

Dynamical Analysis of a Harvesting Model of Phytoplankton-Zooplankton Interaction

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Abstract—In this work, we propose and analyze a model of Phytoplankton-Zooplankton interaction with harvesting considering that some species are exploited commercially for food. Criteria for local stability, instability and global stability are derived and some threshold harvesting levels are explored to maintain the population at an appropriate equilibrium level even if the species are exploited continuously. Further, biological and bionomic equilibria of the system are obtained and an optimal harvesting policy is also analysed using the Pontryagin's Maximum Principle. Finally analytical findings are also supported by some numerical simulations.

Keywords—Phytoplankton-Zooplankton, Global stability, Bionomic Equilibrium, Pontryagin-Maximum Principle.

I. INTRODUCTION

PLANKTON refer to all the plants and animals in marine environment that drift with the oceanic currents as inhabitants of the ocean water. Zooplankton, the planktonic animals, are all weak swimmers, whereas phytoplankton, planktonic plants, do not swim at all. They are the staple item for the food web and are producers and recyclers of most of the energy that flow through the oceanic ecosystem. The phytoplankton species in the pelagic zone are excessive small, microscopic and single-celled, buoyantly supported by the density of the surrounding water which include: Cyanophyta, Bacillariophyta and Xanthophyta. Plankton, especially the phytoplankton play important role not only in aquaculture but they also stabilize environment by consuming half of the universe carbon dioxide and releasing huge oxygen for the living organisms. Aquatic ecologists have long been fascinated by the non-equilibrium dynamics of explosive phytoplankton blooms (i.e., the rapid explosions and declines in their population). Frequent outcome of a planktonic bloom formation, leads to massive cell lysis and rapid disintegration of large planktonic population. This is closely followed by an equally rapid increase in bacterial number, and in turn, by fast deoxygenation of water, which could be detrimental to aquatic plants and animals. Plankton remained fascinated area of the research for the last three decades but now these days some species are exploited for the food such as: Nori, Kelp and Eucheuma are phytoplankton and Jellyfish, Krill and Acetes are zooplankton species. During recent years, many research models were applied to plankton system in the presence of nutrients and role of different

functional forms in phytoplankton-zooplankton interactions were studied [1-7]. In [4] phytoplankton-zooplankton system was studied and it was concluded that the toxin producing phytoplankton may be used as controlling agents for the termination of plankton blooms. So far, not much attention is given on the impact of harvesting on the plankton system. To the best of author's knowledge, recently Lv et al. [8] were the first to propose a harvesting model of toxin producing phytoplankton-zooplankton system in which local and global stability of the various equilibria were studied and concluded that over-exploitation of the system lead to the extinction of the species. Again Lv et al. [9] studied two zooplankton one phytoplankton model with harvesting. They concluded, in the absence of harvesting, the type of zooplankton with the higher biomass conversion ratio and the lower natural death rate persists only whereas harvesting may lead to the persistence of the type of zooplankton with the lower biomass conversion ratio and the higher natural death rate. Following along the lines of Lv et al. [8], in this paper, we assume both the populations grows logistically and the interaction of species are of Holling type-I follows law of mass action [10]. Our paper is organized as follows: In the first section, formation of model, positivity and boundedness is discussed. Second section continues with local and global stability analysis of the boundary and interior equilibrium, in the next section existence of bionomic equilibrium and optimal policy is determined by using Pontryagin's maximal principle. Numerical simulation is carried out in the final section followed by conclusion.

A. Formation of Model

In this section, phytoplankton-zooplankton interaction is modeled with the help of system of simultaneous differential equations with the following assumptions:

- (i) The variable $P(t)$ is the density of the phytoplankton population and Z is the density of zooplankton population at any instant of time t subject to the non-negative initial condition $P(0) = P_0 > 0$ and $Z(0) = Z_0 > 0$.
- (ii) The parameter r_1, r_2 are the intrinsic growth rates and K_1, K_2 are the environmental carrying capacities of phytoplankton and zooplankton population respectively.
- (iii) The constant $\rho_1 > 0$ is the maximum uptake rate for zooplankton species, $\rho_2 > 0$ denotes the ratio of biomass conversion (satisfying the obvious restriction $0 < \rho_2 < \rho_1$).
- (iv) μ_1, μ_2 are the natural death rates of populations and α denotes the rate of toxic substances produced by per unit biomass of phytoplankton.
- (v) The term αPZ describes the distribution of toxic

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substances which ultimately contributes to the death of zooplankton populations where $\rho_2 > \alpha$, i.e. the ratio of biomass consumed by zooplankton is greater than the rate of toxic substance liberation by phytoplankton species.

