



Optimal Control Harvesting in a Deterministic Predator-Prey Model for a Three-Patch Ecosystem

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Abstract

Predator-prey interactions play a pivotal role in shaping ecosystem dynamics, with significant implications for sustainable resource management. While much of the existing literature has focused on deterministic harvesting models in single or two-patch ecosystems, there remains a gap in exploring optimal harvesting strategies within spatially distributed multi-patch systems. This study develops a deterministic predator-prey model across three interconnected patches, representing cage-based aquaculture zones within a lake. The model incorporates prey migration between patches and harvesting applied to the prey population only. We formulate an optimal control problem aimed at maximizing the net economic return from harvesting while ensuring ecological sustainability. Using Pontryagin's Maximum Principle, we derive necessary conditions for optimality and construct a time-dependent control strategy. Numerical simulations, with the help of Python software, reveal that fixed-rate harvesting lead to population decline or instability, while the optimal control strategy stabilizes both predator and prey populations within sustainable bounds. These findings provide valuable insights for fisheries management, aquaculture policy, and the design of ecologically sound harvesting strategies in multi-zone environments.

Keywords: Optimal control, Predator-prey model, Pontryagin's Maximum Principle, harvesting policy, sustainability.

2020 Mathematics Subject Classification: 03Cxx, 34C60, 03C40

1 Introduction

In natural ecosystems, species interact through various biological processes, one of the most fundamental being predation, where a predator feeds on prey [5, 12, 16]. Predator-prey



interactions significantly shape population dynamics, influence community structure, and affect the overall health of ecosystems [19]. Classical models, such as the Lotka–Volterra equations, have been instrumental in describing these interactions and their cyclical population behavior [16]. However, real-world ecosystems are spatially heterogeneous and often exhibit complex dynamics that are not fully captured by basic population models.

One major area of interest in ecological modeling is harvesting, which involves extracting individuals from a biological population [17]. Harvesting may be regulated by quotas (yield-based) or by fishing effort, and it introduces anthropogenic pressures that affect long-term population viability. Constant-yield harvesting assumes fixed removal regardless of stock levels, as shown in [4]:

$$\frac{dN}{dt} = N(r - bN) - \nu, \quad (1)$$

where ν is a constant harvest rate. Alternatively, effort-based harvesting ties extraction rates to available stock levels and fishing intensity, described in [1] by:

$$\frac{dN}{dt} = rN \left(1 - \frac{N}{K}\right) - qEN, \quad (2)$$

where qEN is the harvest rate, q the catchability coefficient, and E the effort level.

Overharvesting, particularly of prey species, can lead to population collapse. Fixed effort policies help mitigate this by reducing harvest as populations decline [29]. Yet, the global threat of overfishing continues to endanger marine ecosystems, highlighting the urgency of adaptive and sustainable management approaches [18].

Spatial heterogeneity, where habitats are partitioned into distinct patches, further complicates predator-prey dynamics [13]. Movement between patches, each with unique environmental conditions, plays a crucial role in population distribution and system resilience. Multi-patch predator-prey models are thus essential in capturing the ecological reality of interconnected zones such as lakes with cage-based fish farming [2, 3, 10, 20, 26]. In such systems, harvesting has a profound influence on population dynamics, and models increasingly incorporate harvesting as a dynamic control variable to better study system behavior [15, 22, 23, 24, 25].

In the context of cage aquaculture, such as that growing rapidly in Lake Victoria, there is a



growing need to understand the interactions between spatial fish populations, prey migration, and harvesting strategies. Despite widespread application, comprehensive deterministic models addressing optimal prey harvesting across multiple patches remain limited.

This paper develops and analyzes a deterministic predator-prey model across three interconnected patches, representing cages within a lake ecosystem. Harvesting is applied exclusively to the prey population, and prey migration between patches is explicitly modeled. The goal is to formulate and solve an optimal control problem that maximizes economic returns from prey harvesting while preserving ecological balance. Using Pontryagin's Maximum Principle, we derive the necessary optimality conditions and propose a dynamic harvesting strategy tailored to population states in each patch. This study contributes to the literature on sustainable resource management and offers insights for policymakers and ecologists interested in multi-zone harvesting frameworks.

