^*),$$

and by Lyapunov's direct method, the equilibrium $P(x^*, y^*, 0, 0, 0)$ is globally asymptotically stable. □

Theorem 5.2.2. The equilibrium point $P(x^*, y^*, z^*, 0, 0)$ *of system (1) is globally asymptotically stable.*

Proof. Set $E_1 = E_2 = 0$. The Lyapunov function simplifies to:

$$V(x,y) = \left(x - x^* - \ln\left(\frac{x}{x^*}\right)\right) + l_1\left(y - y^* - \ln\left(\frac{y}{y^*}\right)\right) + l_2\left(z - z^* - \ln\left(\frac{z}{z^*}\right)\right)$$

Differentiating V along the trajectories of the system:

$$\frac{dV}{dt} = \left(1 - \frac{x^*}{x}\right)\frac{dx}{dt} + l_1\left(1 - \frac{y^*}{y}\right)\frac{dy}{dt} + l_2\left(1 - \frac{z^*}{z}\right)\frac{dz}{dt}$$

From the reduced system (with $E_1 = E_2 = 0$), we have:

$$\begin{aligned} \frac{dx}{dt} &= r_1 x\left(1 - \frac{x}{k}\right) - \sigma_1 x + \sigma_2 y - ux^2, \\ \frac{dy}{dt} &= (r_2 - \sigma_2)y + \sigma_1 x - \nu y^2. \\ \frac{dz}{dt} &= \beta\frac{axz}{b + x^2} - dz - wz, \end{aligned} \tag{25}$$

At equilibrium:

$$\begin{aligned} r_1 x^*\left(1 - \frac{x^*}{k}\right) - \sigma_1 x^* + \sigma_2 y^* - ux^2 - \frac{ax^*z^*}{b + x^{*2}} &= 0, \\ (r_2 - \sigma_2)y^* + \sigma_1 x^* - \nu y^{*2} &= 0, \\ \beta\frac{ax^*z^*}{b + x^{*2}} - dz^* - wz^* &= 0. \end{aligned} \tag{26}$$

Choosing:

$$l_1 = \frac{\sigma_2 y^*}{\sigma_1 x^*},$$

and

$$l_2 = \frac{b + x^{*2}}{\beta b},$$

we obtain:

$$\begin{aligned} \frac{dV}{dt} = \quad & (x - x^*)\left[-\left(\tfrac{r_1}{k} + u\right)(x - x^*) - \sigma_2\left(\tfrac{y^*}{x^*} - \tfrac{y}{x}\right) - a\left(\tfrac{z}{b + x^2} - \tfrac{z^*}{b + x^{*2}}\right)\right] \\ & + \tfrac{\sigma_2 y^*}{\sigma_1 x^*}(y - y^*)\left[-\nu(y - y^*) + \sigma_1\left(\tfrac{x}{y} - \tfrac{x^*}{y^*}\right)\right] \end{aligned}$$

$$+\tfrac{a}{b}(b+x^{*2})(z-z^*)\left(\tfrac{x}{b+x^2}-\tfrac{x^*}{b+x^{*2}}\right)$$

After simplification, we get:

$$\frac{dV}{dt}=(x-x^*)^2\left[\left(\frac{az^*}{b+x^2}\right)-\left(\frac{r_1}{k}+u\right)\right]\ -\nu\frac{\sigma_2 y^*}{\sigma_1 x^*}(y-y^*)^2-\left(\frac{\sigma_2}{xx^*y}(yx^*-y^*x)^2\right)$$

. Therefore:

$$\frac{dV}{dt}<0\quad \text{if } x>\frac{kaz^*}{(b+x^{*2})\,(r_1+ku)}-b,$$

and by Lyapunov's direct method, the equilibrium $P(x^*,y^*,z^*,0,0)$ is globally asymptotically stable. □

Theorem 5.2.3. The equilibrium point $P(x^*,y^*,E_1^*,0,0)$ *of system (1) is globally asymptotically stable.*

Proof. Set $z=E_2=0$. The Lyapunov function reduces to:

$$V(x,y,E_1)=\left(x-x^*-\ln\left(\frac{x}{x^*}\right)\right)+l_1\left(y-y^*-\ln\left(\frac{y}{y^*}\right)\right)$$
$$+l_3\left(E_1-E_1^*-\ln\left(\frac{E_1}{E_1^*}\right)\right).$$

Differentiating V along the system trajectories, we obtain:

$$\frac{dV}{dt}=\left(1-\frac{x^*}{x}\right)\frac{dx}{dt}+l_1\left(1-\frac{y^*}{y}\right)\frac{dy}{dt}+l_3\left(1-\frac{E_1^*}{E_1}\right)\frac{dE_1}{dt}.$$

From the reduced system (with $z=E_2=0$), we have:

(27)
$$\begin{aligned}\frac{dx}{dt}&=r_1x\left(1-\frac{x}{k}\right)-\sigma_1x+\sigma_2y-ux^2-q_1E_1x,\\ \frac{dy}{dt}&=(r_2-\sigma_2)y+\sigma_1x-\nu y^2,\\ \frac{dE_1}{dt}&=\lambda_1\left(q_1x(m_1-\tau_1)-c_1\right)E_1.\end{aligned}$$