(vi) Both populations are subjected to constant harvesting with harvesting terms c_1EP , c_2EZ , where c_1 , c_2 are catchability coefficients and constant E is the harvesting effort.

Thus the phytoplankton-zooplankton interaction with above assumptions are represented by

$$\begin{aligned} \frac{dP}{dt} &= r_1P(1 - \frac{P}{K_1}) - (\mu_1 + c_1E)P - \rho_1PZ \\ \frac{dZ}{dt} &= r_2Z(1 - \frac{Z}{K_2}) - (\mu_2 + c_2E)Z + (\rho_2 - \alpha)PZ \end{aligned} \quad (1)$$

with the initial conditions $P(0) = P_0 > 0$, $Z(0) = Z_0 > 0$.

1) *Positivity and Boundedness of Solution*: In this section we discuss the positivity and boundedness of the system (1) under the given initial conditions for all $t \geq 0$. The system equations (1) yields

$$P(t) = P(0) \exp \int_0^t (r_1(1 - \frac{P}{K_1}) - (\mu_1 + c_1E) - \rho_1Z) ds \geq 0 \text{ and}$$

$$Z(t) = Z(0) \exp \int_0^t (r_2(1 - \frac{Z}{K_2}) - (\mu_2 + c_2E) + (\rho_2 - \alpha)P) ds \geq 0$$

$$\text{Further, } \frac{dP}{dt} \leq r_1P(1 - \frac{P}{K_1}) - c_1EP \text{ and } \frac{dZ}{dt} \leq r_2Z(1 - \frac{Z}{K_2}) - c_2EZ$$

By using a standard comparison theorem [11]

$$\limsup_{t \rightarrow +\infty} P(t) \leq \xi_1 \quad \text{and} \quad \limsup_{t \rightarrow +\infty} Z(t) \leq \xi_2$$

$$\text{where } \xi_1 = \text{Max}[P(0), \frac{K_1(r_1 - c_1E)}{r_1}] \text{ and } \xi_2 = \text{Max}[Z(0), \frac{K_2(r_2 - c_2E)}{r_2}]$$

Thus all solution curves of the system (1) with given initial conditions enter the region, $\Gamma = [(P(t), Z(t)) \in R_+^2 : 0 \leq P(t) \leq \xi_1, 0 \leq Z(t) \leq \xi_2]$.

Remark: In biological context boundedness may be interpreted as natural restriction to growth of species due to limited resources.

2) *Stability of equilibria*: The possible steady states of the system (1) are

(i) $R_0 = (0, 0)$, the extinction equilibrium which always exist

(ii) $R_1 = (\frac{r_1(r_2 - \mu_2 - c_2E)K_1}{(r_1 - \mu_1 - c_1E)K_1}, 0)$, zooplankton free equilibrium exist if $E < \frac{r_1 - \mu_1}{c_1}$,

(iii) $R_2 = (0, \frac{r_2(r_2 - \mu_2 - c_2E)K_2}{r_2 - \mu_2 - c_2E})$, zooplankton dominance equilibria exist if $E < \frac{r_2 - \mu_2}{c_2}$, and

(iv) The interior equilibrium $R_* = (P_*, Z_*)$

$$\text{where } P_* = \frac{\frac{r_2(r_1 - \mu_1 - c_1E)}{\rho_1 K_2} - (r_2 - \mu_2 - c_2E)}{(\frac{r_1 r_2}{K_1 K_2 \rho_1} + \rho_2 - \alpha)} \text{ and}$$

$$Z_* = \frac{(r_1 - \mu_1 - c_1E - \frac{r_1 P_*}{K_1})}{\rho_1} \text{ exist if } \frac{r_2 - \mu_2}{c_2} < E < \frac{(r_1 - \mu_1 - \frac{r_1 P_*}{K_1})}{c_1}.$$

The dynamical behaviour of the system around various equilibria is determined by the nature of the eigen values of community matrix,

$$J = \begin{bmatrix} r_1 - \frac{2r_1 P^*}{K_1} - \mu_1 - \rho_1 Z^* & -\rho_1 P^* \\ -c_1 E & r_2 - \frac{2r_2 Z^*}{K_2} + (\rho_2 - \alpha)P^* - \mu_2 - c_2 E \end{bmatrix}$$

At R_0 , the characteristic equation is

$$J(R_0) = \begin{vmatrix} r_1 - \mu_1 - c_1 E - \lambda & 0 \\ 0 & r_2 - \mu_2 - c_2 E - \lambda \end{vmatrix} = 0.$$

The roots of this equation are $\lambda_1 = r_1 - \mu_1 - c_1 E$ and $\lambda_2 = r_2 - \mu_2 - c_2 E$.