2 Model Formulation

Subsection 2.1 presents the deterministic model for predator-prey interactions across three interconnected patches, as well as the key assumptions made. Subsection 2.2 addresses the positivity of the model, and Subsection 2.3 examines the boundedness of the model.

2.1 The Model

The total fish population under study, denoted by $V(t)$, comprises six interacting components across three distinct patches: prey population in patch-1 (N_1), predator population in patch-1 (M_1), prey population in patch-2 (N_2), predator population in patch-2 (M_2), prey population in patch-3 (N_3), and predator population in patch-3 (M_3). Each patch represents a cage within a lake ecosystem, enclosed with mesh structures that allow migration of fingerlings of the prey species between patches. The model assumes that each patch is environmentally homogeneous with respect to temperature, water quality, food supply, and waste exchange. The prey population in each patch grows logistically with an intrinsic growth rate r_i and carrying capacity K_i . Predators feed on prey at a rate a_i , contributing to predator growth at a rate γ_i , while experiencing natural mortality at rate μ_i . Harvesting is applied to the prey populations



only, with time-dependent effort rates $\nu_i(t)$ in each patch. Migration of prey occurs at constant rates between patches, governed by directional parameters α_1 through α_6 .

Under these conditions, the dynamics of the system are governed by the following set of deterministic ordinary differential equations:

$$\begin{aligned}
 \frac{dN_1}{dt} &= r_1 N_1 \left(1 - \frac{N_1}{K_1}\right) - a_1 N_1 M_1 - \nu_1(t) N_1 + \alpha_4 N_2 + \alpha_3 N_3 - (\alpha_1 + \alpha_6) N_1, \\
 \frac{dM_1}{dt} &= \gamma_1 N_1 M_1 - \mu_1 M_1, \\
 \frac{dN_2}{dt} &= r_2 N_2 \left(1 - \frac{N_2}{K_2}\right) - a_2 N_2 M_2 - \nu_2(t) N_2 + \alpha_1 N_1 + \alpha_5 N_3 - (\alpha_2 + \alpha_4) N_2, \\
 \frac{dM_2}{dt} &= \gamma_2 N_2 M_2 - \mu_2 M_2, \\
 \frac{dN_3}{dt} &= r_3 N_3 \left(1 - \frac{N_3}{K_3}\right) - a_3 N_3 M_3 - \nu_3(t) N_3 + \alpha_2 N_2 + \alpha_6 N_1 - (\alpha_3 + \alpha_5) N_3, \\
 \frac{dM_3}{dt} &= \gamma_3 N_3 M_3 - \mu_3 M_3.
 \end{aligned} \tag{3}$$

with initial conditions:

$$\begin{aligned}
 N_1(0) &= N_1 \geq 0, \\
 N_2(0) &= N_2 \geq 0, \\
 N_3(0) &= N_3 \geq 0, \\
 M_1(0) &= M_1 \geq 0, \\
 M_2(0) &= M_2 \geq 0, \\
 M_3(0) &= M_3 \geq 0.
 \end{aligned} \tag{4}$$

The total population at time t is defined as:

$$V(t) = N_1(t) + N_2(t) + N_3(t) + M_1(t) + M_2(t) + M_3(t). \tag{5}$$

2.2 Positivity of the model

The variables $N_1, M_1, N_2, M_2, N_3, M_3$ represent populations, so they should remain non-negative.



Lemma 1. *Under initial conditions (4), all the solutions $N_1, M_1, N_2, M_2, N_3, M_3$ of the system (3) remain nonnegative for $t \geq 0$*

Proof. For the prey population, the equations for N_1, N_2, N_3 are of the form;

$$\frac{dN_i}{dt} = r_i N_i \left(1 - \frac{N_i}{K_i} \right) - (\text{non-negative terms}) + (\text{migration terms}).$$

The term $r_i N_i \left(1 - \frac{N_i}{K_i} \right)$ is non-negative when $N_i \geq 0$, as the logistic growth ensures $N_i \geq 0$. Predation ($-a_i N_i M_i$) and harvesting ($-\nu_i N_i$), act as sinks but cannot make N_i negative if $N_i \geq 0$. Migration input terms ($\alpha_{ij} N_j$) are non-negative, adding to the population. Thus, if $N_i(0) \geq 0$, then $\frac{dN_i}{dt}$ ensures $N_i(t) \geq 0$ for all $t \geq 0$.