At equilibrium, the following conditions hold:

(28)
$$\begin{aligned}r_1x^*\left(1-\frac{x^*}{k}\right)-\sigma_1x^*+\sigma_2y^*-u(x^*)^2-q_1E_1^*x^*&=0,\\ (r_2-\sigma_2)y^*+\sigma_1x^*-\nu(y^*)^2&=0,\\ q_1x^*(m_1-\tau_1)-c_1&=0.\end{aligned}$$

Choose:

$$l_1 = \frac{\sigma_2 y^*}{\sigma_1 x^*}, \qquad l_3 = \frac{1}{\lambda_1(m_1 - \tau_1)}.$$

Substituting into $\frac{dV}{dt}$, we get:

$$\frac{dV}{dt} = -\left(\frac{r_1}{k} + u\right)(x - x^*)^2 - \nu \cdot \frac{\sigma_2 y^*}{\sigma_1 x^*}(y - y^*)^2 - \frac{\sigma_2}{xx^*y}(x^*y - xy^*)^2.$$

All terms are non-positive and vanish only when $x = x^*$, $y = y^*$, and $E_1 = E_1^*$. Hence:

$$\frac{dV}{dt} < 0 \quad \text{for all} \quad (x, y, E_1) \neq (x^*, y^*, E_1^*),$$

which implies that the equilibrium point $P(x^*, y^*, E_1^*, 0, 0)$ is globally asymptotically stable. □

Theorem 5.2.4. The equilibrium point $P(x^*, y^*, z^*, 0, E_2^*)$ of system (1) is globally asymptotically stable.

Proof. Set $E_1^* = 0$. The Lyapunov function simplifies to:

$$\begin{aligned} V(x,y,z,E_2) \quad &= \quad \left(x - x^* - \ln\left(\frac{x}{x^*}\right)\right) + l_1\left(y - y^* - \ln\left(\frac{y}{y^*}\right)\right) + l_2\left(z - z^* - \ln\left(\frac{z}{z^*}\right)\right) \\ &\quad + l_4\left(E_2 - E_2^* - \ln\left(\frac{E_2}{E_2^*}\right)\right). \end{aligned}$$

Differentiating V along trajectories of the system, we get:

$$\frac{dV}{dt} = \left(1 - \frac{x^*}{x}\right)\frac{dx}{dt} + l_1\left(1 - \frac{y^*}{y}\right)\frac{dy}{dt} + l_2\left(1 - \frac{z^*}{z}\right)\frac{dz}{dt} + l_4\left(1 - \frac{E_2^*}{E_2}\right)\frac{dE_2}{dt}.$$

From the reduced system (with $E_1 = 0$):

$$\begin{aligned} \frac{dx}{dt} &= r_1 x\left(1 - \frac{x}{k}\right) - \sigma_1 x + \sigma_2 y - ux^2 - \frac{axz}{b + x^2}, \\ \frac{dy}{dt} &= (r_2 - \sigma_2)y + \sigma_1 x - \nu y^2, \\ \frac{dz}{dt} &= \beta\frac{axz}{b + x^2} - dz - wz - q_2 E_2 z, \\ \frac{dE_2}{dt} &= \lambda_2 E_2\left(q_2 z(m_2 - \tau_2) - c_1\right). \end{aligned} \tag{29}$$

At equilibrium:

$$\begin{aligned} r_1 x^*\left(1 - \frac{x^*}{k}\right) - \sigma_1 x^* + \sigma_2 y^* - ux^{*2} - \frac{ax^*z^*}{b + x^{*2}} &= 0, \\ (r_2 - \sigma_2)y^* + \sigma_1 x^* - \nu y^{*2} &= 0, \end{aligned} \tag{30}$$

$$\begin{aligned} \beta \frac{ax^*z^*}{b+x^{*2}} - dz^* - wz^* - q_2E_2^*z^* &= 0, \\ q_2z^*(m_2-\tau_2) - c_2 &= 0. \end{aligned}$$

Choose the coefficients:

$$l_1 = \frac{\sigma_2 y^*}{\sigma_1 x^*}, \quad l_2 = \frac{b+x^{*2}}{\beta b}, \quad l_4 = \frac{b+x^{*2}}{\beta b \lambda_2 (m_2-\tau_2)}.$$

Substituting into $\frac{dV}{dt}$, we obtain:

$$\begin{aligned} \frac{dV}{dt} = (x-x^*) &\left[-\left(\frac{r_1}{k}+u\right)(x-x^*) - \sigma_2\left(\frac{y^*}{x^*}-\frac{y}{x}\right) - a\left(\frac{z}{b+x^2}-\frac{z^*}{b+x^{*2}}\right)\right] \\ &+ \frac{\sigma_2 y^*}{\sigma_1 x^*}(y-y^*)\left[-\nu(y-y^*)+\sigma_1\left(\frac{x}{y}-\frac{x^*}{y^*}\right)\right] \\ &+ \frac{b+x^{*2}}{\beta b}(z-z^*)\left[\frac{\beta ax}{b+x^2}-\frac{\beta ax^*}{b+x^{*2}}-q_2(E_2-E_2^*)\right] \\ &+ \frac{b+x^{*2}}{\beta b} q_2(z-z^*)(E_2-E_2^*). \end{aligned}$$