Thus R_0 is a stable node if $r_1 - \mu_1 - c_1 E < 0$ and $r_2 - \mu_2 - c_2 E < 0$.

$$\text{i.e. } E > \max[\frac{r_1 - \mu_1}{c_1}, \frac{r_2 - \mu_2}{c_2}].$$

Remark: The biological significance of the above theorem is that, if E crosses a threshold level, the extinction equilibria R_0 becomes stable which further reaffirms the ecologically well known fact that over exploitation would result in population extinction.

Proposition 1. For the system (1), $R_0 = (0, 0)$ always exist and when $E > \max(\frac{r_1 - \mu_1}{c_1}, \frac{r_2 - \mu_2}{c_2})$, it is asymptotically stable. Further when $E < \frac{r_1 - \mu_1}{c_1}$ always hold, R_0, R_1 exists and if $E < \frac{r_1(r_2 - \mu_2) - (r_1 - \mu_1)K_1(\rho_2 - \alpha)}{r_1 c_2 - c_1 K_1(\rho_2 - \alpha)}$, the zooplankton free equilibrium R_1 becomes locally asymptotically stable.

Proposition 2. For the system (1), if $\frac{r_1(r_2 - \mu_2) - (r_1 - \mu_1)K_1(\rho_2 - \alpha)}{r_1 c_2 - c_1 K_1(\rho_2 - \alpha)} < E < \min(\frac{r_1 - \mu_1}{c_1}, \frac{r_2 - \mu_2}{c_2})$, then R_0, R_1 and R_2 exist, and R_0, R_1 become unstable, R_2 is locally asymptotically stable if $E > \frac{r_2(r_1 - \mu_1) - (r_2 - \mu_2)K_2 \rho_1}{r_2 c_1 - c_2 K_2 \rho_1}$.

Next, if the interior equilibrium R_* exists, then the characteristic equation at R_* is,

$$\lambda^2 - \text{trace}J\lambda + \det J = 0 \quad (2)$$

$$\text{where, } \text{Trace}J = (r_1 - \mu_1 - c_1 E) - \frac{2r_1 P^*}{K_1} - \rho_1 Z^* +$$

$$(r_2 - \mu_2 - c_2 E) - \frac{2r_2 Z^*}{K_2} + (\rho_2 - \alpha)P^*$$

$$\text{and } \det J = [(r_1 - \mu_1 - c_1 E) - \frac{2r_1 P^*}{K_1} - \rho_1 Z^*]$$

$$[(r_2 - \mu_2 - c_2 E) - \frac{2r_2 Z^*}{K_2} + (\rho_2 - \alpha)P^*] + \rho_1(\rho_2 - \alpha)P^*Z^*.$$

Theorem 1. For the system (1), if

$$\frac{r_2 - \mu_2}{c_2} < E < \frac{r_1 - \mu_1}{c_1} - \frac{r_1 P_*}{c_1 K_1}, \text{ then } R_* \text{ exists and is locally asymptotically stable if } \text{Trace}J < 0 \text{ and } \det J > 0.$$

For the global stability of the equilibria, we have the following theorem's.

Theorem 2. The extinction equilibria R_0 is globally asymptotically stable (GAS) if

$$E > \max[\frac{r_1 - \mu_1}{c_1}, \frac{r_2 - \mu_2}{c_2}].$$

Proof: Consider the following Lyapunov function

$$V(P, Z) = \frac{1}{\rho_1} P(t) + \frac{1}{\rho_2 - \alpha} Z(t)$$

Its time derivative along the solutions of system (1) yields

$$\begin{aligned} \frac{dV}{dt} &= \frac{(r_1 - \mu_1 - c_1 E)P}{\rho_1} - \frac{r_1 P^2}{\rho_1 K_1} \\ &+ \frac{(r_2 - \mu_2 - c_2 E)Z}{\rho_2 - \alpha} - \frac{r_2 Z^2}{(\rho_2 - \alpha)K_2} \\ &\leq \frac{(r_1 - \mu_1 - c_1 E)P}{\rho_1} + \frac{(r_2 - \mu_2 - c_2 E)Z}{\rho_2 - \alpha} \end{aligned}$$

If $r_1 - \mu_1 - c_1 E < 0$ and $r_2 - \mu_2 - c_2 E < 0$,

then we obtain $\frac{dV}{dt} < 0$.