For the predator population, the equations for M_1, M_2, M_3 are of the form;

$$\frac{dM_i}{dt} = \gamma_i N_i M_i - (\mu_i + \nu_i) M_i.$$

The term $\gamma_i N_i M_i$ is non-negative for $N_i \geq 0$ and $M_i \geq 0$. The mortality terms ($-\mu_i M_i$ and $-\nu_i M_i$) act as sinks but cannot make M_i negative if $M_i \geq 0$. Thus, if $M_i(0) \geq 0$, then $\frac{dM_i}{dt}$ ensures $M_i(t) \geq 0$ for all $t \geq 0$.

The initial conditions $N_i(0) \geq 0$ and $M_i(0) \geq 0$ hold, the structure of the equations ensures that all solutions $N_i(t)$ and $M_i(t)$ remain non-negative for all $t \geq 0$. Thus, positivity of the system. \square

2.3 Boundedness of the model

Proposition 1. *Under initial conditions (4), the total population function*

$$V(t) = \sum_{i=1}^3 (N_i(t) + M_i(t))$$

remains bounded for all $t \geq 0$.

Proof. To prove the boundedness of the solutions for the given system of differential equations, we used the LaSalle Invariance Principle [14] and analyzed the structure of the system. We need



to sought a function that is non-negative and has the following properties; decreases along the trajectories of the system, and bounds the populations, meaning it does not increase without bound as $t \rightarrow \infty$.

Let the total population of the system be represented by the function;

$$V(t) = N_1(t) + N_2(t) + N_3(t) + M_1(t) + M_2(t) + M_3(t)$$

where $N_i(t)$ and $M_i(t)$ denote the prey and predator populations in patch i respectively, for $i = 1, 2, 3$. We aim to show that $V(t)$ remains bounded for all $t \geq 0$. This function was always non-negative because populations cannot be negative.

Differentiating $V(t)$ with respect to time gives;

$$\frac{dV}{dt} = \frac{dN_1}{dt} + \frac{dM_1}{dt} + \frac{dN_2}{dt} + \frac{dM_2}{dt} + \frac{dN_3}{dt} + \frac{dM_3}{dt}$$

Substituting the system of equations into this derivative;

$$\begin{aligned} \frac{dV}{dt} = & \left(r_1 N_1 \left(1 - \frac{N_1}{K_1} \right) - a_1 N_1 M_1 - \nu_1 N_1 + \alpha_4 N_2 + \alpha_3 N_3 - (\alpha_1 + \alpha_6) N_1 \right) \\ & + (\gamma_1 N_1 M_1 - \mu_1 M_1 - \nu_1 M_1) \\ & + \left(r_2 N_2 \left(1 - \frac{N_2}{K_2} \right) - a_2 N_2 M_2 - \nu_2 N_2 + \alpha_1 N_1 + \alpha_5 N_3 - (\alpha_2 + \alpha_4) N_2 \right) \\ & + (\gamma_2 N_2 M_2 - \mu_2 M_2 - \nu_2 M_2) \\ & + \left(r_3 N_3 \left(1 - \frac{N_3}{K_3} \right) - a_3 N_3 M_3 - \nu_3 N_3 + \alpha_2 N_2 + \alpha_6 N_1 - (\alpha_3 + \alpha_5) N_3 \right) \\ & + (\gamma_3 N_3 M_3 - \mu_3 M_3 - \nu_3 M_3) \end{aligned}$$

The right-hand side of the equation is a sum of terms that include logistic growth terms which are self-limiting and ensure prey growth does not exceed the carrying capacity K_i , negative interaction terms like $-a_i N_i M_i$, representing predation and reduce prey population when predator numbers increase, mortality and harvesting terms which continuously act to reduce the population sizes, and migration terms which redistribute prey among patches without introducing unbounded growth. The logistic terms inherently bound the prey population by their respective carrying capacities. The mortality and harvesting terms act as sinks, further limiting unbounded growth. Predation introduces nonlinear decay effects, ensuring that even in the presence of high prey numbers, predator pressure helps regulate population sizes.



The predator equations similarly contain death and harvesting terms that prevent unbounded growth.