After simplification:

$$\frac{dV}{dt} = (x-x^*)^2\left[\frac{az^*}{b+x^2}-\left(\frac{r_1}{k}+u\right)\right] \quad -\nu\frac{\sigma_2 y^*}{\sigma_1 x^*}(y-y^*)^2 - \frac{\sigma_2}{xx^*y}(yx^*-y^*x)^2.$$

Therefore,

$$\frac{dV}{dt} < 0 \quad \text{if} \quad x > \frac{kaz^*}{(b+x^{*2})(r_1+ku)} - b.$$

By Lyapunov's direct method, the equilibrium point $P(x^*,y^*,z^*,0,E_2^*)$ is globally asymptotically stable. ☐

Theorem 5.2.5. The equilibrium point $P(x^*,y^*,z^*,E_1^*,E_2^*)$ of system (1) is globally asymptotically stable.

Proof. We define the Lyapunov function:

$$\begin{aligned} V(x,y,z,E_1,E_2) = &\left(x-x^*-\ln\left(\frac{x}{x^*}\right)\right) + l_1\left(y-y^*-\ln\left(\frac{y}{y^*}\right)\right) \\ &+ l_2\left(z-z^*-\ln\left(\frac{z}{z^*}\right)\right) + l_3\left(E_1-E_1^*-\ln\left(\frac{E_1}{E_1^*}\right)\right) \\ &+ l_4\left(E_2-E_2^*-\ln\left(\frac{E_2}{E_2^*}\right)\right). \end{aligned}$$

Differentiating V along the trajectories of the system:

$$\frac{dV}{dt} = \left(1-\frac{x^*}{x}\right)\frac{dx}{dt} + l_1\left(1-\frac{y^*}{y}\right)\frac{dy}{dt} + l_2\left(1-\frac{z^*}{z}\right)\frac{dz}{dt} + l_3\left(1-\frac{E_1^*}{E_1}\right)\frac{dE_1}{dt} + l_4\left(1-\frac{E_2^*}{E_2}\right)\frac{dE_2}{dt}.$$

The full system is:

$$\begin{aligned} \frac{dx}{dt} &= r_1 x\left(1-\frac{x}{k}\right) - \sigma_1 x + \sigma_2 y - ux^2 - \frac{axz}{b+x^2} - q_1 E_1 x, \\ \frac{dy}{dt} &= (r_2-\sigma_2)y + \sigma_1 x - \nu y^2, \\ \frac{dz}{dt} &= \beta\frac{axz}{b+x^2} - dz - wz - q_2 E_2 z, \\ \frac{dE_1}{dt} &= \lambda_1\left(q_1 x(m_1-\tau_1) - c_1\right)E_1, \\ \frac{dE_2}{dt} &= \lambda_2\left(q_2 z(m_2-\tau_2) - c_2\right)E_2. \end{aligned} \tag{31}$$

At equilibrium, we have:

$$\begin{aligned} r_1 x^*\left(1-\frac{x^*}{k}\right) - \sigma_1 x^* + \sigma_2 y^* - ux^{*2} - \frac{ax^*z^*}{b+x^{*2}} - q_1 E_1^* x^* &= 0, \\ (r_2-\sigma_2)y^* + \sigma_1 x^* - \nu y^{*2} &= 0, \\ \beta\frac{ax^*z^*}{b+x^{*2}} - dz^* - wz^* - q_2 E_2^* z^* &= 0, \\ q_1 x^*(m_1-\tau_1) - c_1 &= 0, \\ q_2 z^*(m_2-\tau_2) - c_2 &= 0. \end{aligned} \tag{32}$$

We choose the constants as:

$$l_1 = \frac{\sigma_2 y^*}{\sigma_1 x^*}, \quad l_2 = \frac{b+x^{*2}}{\beta b}, \quad l_3 = \frac{1}{\lambda_1(m_1-\tau_1)}, \quad l_4 = \frac{b+x^{*2}}{\beta b\lambda_2(m_2-\tau_2)}.$$

Substituting into $\frac{dV}{dt}$, we obtain:

$$\begin{aligned} \frac{dV}{dt} = {} & (x-x^*)\left[-\left(\frac{r_1}{k}+u\right)(x-x^*) - \sigma_2\left(\frac{y^*}{x^*}-\frac{y}{x}\right) - a\left(\frac{z}{b+x^2}-\frac{z^*}{b+x^{*2}}\right) - q_1(E_1-E_1^*)\right] \\ & + l_3 q_1(m_1-\tau_1)(x-x^*)(E_1-E_1^*) + l_1(y-y^*)\left[-\nu(y-y^*) + \sigma_1\left(\frac{x}{y}-\frac{x^*}{y^*}\right)\right] \\ & + l_2(z-z^*)\left[\frac{\beta ax}{b+x^2} - \frac{\beta ax^*}{b+x^{*2}} - q_2(E_2-E_2^*)\right] + l_2 q_2(z-z^*)(E_2-E_2^*). \end{aligned}$$