Further, the Lyapunov theorem on stability [12] implies that all solutions ultimately approach the equilibrium R_0 . This establishes our global result of the equilibrium R_0 .

Theorem 3. The interior equilibrium R^* is globally asymptotically stable (GAS) in the positive quadrant.

Proof of theorem: Let us define a lyapunov function

$$V(P, Z) = \int_{P^*}^P \frac{x - P^*}{x} dx + \frac{\rho_1}{(\rho_2 - \alpha)} \int_{Z^*}^Z \frac{x - Z^*}{x} dx$$

Then $V(P, Z) = 0$ if and only if $P = P^*, Z = Z^*$ and $V(P, Z) \geq 0$ in pz -plane.

The time derivative of V along the trajectories of system is

$$\begin{aligned} \frac{dV}{dt} &= \frac{P - P^*}{P^*} \frac{dP}{dt} + \frac{\rho_1}{(\rho_2 - \alpha)} \frac{Z - Z^*}{Z^*} \frac{dZ}{dt} \\ &= (P - P^*) \left[r_1 - \frac{r_1 P}{K_1} - (\mu_1 + c_1 E) - \rho_1 Z \right] \\ &+ \frac{\rho_1}{(\rho_2 - \alpha)} (Z - Z^*) \left[r_2 - \frac{r_2 Z}{K_2} - (\mu_2 + c_2 E) \right] \\ &+ (\rho_2 - \alpha) P \end{aligned}$$

After some algebraic calculations, we can obtain

$$\frac{dV}{dt} = -\frac{r_1(P - P^*)^2}{K_1} - \frac{\rho_1}{(\rho_2 - \alpha)} \frac{r_2(Z - Z^*)^2}{K_2} < 0$$

Thus $\frac{dV}{dt} \leq 0$ and $\frac{dV}{dt} = 0$ iff $P = P^*$ and $Z = Z^*$. Thus by lasalle's theorem [12], R^* is globally asymptotically stable (GAS) in some neighbour of pz -plane.

B. Non Existence of Periodic Solutions

Theorem 4. System (1) does not have any limit cycle in the positive quadrant of pz -plane.

Proof: For the proof of the above theorem, consider a continuous and differentiable function $D(P, Z) = \frac{1}{PZ}$ in the simple connected domain Ω of the region Γ in the positive quadrant of pz plane.

$$\begin{aligned} \text{Let } H(P, Z) &= r_1 P \left(1 - \frac{P}{K_1} \right) - (\mu_1 + c_1 E) P \\ &- \rho_1 P Z \\ \text{and } G(P, Z) &= r_2 Z \left(1 - \frac{Z}{K_2} \right) - (\mu_2 + c_2 E) Z \\ &+ (\rho_2 - \alpha) P Z \end{aligned}$$

Then

$$\begin{aligned} \Delta(P(t), Z(t)) &= \frac{\partial(DH)}{\partial P} + \frac{\partial(DG)}{\partial Z} \\ &= -\frac{r_1}{K_1 Z} - \frac{r_2}{K_2 P} < 0 \end{aligned}$$

, which is negative. Thus $\Delta(P(t), Z(t))$ neither change sign nor identically zero in the positive quadrant of pz -plane. Therefore Bendixon-Dulac criteria confirm the non-existence of any limit cycles or closed trajectory in the positive quadrant of pz -plane.

C. Bionomic Equilibrium

The bionomic equilibrium is said to be achieved when the total revenue obtained by selling the harvested biomass equals the total cost of harvesting it. Let C be the harvesting cost per unit effort; p_1, p_2 are the prices per unit biomass of the phytoplankton and zooplankton respectively. Then net economic revenue or economic rent at any time t is given by,