Formalizing this by constructing a Lyapunov-like function,

$$V(t) = \sum_{i=1}^3 (N_i(t) + M_i(t)),$$

and analyze its derivative,

$$\frac{dV}{dt} \leq C - DV(t),$$

where $C > 0$ is a constant representing the maximum cumulative contribution from logistic and migration terms, and $D > 0$ is a constant representing the decay effect due to mortality, harvesting, and predation. This inequality implies that $V(t)$ grows at a rate bounded above by a linear function that decreases in V , leading to the conclusion (by the Comparison Theorem [6]) that;

$$V(t) \leq \max \left(V(0), \frac{C}{D} \right), \quad \text{for all } t \geq 0.$$

Hence, all individual population components $N_i(t)$ and $M_i(t)$ are bounded above by finite constants. □

3 Optimal Control Problem

This section presents the formulation and analysis of an optimal control harvesting strategy. The goal is to determine the optimal harvesting strategy for the prey population in the three interconnected patches, maximizing economic returns while preserving ecological sustainability. Subsection 3.1 introduces the controlled model formulation, where the harvesting efforts are incorporated into the system dynamics as control variables. In Subsection 3.2, we define the objective functional that captures the trade-off between economic gain from harvesting and the cost associated with effort. Subsection 3.3 outlines the optimal control problem, setting up the necessary constraints and admissible control set. Subsection 3.4 presents the Pontryagin's Maximum Principle and derives the necessary conditions for optimality.



3.1 Controlled Model Formulation

Let $x_i(t)$ and $y_i(t)$ denote the prey and predator populations in patch i ($i = 1, 2, 3$) at time t . The system of nonlinear ordinary differential equations is given by;

$$\frac{dx_i}{dt} = r_i x_i \left(1 - \frac{x_i}{K_i} \right) - a_i x_i y_i - u_i(t) x_i, \quad (6)$$

$$\frac{dy_i}{dt} = b_i x_i y_i - d_i y_i, \quad (7)$$

where, r_i is the intrinsic growth rate of the prey, K_i is the carrying capacity of the prey, a_i is the predation rate, b_i is the conversion efficiency of prey to predator biomass, d_i is the natural death rate of the predator, and $u_i(t)$ is the control function representing harvesting effort, bounded by $0 \leq u_i(t) \leq u_{\max}$.

3.2 Objective Functional

We aim to maximize the economic benefits from harvesting prey while accounting for harvesting costs. The objective functional is;

$$J(u) = \int_0^T \sum_{i=1}^3 \left[\alpha_i u_i(t) x_i(t) - \frac{1}{2} \beta_i u_i^2(t) \right] dt, \quad (8)$$

where α_i is the price per unit harvest from patch i , and β_i is a cost coefficient penalizing the harvesting effort.

3.3 Hamiltonian and Optimality Conditions

Let $\lambda_i(t)$ and $\mu_i(t)$ be the adjoint variables corresponding to $x_i(t)$ and $y_i(t)$, respectively. The Hamiltonian for patch i is defined as;

$$\begin{aligned} \mathcal{H}_i = & \alpha_i u_i x_i - \frac{1}{2} \beta_i u_i^2 \\ & + \lambda_i \left[r_i x_i \left(1 - \frac{x_i}{K_i} \right) - a_i x_i y_i - u_i x_i \right] \\ & + \mu_i [b_i x_i y_i - d_i y_i]. \end{aligned} \quad (9)$$

The necessary condition for optimality from Pontryagin's Maximum Principle [27] is;



$$\frac{\partial \mathcal{H}_i}{\partial u_i} = \alpha_i x_i - \beta_i u_i - \lambda_i x_i = 0. \quad (10)$$

Solving for u_i gives the optimal control;

$$u_i^*(t) = \frac{1}{\beta_i} (\alpha_i - \lambda_i) x_i. \quad (11)$$

With bounds applied, the optimal control becomes;

$$u_i^*(t) = \min \left\{ u_{\max}, \max \left\{ 0, \frac{1}{\beta_i} (\alpha_i - \lambda_i) x_i \right\} \right\}. \quad (12)$$

3.4 Adjoint Equations

The adjoint equations are derived as;

$$\frac{d\lambda_i}{dt} = -\frac{\partial \mathcal{H}_i}{\partial x_i}, \quad \frac{d\mu_i}{dt} = -\frac{\partial \mathcal{H}_i}{\partial y_i}. \quad (13)$$