After simplification:

$$\frac{dV}{dt} = (x-x^*)^2\left[\frac{az^*}{b+x^2}-\left(\frac{r_1}{k}+u\right)\right] \qquad -\nu\frac{\sigma_2 y^*}{\sigma_1 x^*}(y-y^*)^2 \quad -\frac{\sigma_2}{xx^*y}(yx^*-y^*x)^2.$$

Thus, the Lyapunov derivative is negative definite if

$$x > \frac{kaz^*}{(b+x^{*2})(r_1+ku)} - b,$$

and by Lyapunov's direct method, the equilibrium point $P(x^*,y^*,z^*,E_1^*,E_2^*)$ is globally asymptotically stable. □

5.3 Optimal Harvesting Strategy.

Consider I to be the present value of a continuous-time stream of revenues. Let δ be the instantaneous rate of discount, and $E_{1\delta}$ the optimal harvesting control with corresponding state variables x_δ, and y_δ.

The objective is:

$$I(E_{1\delta}) = \max\{I(E) : E \in U\}, \quad \text{where } U = \left\{E : [0,t_f] \to [0,E_{\max}] \mid E \in L[0,1]\right\}$$

We write the Hamiltonian:

$$H(t) = e^{-\delta t}(p_1q_1x - D)E_1(t) + \lambda_1(t)\left[r_1x\left(1-\frac{x}{k}\right) - \sigma_1x + \sigma_2y - ux^2 - q_1E_1x\right]$$
$$+\lambda_2(t)\left[(r_2-\sigma_2)y + \sigma_1x - \nu y^2\right]$$

Let $\lambda_1(t)$ and $\lambda_2(t)$ be the adjoint variables.

Switching Function

$$\psi(t) = \frac{\partial H}{\partial E_1} = (p_1q_1x - D)e^{-\delta t} - \lambda_1q_1x$$

Adjoint Equations

$$\frac{d\lambda_1}{dt} = -\frac{\partial H}{\partial x}, \qquad \frac{d\lambda_2}{dt} = -\frac{\partial H}{\partial y}$$

When $\psi = 0$:

$$\lambda_1q_1x = (p_1q_1x - D)e^{-\delta t} \quad \Rightarrow \quad \lambda_1 = \left(p_1 - \frac{D}{q_1x}\right)e^{-\delta t}$$

Evaluate $\frac{d\lambda_1}{dt}$

$$\frac{d\lambda_1}{dt} = -e^{-\delta t}E_1p_1q_1 + \lambda_1\left[r_1 - \frac{2r_1}{k}x - \sigma_1 - 2ux - q_1E_1\right] + \lambda_2\sigma_2x$$

Evaluate $\frac{d\lambda_2}{dt}$

$$\frac{d\lambda_2}{dt} = -\lambda_1\sigma_2 + \lambda_2(r_2 - \sigma_2 - 2\nu y)$$

At the interior equilibrium point $P(x^*, y^*)$, when $\frac{\partial H}{\partial E} = 0$, we have:

$$\lambda_1 = A_1 e^{-\delta t}, \quad \text{where } A_1 = p_1 - \frac{D}{q_1 x^*}$$

Substituting into the equation for λ_2:

$$\frac{d\lambda_2}{dt} - \lambda_2 A_2 = -A_1\sigma_2 e^{-\delta t}, \quad A_2 = (r_2 - \sigma_2) - 2\nu y^* \Rightarrow \lambda_2 = \frac{A_1\sigma_2}{A_2 + \delta} e^{-\delta t}$$

Now for λ_1:

$$\frac{d\lambda_1}{dt} - \lambda_1 A_4 = -A_5 e^{-\delta t}$$

Where:

$$A_4 = r_1 - \frac{2r_1}{k}x - \sigma_1 - 2ux - q_1 E_1, \quad A_5 = E_1 p_1 q_1 + \frac{A_1\sigma_2}{A_2 + \delta}$$

Then:

$$\lambda_1 = \frac{A_5}{A_4 + \delta} e^{-\delta t}$$

Compare with:

$$\lambda_1 = \left(p_1 - \frac{D}{q_1 x}\right) e^{-\delta t} \Rightarrow p_1 q_1 x^* - D = \frac{A_5 q_1 x^*}{A_4 + \delta}$$

Define the function:

$$F(x^*) = h(x^*) - (p_1 q_1 x^* - D)$$

The positive roots of $F(x^*)$ give the optimal fish population $x^* = x_\delta$. The solution is unique if:

$$F(0) < 0, \quad F(K) > 0, \quad F'(x^*) > 0, \quad 0 < x_\delta < K$$

Optimal Prey Population

$$y^* = y_\delta = \frac{(r_2 - \sigma_2) + \sqrt{(r_2 - \sigma_2)^2 + 4\nu\sigma_1 x_\delta}}{2\nu}$$

Optimal Effort Level

$$E^*_{1,\delta} = \frac{1}{q_1 x_\delta}\left[r x_\delta \left(1 - \frac{x_\delta}{K}\right) - \sigma_1 x_\delta + \sigma_2 y_\delta\right]$$

Asymptotic Behavior

As $\delta \to \infty$:

$$\frac{A_5 q_1 x^*}{A_4 + \delta} \to 0 \quad \Rightarrow \quad \pi(x_\infty, y_\infty, E_\infty, t) = 0$$

5.4 Simulation Results and Interpretation.

5.4.1 Equilibrium Point $P_1(x, y, 0, 0, 0)$. The simulation results for the simplified fishery model $P_1(x, y, 0, 0, 0)$ help us understand the behavior of fish populations under spatial separation and no external effort.