$\pi(P, Z, E, t) = (p_1 c_1 P + p_2 c_2 Z - C)E$
The Bionomic equilibrium $(P_\infty, Z_\infty, E_\infty)$, of the phytoplankton-zooplankton system is the solution of the biological equilibrium given by $\frac{dP}{dt} = 0$, $\frac{dZ}{dt} = 0$, which yields

$$\begin{aligned} E &= \frac{r_1}{c_1} \left[\left(1 - \frac{P}{K_1} \right) - \mu_1 - \rho_1 Z \right] \\ &= \frac{r_2}{c_2} \left[\left(1 - \frac{Z}{K_2} \right) + (\rho_2 - \alpha) P - \mu_2 \right] \end{aligned} \quad (3)$$

or

$$\begin{aligned} \left(\frac{r_1}{K_1} + \frac{c_1(\rho_2 - \alpha)}{c_2} \right) P + \left(\rho_1 - \frac{c_1 r_2}{c_2 K_2} \right) Z \\ + \left(\frac{c_1(r_2 - \mu_2)}{c_2} - (r_2 - \mu_1) \right) = 0. \end{aligned} \quad (4)$$

and the economic equilibrium which is said to be achieved when the economic rent is completely dissipated, i.e.

$$\pi(P, Z, E, t) = (p_1 c_1 P + p_2 c_2 Z - C)E = 0. \quad (5)$$

On solving (4), (5) and using (3), we can find the bionomic equilibrium

$$P_\infty = \frac{(r_1 - \mu_1)c_2 - c_1(r_2 - \mu_2) + \frac{C(c_1 r_2 - \rho_1 c_2 K_2)}{c_2^2 p_2 K_2}}{\frac{r_1 c_2}{K_1} + c_1(\rho_2 - \alpha) + \frac{c_1 p_1 (c_1 r_2 - \rho_1 c_2 K_2)}{c_2 p_2 K_2}},$$

which is positive if $\frac{c_1}{c_2} < \min\left(\frac{r_1 - \mu_1}{r_2 - \mu_2}, \frac{\rho_1 K_2}{r_2}\right)$,

$$\begin{aligned} Z_\infty &= \frac{C - c_1 p_1 P_\infty}{c_2 p_2} \text{ exist if } P_\infty < \frac{C}{c_1 p_1} \\ \text{and } E_\infty &= \frac{r_1}{c_1} \left[\left(1 - \frac{P_\infty}{K_1} \right) - \mu_1 - \rho_1 Z_\infty \right] \text{ exist if} \\ P_\infty &< \frac{K_1}{r_1} (r_1 - \mu_1 - \rho_1 Z_\infty). \end{aligned}$$

D. Optimal Harvesting Policy

In this section, the aim is to find an optimal harvesting policy for maximum sustainable yield by; assurance to regulatory agency to achieve its objective. We consider the present value $\mathfrak{R}$ of a continuous time-stream of revenues given by :

$$\mathfrak{R} = \int_0^\infty e^{-\delta t} (p_1 c_1 P(t) + p_2 c_2 Z(t) - C) E(t) dt$$

where δ is the instantaneous rate of annual discount. Thus, our objective is to maximize $\mathfrak{R}$ subject to (1) and to the control constraints $0 \leq E \leq E_{max}$, here E_{max} is the upper limit for the harvesting effort.

By using the Pontryagin Maximum Principle [13], the associated hamiltonian function is given by:

$$\begin{aligned} H = & e^{-\delta t} (p_1 c_1 P + p_2 c_2 Z - C) E + \lambda_1 (r_1 P (1 - \frac{P}{K_1}) \\ & - (\mu_1 + c_1 E) P - \rho_1 P Z) + \lambda_2 (r_2 Z (1 - \frac{Z}{K_2}) \\ & - (\mu_2 + c_2 E) Z + (\rho_2 - \alpha) P Z) \\ = & \sigma(t) E + \lambda_1 (r_1 P (1 - \frac{P}{K_1}) - \mu_1 P - \rho_1 P Z) \\ & + \lambda_2 (r_2 Z (1 - \frac{Z}{K_2}) - \mu_2 Z + \rho_2 P Z - \alpha P Z) \end{aligned}$$

where λ_1, λ_2 are the adjoint operators which satisfy the equations

$$\frac{d\lambda_1}{dt} = -\frac{\partial H}{\partial P}, \quad (6)$$

$$\frac{d\lambda_2}{dt} = -\frac{\partial H}{\partial Z}, \quad (7)$$

and $\sigma(t) = (e^{-\delta t} (p_1 c_1 P + p_2 c_2 Z - C) - \lambda_1 c_1 P - \lambda_2 c_2 Z) E$ represents the switching function [15]. Since the Hamiltonian H is linear in control variable $E(t)$ so in this case only singular control for optimisation problem will be obtained. Thus the necessary condition to maximize the hamiltonian H under the singular control variable $E(t)$ is

$$\frac{\partial H}{\partial E} = 0 \quad (8)$$

So (8) gives:

$$e^{-\delta t} (p_1 c_1 P + p_2 c_2 Z - C) - \lambda_1 c_1 P - \lambda_2 c_2 Z = 0. \quad (9)$$

or it can be written as, $(\lambda_1 c_1 P + \lambda_2 c_2 Z) = e^{-\delta t} \frac{\partial \pi}{\partial E}$, which implies that the total user's cost of harvesting per unit effort is equal to the discounted values of the future price at the steady state effort level.