Computing the derivatives;

$$\begin{aligned} \frac{d\lambda_i}{dt} &= - \left[\alpha_i u_i - \lambda_i \left(r_i \left(1 - \frac{2x_i}{K_i} \right) - a_i y_i - u_i \right) - \mu_i b_i y_i \right], \\ \frac{d\mu_i}{dt} &= \lambda_i a_i x_i + \mu_i (b_i x_i - d_i). \end{aligned} \quad (14)$$

With transversality conditions;

$$\lambda_i(T) = 0, \quad \mu_i(T) = 0. \quad (15)$$

4 Numerical Simulations

This section presents numerical simulations to illustrate the behavior of the predator-prey system under both constant and optimal harvesting strategies. Subsection 4.1 presents the time evolution of prey and predator populations across the three spatial patches under constant harvesting rates. Subsection 4.2 analyzes the behavior of the system under optimal harvesting policies, and compare scenarios with and without control.



4.1 Time-Series Evaluation of Population Dynamics

In this subsection, we present the time evolution of prey and predator populations across the three spatial patches under constant harvesting rates. The goal is to observe the behavior of individual species over time, considering the effects of logistic growth, predation, mortality, and inter-patch migration. The system was simulated using the parameter values shown in table below. Initial population values were set as follows: $N_1(0) = 50$, $M_1(0) = 10$, $N_2(0) = 40$, $M_2(0) = 5$, $N_3(0) = 20$, and $M_3(0) = 2$.

Table 1: Parameter values used for numerical simulations

Parameter/Variable	Description	Value	Source
ν_1, ν_2, ν_3	Harvesting rates in patches 1-3	0.02	Estimated
K_1, K_2, K_3	Carrying capacities in patches 1-3	10, 8, 6	Estimated
a_1, a_2, a_3	Predation rates in patches 1-3	0.2, 0.3, 0.4	Estimated
r_1, r_2, r_3	Prey growth rates in patches 1-3	0.5, 0.4, 0.3	[7]
μ_1, μ_2, μ_3	Predator death rates in patches 1-3	0.1	[28]
$\gamma_1, \gamma_2, \gamma_3$	Predator growth rates in patches 1-3	0.01	Estimated
α_1 to α_6	Prey migration rates between patches	0.03	Estimated

The resulting population trajectories for prey and predators, with the help of Python software, are shown in Figure 1:

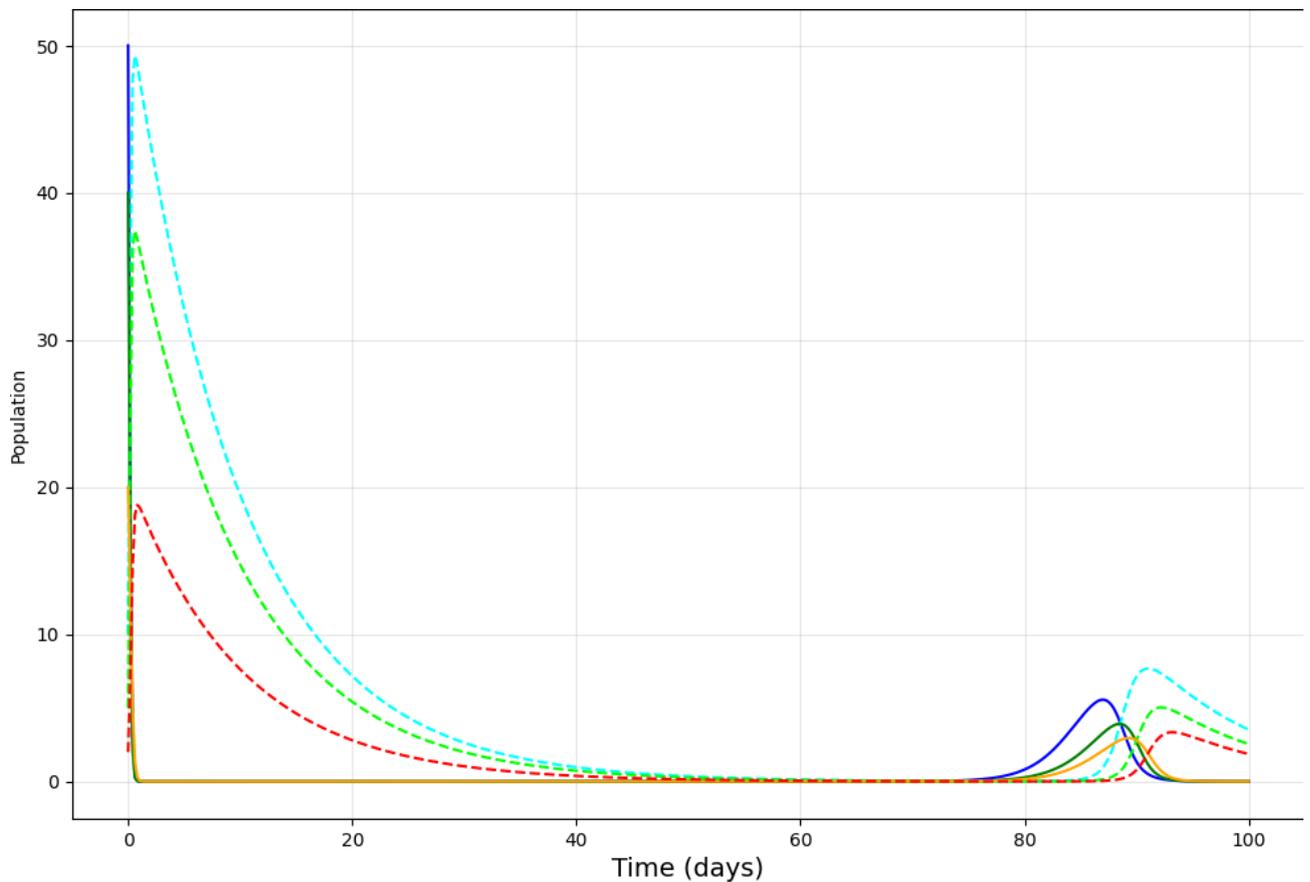


Figure 1: Time evaluation of the population $N_1, M_1, N_2, M_2, N_3, M_3$ with initial values 50, 10, 40, 5, 20, 2 respectively.

Figure 1 shows the time evaluation of population $N_1, M_1, N_2, M_2, N_3, M_3$ with initial values 50, 10, 40, 5, 20, 2 respectively. Predator populations increase as they feed on the prey, creating predator-prey oscillations. Migration between patches introduces interdependence among the populations, with prey and predators influencing each other's dynamics across the 3 patches. Over time, the populations stabilize reflecting the balance of growth, predation, and migration. These graphs serve as a baseline for understanding system behavior under fixed harvesting and provide a reference for subsequent comparison with optimal harvesting strategies.



4.2 Constant and Optimal harvesting control graphs

Figures 2 and 3 analyze the behavior of the system under optimal harvesting policies, and compare scenarios with and without control.