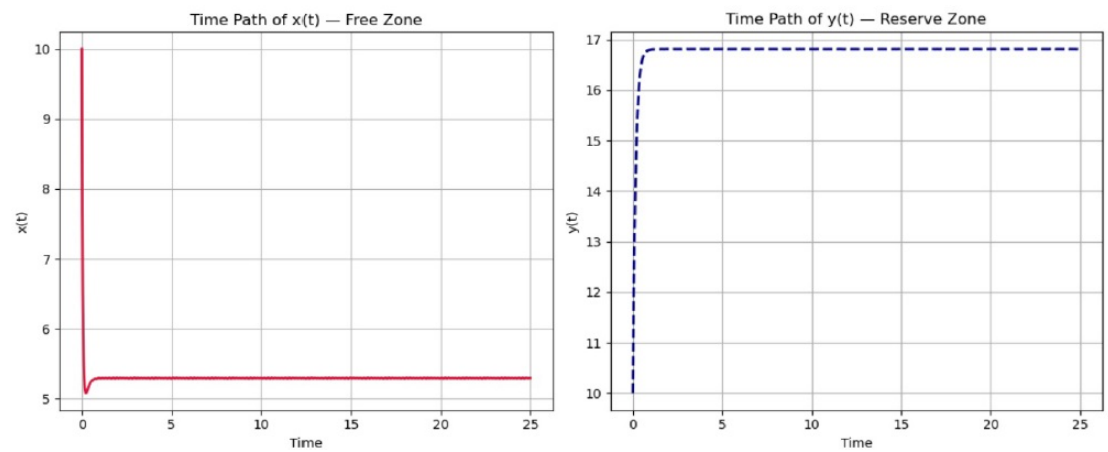

FIGURE 1. Time paths for $x(t)$ and $y(t)$

Initially, the fish population in the free fishing zone is high ($x(0) = 10$), but it declines rapidly due to strong competition, movement to the reserve zone, and the absence of protection. This sharp decrease is followed by a stabilization around a lower steady-state value near $x^* \approx 5.2$. In contrast, the reserve zone starts with the same initial value ($y(0) = 10$), but without fishing pressure, its population grows quickly, benefiting from migration and lack of exploitation. It eventually stabilizes around $y^* \approx 16.8$. These results suggest that spatial separation into fishing and protected zones creates a self-balancing dynamic. The reserve supports biomass recovery, while the exploited zone maintains a lower but steady population. This confirms the practical value of marine protected areas (MPAs) in promoting long-term fishery sustainability.

5.4.2 Equilibrium Point $P_2(x, y, z, 0, 0)$. The dynamics under $P_2(x, y, z, 0, 0)$ include the effects of predator-prey interactions in addition to spatial management.

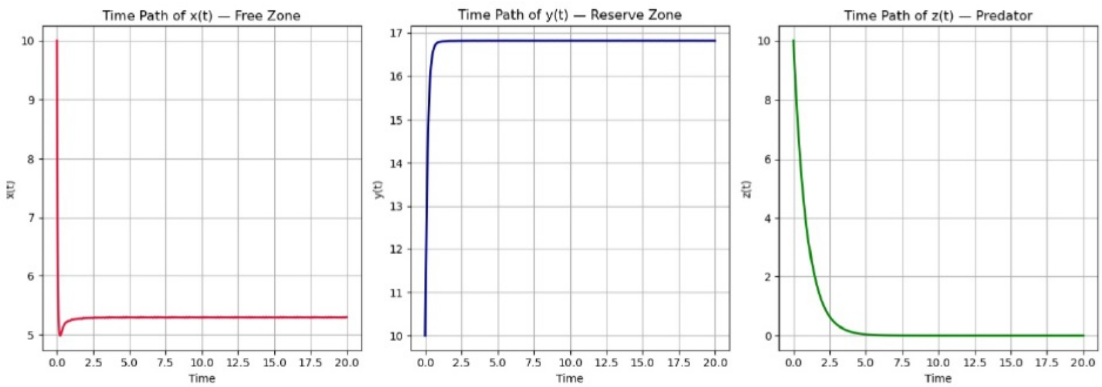

FIGURE 2. Time paths for $x(t)$, $y(t)$, and $z(t)$

In the free fishing zone, the fish population initially decreases quickly, driven by both competition and predation. It stabilizes at a lower level after a brief transient period. The reserve zone benefits again from the lack of fishing, allowing fish populations to increase and settle at a higher equilibrium. The predator population, however, declines steadily. As the prey base in the free zone diminishes, and with no access to the reserve, the predators experience a shortage of food, leading to population collapse.