Now from (6) and (7), we have

$$\begin{aligned} \frac{d\lambda_1}{dt} = & -c_1 p_1 E e^{-\delta t} - \lambda_1 (r_1 - \frac{2r_1 P}{K_1} - (\mu_1 + c_1 E) \\ & - \rho_1 Z) - (\rho_2 - \alpha) Z \lambda_2 \end{aligned} \quad (10)$$

$$\begin{aligned} \frac{d\lambda_2}{dt} = & -c_2 p_2 E e^{-\delta t} + \rho_1 P \lambda_1 - \lambda_2 (r_2 - \frac{2r_2 Z}{K_2} \\ & - (\mu_2 + c_2 E) + (\rho_2 - \alpha) P) \end{aligned} \quad (11)$$

Now in order to find the optimal equilibrium we consider the equilibrium value of E from (3) at R^* as

$$E = \frac{r_1}{c_1} [(1 - \frac{P^*}{K_1}) - \mu_1 - \rho_1 Z^*] = \frac{r_2}{c_2} [(1 - \frac{Z^*}{K_2}) - \mu_2 + (\rho_2 - \alpha) P^*] \quad (12)$$

and using it in (10) and (11), the following system of simultaneous linear equations can be obtained,

$$\frac{d\lambda_1}{dt} = -c_1 p_1 E e^{-\delta t} + \frac{r_1 P^* \lambda_1}{K_1} - (\rho_2 - \alpha) Z^* \lambda_2 \quad (13)$$

$$\frac{d\lambda_2}{dt} = -c_2 p_2 E e^{-\delta t} + \rho_1 P^* \lambda_1 + \frac{r_2 Z^* \lambda_2}{K_2} \quad (14)$$

Eliminating λ_2 from (13) and (14), we have

$$\frac{d\lambda_1}{dt} - M_1 \lambda_1 = -M_2 e^{-\delta t}, \quad (15)$$

$$\begin{aligned} \text{where, } M_1 &= (\frac{r_1}{K_1} + \frac{(\rho_2 - \alpha)c_1}{c_2}) P^* \quad \text{and} \\ M_2 &= c_1 p_1 E + \frac{(\rho_2 - \alpha)}{c_2} (c_1 p_1 P^* + c_2 p_2 Z^* - C) \end{aligned}$$

On solving (15), we get $\lambda_1 = \frac{M_2}{M_1 + \delta} e^{-\delta t}$ and using this value in (14), we obtain

$$\frac{d\lambda_2}{dt} - N_1 \lambda_1 = -N_2 e^{-\delta t} \quad (16)$$

which results into $\lambda_2 = \frac{N_2}{N_1 + \delta} e^{-\delta t}$

$$\text{where } N_1 = \frac{r_2 Z^*}{K_2} \quad \text{and} \quad N_2 = c_2 p_2 E - \rho_1 \frac{M_2}{M_1 + \delta} P^*$$

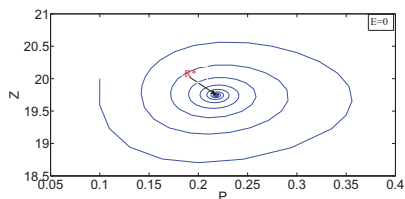
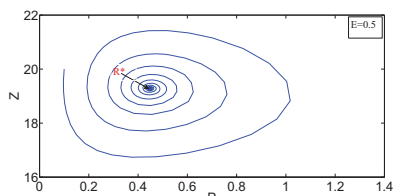
Here $\lambda_i e^{\delta t}$ represents shadow prices [16] along the singular path and from the solution of (15) and (16), it is clear that shadow prices remains constant over time interval in optimal equilibrium when they strictly satisfy the transversality condition at ∞ [14-15]. It implies they remain bounded as $t \rightarrow \infty$. Using the values of λ_1 and λ_2 in (9), the equation of the path of singular control is:

$$c_1 (p_1 - \frac{M_2}{M_1 + \delta}) P + c_2 (p_2 - \frac{N_2}{N_1 + \delta}) Z = C \quad (17)$$