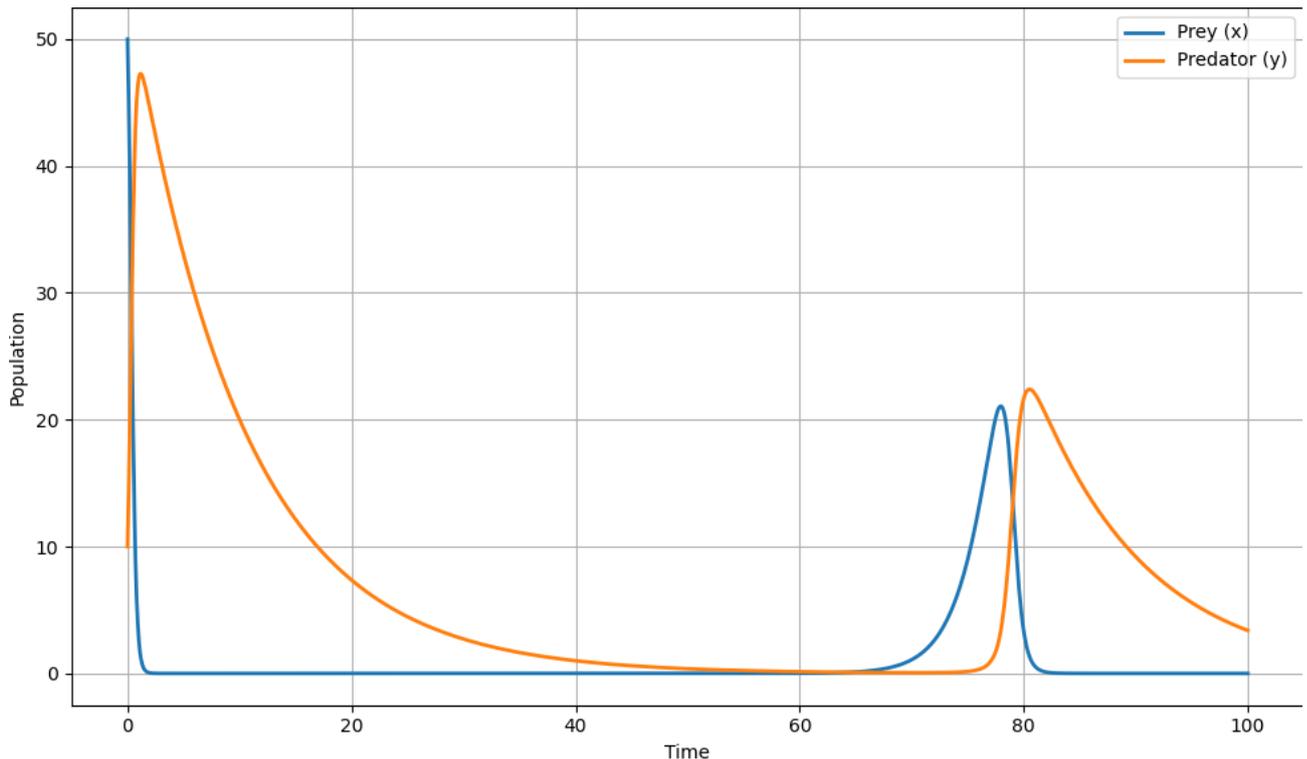


Figure 2: Predator-prey Dynamics with constant harvesting efforts.

Figure 2 shows how prey and predator populations evolve over time when harvesting is applied at a fixed rate. The prey population decreases due to continuous harvesting, while the predator population follows a similar decline as it depends on the availability of prey demonstrating the limitations of constant harvesting in maintaining long-term ecological balance. This analysis provides a baseline for comparison, showing the need for a more dynamic strategy, which is addressed in the optimal control approach.