These outcomes show how predator-prey dynamics can amplify the benefits of spatial protection. Predators are highly sensitive to changes in prey availability, and their collapse here highlights the importance of maintaining healthy prey populations across zones.

5.4.3 Equilibrium Point $P_3(x,y,0,E_1,0)$. This simulation introduces economic effort targeting the fish population in the free zone. We analyze the evolution of fish in both zones and the effort variable $E_1(t)$.

The fish population in the free zone starts high but declines sharply due to intense harvesting pressure. After this initial fall, it reaches a steady equilibrium. Meanwhile, the reserve zone population grows rapidly, supported by migration and protection, and then stabilizes at a high level.

Importantly, the fishing effort $E_1(t)$ also falls over time. Initially active, it collapses as the resource becomes scarce and unprofitable. This demonstrates how economic incentives are naturally constrained by ecological conditions, if a population can't support harvesting, effort

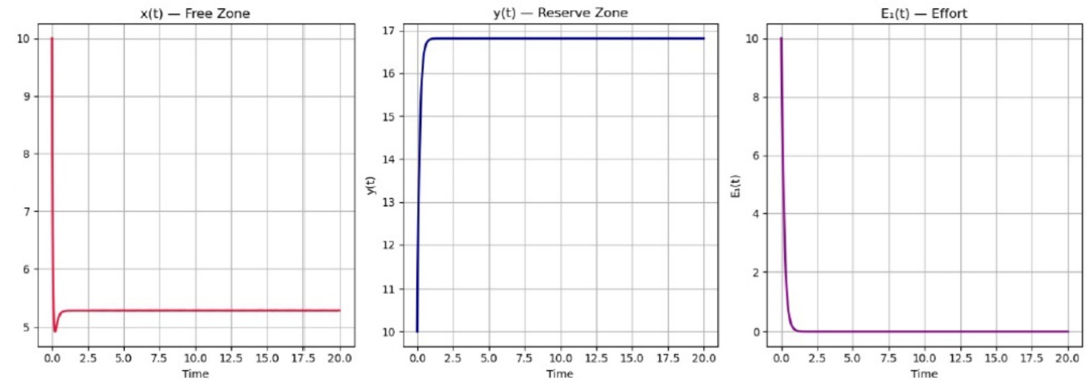

FIGURE 3. Time paths for $x(t)$, $y(t)$, and $E_1(t)$

declines as well. The reserve again provides resilience by maintaining biomass, even when effort collapses.

5.4.4 Equilibrium Point $P_4(x,y,z,0,E_2)$. This case models targeted fishing effort on the predator population, in addition to prey dynamics and spatial effects.

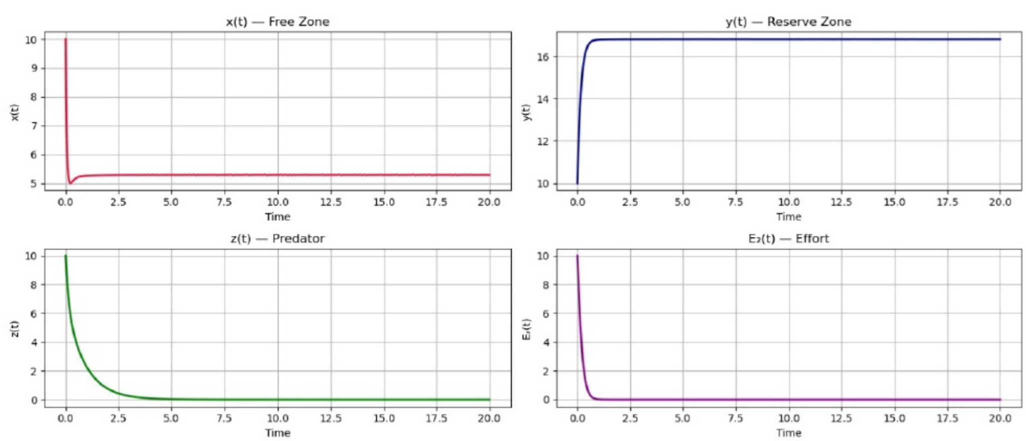

FIGURE 4. Time paths for $x(t)$, $y(t)$, $z(t)$, and $E_2(t)$

The free zone population falls rapidly due to predation and internal pressures, stabilizing at a lower level. In contrast, the reserve fish population increases and maintains a higher equilibrium. The predator population declines drastically, collapsing entirely due to both a lack of food and the impact of fishing effort $E_2(t)$.

Effort $E_2(t)$ mirrors the predator trend starting high but decreasing as the economic return on harvesting predators diminishes. This simulation again emphasizes the importance of resource availability in determining economic effort, and how protected areas play a stabilizing role in the broader system.

5.4.5 Equilibrium Point $P_5(x,y,z,E_1,E_2)$. This final simulation integrates both fishing efforts and the full ecological interaction among fish, predators, and spatial zones.