Considering the values of M_1, M_2, N_1 and N_2 at the equilibrium value of E ; (5) and (17) gives the optimal equilibrium of the population of phytoplankton and zooplankton i.e. (P_δ, Z_δ) . Moreover from (3), the corresponding optimal harvesting effort E_δ can be estimated. Now from (17), it can be concluded that

$$\begin{aligned} \pi(P, Z, E) &= c_1 p_1 P + c_2 p_2 Z - C \\ &= (\frac{c_1 M_2}{M_1 + \delta}) P + (\frac{c_2 N_2}{N_1 + \delta}) Z \rightarrow 0 \\ \text{as } \delta &\rightarrow \infty \end{aligned} \quad (18)$$

Therefore, the net economic revenue $\pi(P_\infty, Z_\infty, E, t) = 0$. This implies that in case of infinite discount rate, the net economic revenue becomes zero and harvesting will no longer take place [16]. Moreover (18) shows that, the net economic rent only be maximised in the optimal equilibrium if zero discount rate being offered.

Fig. 1. Stability of the interior equilibrium R_* Fig. 2. Stability of the interior equilibrium R_*

Again equation (18) shows that, $c_1 M_2 (N_1 + \delta) P + c_2 N_2 (M_1 + \delta)$ is of $O(\delta)$ and $(M_1 + \delta)(N_1 + \delta)Z$ of $O(\delta^2)$, thus π is of $O(\delta^{-1})$ and this implies, π (the economic rent function) is a decreasing function of the instantaneous annual rate of discount δ . Hence, $\delta = 0$ leads to maximization of π .

E. Numerical Simulation

(i) Consider the following set of parametric values of the given system ,

$r_1 = 6$, $r_2 = 0.1$, $K_1 = 50$, $K_2 = 30$, $\rho_1 = 0.3$, $\rho_2 = 0.25$, $\alpha = 0.04$, $\mu_1 = 0.05$, $\mu_2 = 0.08$, $c_1 = 0.22$, $c_2 = 0.1$, $E = 0.5$.

It is easy to find

$\frac{r_1 - u_1}{c_1} = 27.0455$, $\frac{r_2 - u_2}{c_2} = 0.2$, $\frac{r_1 - u_1}{c_1} - \frac{r_1 P_*}{c_1 K_1} = 26.8005$, $\text{Trace} J = -0.1182 < 0$ and $\text{Det} J = 0.5490 > 0$.

So, the condition of Theorem 1 holds, then the interior equilibrium $R_* = (0.4490, 19.2871)$ is globally asymptotically stable, which is shown in fig. 1. In the absence of harvesting effort ($E=0$), the globally asymptotically stable equilibrium R_* exists at $(0.2184, 19.7419)$ (see fig. 2).

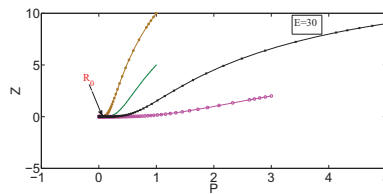
(ii) Choosing $E = 30$, keeping the other parametric values as in (i)

It is easy to verify that $E > \max(\frac{r_1 - u_1}{c_1}, \frac{r_2 - u_2}{c_2}) = \max(27.0455, 0.2) = 27.0455$.

Then the conditions of Theorem 2 are satisfied. Hence the extinction equilibrium R_0 is globally asymptotically stable, which is shown in fig. 3.

(iii) Taking the same set of parametric values in (i) with $p_1 = 2$, $p_2 = 3$, $C = 5.9$, $\delta = 0.03$ and

$E = \frac{r_1}{c_1}[(1 - \frac{P_*}{K_1}) - \mu_1 - \rho_1 Z^*]$ instead taking $E = 0.5$ or 1, we obtain the bionomic equilibrium is $(P_\infty, Z_\infty) = (0.9834, 18.2243)$ and effort value to reach this equilibrium is $E_\infty = 1.6577$. The optimal equilibrium solution is $(P_\delta, Z_\delta) = (0.5137, 18.9132)$ and the effort value to reach this equilibrium is $E_\delta = 0.9745$.