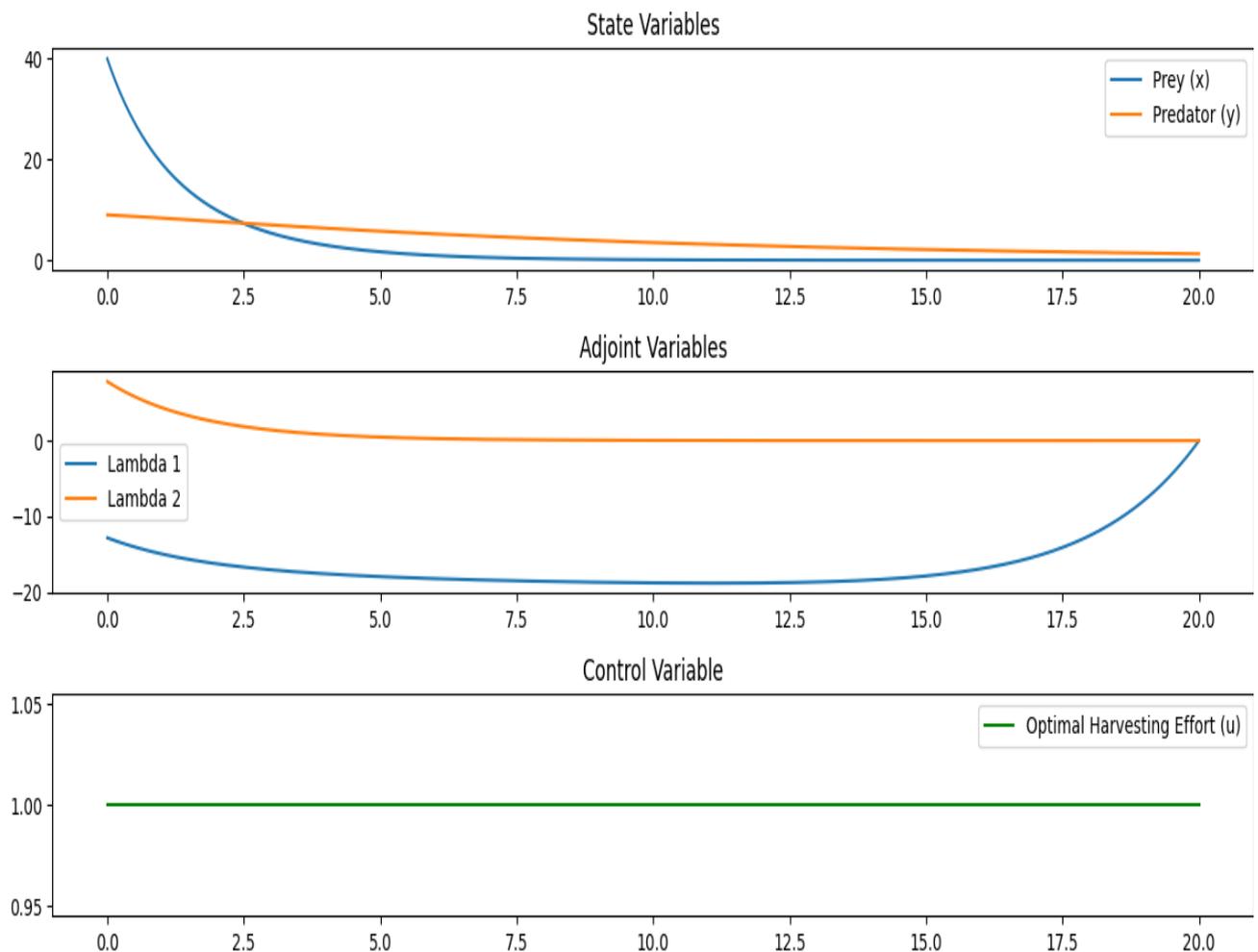


Figure 3: Numerical simulation of optimal harvesting.

Figure 3 illustrates the dynamics of the predator and prey populations under an optimal harvesting strategy, where the harvesting effort is adjusted over time. The top plot shows that both populations remain stable, with the prey population fluctuating within a sustainable range and the predator population responding to changes in prey availability. The middle plot reveals the evolution of the adjoint variables, $\lambda_x(t)(1)$ and $\lambda_y(t)(2)$, which quantify the sensitivity of the optimal control to variations in the prey and predator populations. Finally, the bottom plot demonstrates how the optimal harvesting effort fluctuates over time to balance economic gains with ecological sustainability. This dynamic strategy ensures that both populations are



preserved in the long term, preventing overharvesting and promoting ecological stability, in contrast to the fixed harvesting rate shown in Figure 1.

5 Discussion

This study aimed to derive an optimal harvesting strategy within a deterministic predator-prey model distributed across three interconnected patches that maximizes economic benefits while ensuring ecological sustainability in a three-patch predator-prey ecosystem. An objective functional was formulated to capture the trade-off between harvesting revenue and the cost associated with harvesting effort. Using Pontryagin's Maximum Principle, the Hamiltonian was constructed for each patch, and necessary conditions for optimality were derived. The resulting control law adjusts harvesting effort dynamically in response to real-time prey population levels and adjoint variables. This ensures that prey are not overexploited, which in turn helps sustain predator populations, thus maintaining overall ecological balance.

Numerical simulations for the optimal control problem demonstrated that, unlike fixed-rate harvesting which leads to a gradual decline in both prey and predator populations, the optimal harvesting approach promotes long-term sustainability. Population densities remained within biologically feasible limits, and the system achieved dynamic stability under the optimal control policy. The adjoint variables revealed how control decisions respond sensitively to ecosystem changes, underscoring the benefits of adaptive strategies in resource management. These results highlight the potential of optimal control theory to inform more effective and ecologically sound harvesting policies in spatially structured ecosystems such as cage aquaculture.

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AUTHORS' CONTRIBUTIONS

This work was carried out in collaboration between all authors. All authors read and approved the final manuscript.

Conflict of Interest

Authors have declared that no competing interests exist.



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