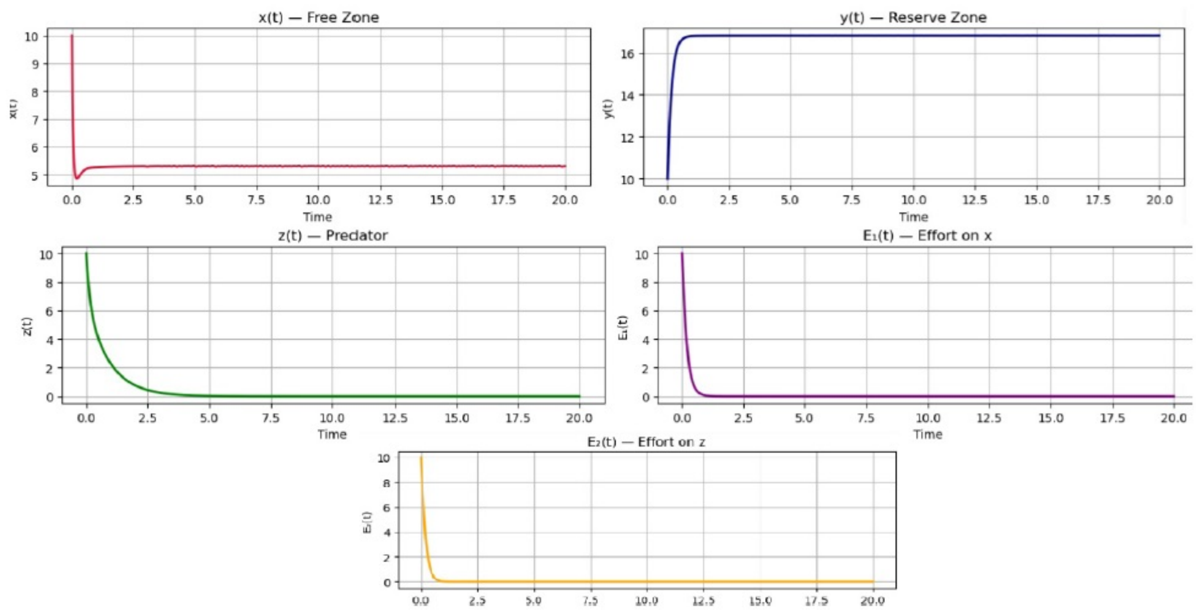

FIGURE 5. Time paths for $x(t)$, $y(t)$, $z(t)$, $E_1(t)$, and $E_2(t)$

The free zone fish population declines sharply and stabilizes at a lower level. The reserve fish population increases quickly and levels off at a higher value. Predator numbers drop steadily and eventually collapse due to lack of prey and harvesting. Both fishing efforts $E_1(t)$ and $E_2(t)$ begin at high levels but fall rapidly as the populations they target become economically unviable.

The model underscores a key insight: ecosystems and economic systems are deeply connected. When prey populations shrink, predator survival and economic interest in harvesting them also decline. Marine reserves play a vital role in maintaining system-wide balance, providing refuge and ensuring that collapse in one part of the system doesn't lead to total failure.

CONCLUSION

We developed and analyzed a bioeconomic model for a three-species marine ecosystem, integrating spatial zoning and dynamic harvesting efforts. Unlike traditional fixed-effort models, our formulation allows fishing pressure to evolve based on ecological feedback and economic return, thereby better capturing real-world decision-making dynamics.

Through rigorous stability analysis including equilibrium classification, Jacobian evaluation, and Lyapunov-based global stability proofs we identified conditions under which the system can reach ecologically meaningful and economically viable steady states. The inclusion of a Holling type IV functional response enriches the model by accounting for predator saturation and efficiency thresholds.

The application of Pontryagin's Maximum Principle allowed us to explore optimal harvesting under cost, revenue, and discounting constraints. This formalism provided critical insights into how prey biomass and fishing effort can be tuned to maximize long term returns without jeopardizing species persistence.

Numerical simulations complemented the theory, demonstrating how spatial protection zones can act as ecological buffers, particularly when prey collapse threatens predator viability or harvesting profitability. The sharp drop in effort levels observed in some scenarios reflects a natural economic feedback mechanism a system halting exploitation when it becomes unprofitable.

Taken together, these results support the argument for integrated management strategies that combine spatial protection, dynamic regulation, and economic adaptation. Future extensions could explore stochastic perturbations, delayed feedback, or agent-based implementations to reflect even richer behavioral patterns. We hope this work contributes to the growing literature on sustainable fisheries and offers practical guidance for policymakers and resource managers.

Conflict of Interests

The authors declare that there is no conflict of interests.

References

[1] V.I. Arnol'd, Ordinary Differential Equations, Springer, (1992).

[2] S. Toaha, J. Kusuma, Khaeruddin, M. Bahri, Stability Analysis and Optimal Harvesting Policy of Prey-Predator Model with Stage Structure for Predator, Appl. Math. Sci. 8 (2014), 7923–7934. https://doi.org/10.12988/ams.2014.410792.

[3] K. Belkhodja, A. Moussaoui, M.A. Alaoui, Optimal Harvesting and Stability for a Prey–predator Model, Nonlinear Anal.: Real World Appl. 39 (2018), 321–336. https://doi.org/10.1016/j.nonrwa.2017.07.004.