Fig. 3. Stability of the extinction equilibrium R_0

II. CONCLUSION

In this paper, a mathematical model of phytoplankton zoo plankton interactions with harvesting (i.e some species are exploited commercially for food supply) is analysed. It is assumed that, both populations grow logistically and some species of phytoplankton releases toxic substances which reduces the predator's grazing pressure on their prey (phyto plankton) species. Using stability theory of ordinary differential equations the dynamical properties (local and global) of the system along with the effects of harvesting efforts are discussed. It is shown, in case of excessive harvest ing the system never recovered and entire populations goes to extinction. Further, it has been proved that the interior equilibrium exists under certain conditions and it is globally asymptotically stable. Moreover, numerical results shows that, in the absence of harvesting ($E=0$) interior equilibrium exists at lower population level $R_* = (0.0575, 19.8102)$ compared to $R_* = (0.2815, 19.3555)$ (in the presence of harvesting) for the phytoplankton but at a higher population level for the zooplankton. It has also been shown that the system under consideration does not have any limit cycle by using dulac's criterion. Next, the existence of bionomic equilibria (intersection of the zero profit line and the biological equilibrium) and optimal harvesting policy are discussed. The present value of revenues is maximized by using Pontryagin's maximum principle subject to the state equations and the control constraints. It is found that the shadow prices remain constant over time in optimal equilibrium when they satisfy the transversality condition. It is established that the zero discounting leads to the maximization of economic revenue and that an infinite discount rate leads to complete dissipation of economic rent.

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REFERENCES

- [1] A. M. Edwards and J. Brindley, *Oscillatory behaviour in three component plankton population model.*, Dyn. Syst., (1996);11(4):347-370.
- [2] S. Ruan, *Persistence and co-existence in zooplankton-phytoplankton-nutrient models with instantaneous nutrient recycling.*, J. Math. Biol.(1993);31:633-654.

- [3] S. Busenberg, K. S. Kishore, P. Austin, G. Wake, *The dynamics of a model of a plankton-nutrient interaction.*, J. Math. Biol. (1990);52(5): 677-696.
- [4] Chakarborty, S. Roy, J. Chattopadhyay, *Nutrient-limiting toxin producing and the dynamics of two phytoplankton in culture media: A mathematical instantaneous nutrient recycling.*, J. Ecological Modelling. (2008);213(2):191-201.
- [5] S. Pal, S. Chatterjee, J. Chattopadhyay, *Role of toxin and nutrient for the occurrence and termination of plankton bloom-results drawn from field observations and a mathematical model.*, J. Biosystem. (2007);90:87-100.
- [6] R. R. Sarkar, S. Pal, J. Chattopadhyay, *Role of two toxin-producing plankton and their effect on phytoplankton-zooplankton system-a mathematical study by experimental findings.*, J. Biosystem. (2005);80:11-23.
- [7] J. Chattopadhyay, R. R. Sarkar, S. Mandal, *Toxin producing plankton may act as a biological control for planktonic blooms-field study and mathematical modelling.*, J. Biol. Theor. (2002);215(3):333-344.
- [8] Y. F. Lv, Y. Z. Pei, S. J. Gao, C. G. Li, *Harvesting of a phytoplankton-zooplankton model.*, Nonlinear Anal. RWA. (2010);11:3608-3619.
- [9] Y. F. Lv, Y. Z. Pei, C. G. Li, *Evolutionary consequences of harvesting for a two-zooplankton one-phytoplankton system.*, Appl. Math. Modelling (2012);36:1752-1765.
- [10] J. D. Murray, *Mathematical Biology.*, Springer;(2002).
- [11] G. Birkhoff, G. S. Rota, *Ordinary Differential Equations.*, Ginn, Boston; 1882.
- [12] J. La Salle, S. Lefschetz, *Stability by Liapunov's Direct Method with Applications.*, Academic Press: New York, London: 1961.
- [13] L. S. Pontryagin, V. G. Boltyanskii, R. V. Gamkrelidze, E. F. Mishchenko, *The Mathematical Theory of Optimal Processes.*, Pergamon Press: London, 1964.
- [14] C. W. Clark, *Bioeconomic Modelling and Fisheries Management.*, John Wiley and Sons; 1985.
- [15] T. K. Kar, K. S. Chaudhuri, *On non-selective harvesting of a multispecies fishery.*, int. J. Math. Educ. Sci. Technol. 33(2002) 543-556.
- [16] C. W. Clark, *Mathematical Bioeconomics: The Optimal Management of Renewable Resources.*, Wiley, New York: 1976.