[4] R.J.H. Beverton, S.J. Holt, On the Dynamics of Exploited Fish Populations, Springer, (1993). https://doi.org/10.1007/978-94-011-2106-4.

[5] K. Chakraborty, S. Das, T. Kar, Optimal Control of Effort of a Stage Structured Prey–predator Fishery Model with Harvesting, Nonlinear Anal.: Real World Appl. 12 (2011), 3452–3467. https://doi.org/10.1016/j.nonrwa.2011.06.007.

[6] C. Chicone, Stability Theory of Ordinary Differential Equations, in: Mathematics of Complexity and Dynamical Systems, Springer New York, 2012: pp. 1653–1671. https://doi.org/10.1007/978-1-4614-1806-1_106.

[7] D.R. Curtiss, Recent Extentions of Descartes' Rule of Signs, Ann. Math. 19 (1918), 251–278. https://doi.org/10.2307/1967494.

[8] T. Das, R. Mukherjee, K. Chaudhuri, Harvesting of a Prey–predator Fishery in the Presence of Toxicity, Appl. Math. Model. 33 (2009), 2282–2292. https://doi.org/10.1016/j.apm.2008.06.008.

[9] B. Dubey, P. Chandra, P. Sinha, A Model for Fishery Resource with Reserve Area, Nonlinear Anal.: Real World Appl. 4 (2003), 625–637. https://doi.org/10.1016/s1468-1218(02)00082-2.

[10] B. Dubey, A Prey-Predator Model with a Reserved Area, Nonlinear Anal.: Model. Control. 12 (2007), 479–494. https://doi.org/10.15388/na.2007.12.4.14679.

[11] S. Guénette, T. Lauck, C. Clark, Marine Reserves: From Beverton and Holt to the Present, Rev. Fish Biol. Fish. 8 (1998), 251–272. https://doi.org/10.1023/a:1008859130275.

[12] H. Huo, H. Jiang, X. Meng, A Dynamic Model for Fishery Resource with Reserve Area and Taxation, J. Appl. Math. 2012 (2012), 794719. https://doi.org/10.1155/2012/794719.

[13] H. Huo, H. Jiang, X. Meng, A Dynamic Model for Fishery Resource with Reserve Area and Taxation, J. Appl. Math. 2012 (2012), 794719. https://doi.org/10.1155/2012/794719.

[14] G.M.V. Lakshmi, M. Gunasekaran, S. Vijaya, Bifurcation Analysis of Predator Model With Harvested Predator, Int. J. Eng. Res. Dev. 10 (2014), 42–51.

[15] A.J. Lotka, Contribution to the Theory of Periodic Reactions, J. Phys. Chem. 14 (1910), 271–274. https://doi.org/10.1021/j150111a004.

[16] A.J. Lotka, Analytical Note on Certain Rhythmic Relations in Organic Systems, Proc. Natl. Acad. Sci. 6 (1920), 410–415. https://doi.org/10.1073/pnas.6.7.410.

[17] Y. Louartassi, E.H. El Mazoudi, N. Elalami, A New Generalization of Lemma Gronwall-Bellman, Appl. Math. Sci, 6 (2012), 621–628.

[18] Y. Louartassi, A. Alla, K. Hattaf, A. Nabil, Dynamics of a Predator–prey Model with Harvesting and Reserve Area for Prey in the Presence of Competition and Toxicity, J. Appl. Math. Comput. 59 (2018), 305–321. https://doi.org/10.1007/s12190-018-1181-0.

[19] M.R. Lemnaouar, M. Khalfaoui, Y. Louartassi, I. Tolaimate, Harvesting of a Prey-Predator Model Fishery in the Presence of Competition and Toxicity With Two Effort Functions, Commun. Math. Biol. Neurosci. 2019 (2019), 29. https://doi.org/10.28919/cmbn/4203.

[20] R.M. May, Stability and Complexity in Model Ecosystems, Princeton University Press, 2001. https://doi.org/10.1515/9780691206912.

[21] L. Pontryagin, Mathematical Theory of Optimal Processes, Routledge, 2018. https://doi.org/10.1201/9780203749319.

[22] A.K. Sardar, M. Hanif, M. Asaduzzaman, M.H.A. Biswas, Mathematical Analysis of the Two Species Lotka-Volterra Predator-Prey Inter-Specific Game Theoretic Competition Model, Adv. Model. Optim. 18 (2016), 231–242.

[23] P.F. Verhulst, Notice on the Law That a Population Follows in Its Growth, Corr. Math. Phys. 10 (1838), 113–121.

[24] V. Volterra, Variations and Fluctuations of the Number of Individuals in Animal Species Living Together, ICES J. Mar. Sci. 3 (1928), 3–51. https://doi.org/10.1093/icesjms/3.1.3.

[25] H. Yang, J. Jia, Harvesting of a Predator–prey Model with Reserve Area for Prey and in the Presence of Toxicity, J. Appl. Math. Comput. 53 (2016), 693–708. https://doi.org/10.1007/s12190-016-0989-8.