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Dynamics of Phytoplankton, Zooplankton and Fishery Resource Model

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Abstract

In this paper, a new mathematical model has been proposed and analyzed to study the interaction of phytoplankton- zooplankton-fish population in an aquatic environment with Holloing's types II, III and IV functional responses. It is assumed that the growth rate of phytoplankton depends upon the constant level of nutrient and the fish population is harvested according to CPUE (catch per unit effort) hypothesis. Biological and bionomical equilibrium of the system has been investigated. Using Pontryagin's Maximum Principal, the optimal harvesting policy is discussed. Chaotic nature and bifurcation analysis of the model system for a control parameter have been observed through a numerical simulation.

Keywords: Stability; control variable; maximum sustainable yield; chaotic behavior; bifurcation

MSC 2010 No.: 34K20, 92D25, 49K15

1. Introduction

The study of prey-predator models have been of great interest for ecologists in the past few decades. The prey-predator models have also been used in phytoplankton-zooplankton-fish interactions to study the spatiotemporal pattern [Steele and Henderson (1981); Scheffer (1991);

Pascual (1993)] and local and temporal chaos [Sherratt et al. (1995); Petrovskii and Malchow (1999, 2001); Malchow et al. (2002); Upadhay et al. (2008)]. Modeling of phytoplankton-zooplankton interaction takes into account zooplankton grazing with saturating functional response to phytoplankton abundance called Michaelis-Menten models of enzyme kinetics [Michaelis and Menten (1913)]. The oscillatory behavior of phytoplankton and zooplankton has extensively been studied by several researchers [Steele and Handerson (1981, 1992a, 1992b), Scheffer (1991, 1998), Truscott and Brindley (1994a, 1994b)]. Dubois (1975) proposed a nonlinear partial differential equation model with the Lotka-Volterra type ecological interaction taking into account advection and eddy diffusivity. Vilar et al. (2003) showed that biotic fluctuations and turbulent diffusion in standard prey-predator models are able to explain plankton field observations which include not only the spatial pattern but also its temporal evolution. Morozov and Arashkevich (2008) proposed a simple model explaining the observed alternations of functional response. They observed that the overall response of zooplankton exhibits different behavior compared to the patterns of the local response.

To study the effects of space and time on the interacting species, Jansen (1995) extended the scope of the simple Lotka-Volterra system and Rosenzweig-McAurthur model to a patchy environment. Temporal and spatiotemporal chaos in population dynamics have been observed by many authors [Hanski et al. (1993); Becks et al. (2005); Xiao et al. (2006); Liu et al. (2008); Malchow et al. (2008)]. Upadhyay et al. (2008) proposed a phytoplankton- zooplankton -fish interaction model with Holling type IV functional response and studied the wave of chaos and pattern formation. Comparing with the empirical evidence from a different predator-prey model, Skalski and Gilliam (2001) pointed out that the predator-dependent functional responses could provide better descriptions of predator feeding over a range of predator-prey abundance, and in some cases, the Beddington –DeAngelis type functional response performed even better [Liu and Edoardo (2006)]. Upadhyay et al. (2009, 2010) investigated the wave phenomena and nonlinear non-equilibrium pattern formation in a spatial plankton-fish system with Holling type II and IV functional responses.

Holling type III functional response has also been used to demonstrate cyclic collapses for representing the behavior of predator hunting [Real (1977); Ludwig et al. (1978)]. This response function is sigmoid, rising slowly when prey are rare, accelerating when they become more abundant, and finally reaching a saturated upper limit. Keeping the above mentioned properties in mind, we have considered the zooplankton grazing rate on phytoplankton and the zooplankton predation by fish follows a sigmoidal functional response of Holling type III. Misra (2011) also studied the depletion of dissolved oxygen due to algal boom in a lake with Holling type III interaction. Shukla et al. (2011) proposed and analyzed a mathematical model to study the depletion of a renewable resource by population and industrialization. They showed that density of the resource biomass decreases due to increase in densities of population and industrialization. It decreases further as the resource dependent industrial migration increases. However, the resource biomass can be maintained at an appropriate level if suitable technological efforts are applied for its conservation. Recently, Shukla et al. (2012) studied the effect of acid rain formed by precipitation on the plant species. They showed that the plant species may become extinct if the rate of formation of acid rain is very high. In these studies [Misra (2008, 2011); Shukla et al. (2007, 2011, 2012)] the interaction considered are either linear or bilinear. Kar and Chudhuri (2004) studied the bio-economic equilibrium and optimal harvesting policy of Lotka-Volterra model consisting of two prey species in the presence of a predator. In this article, they have considered the predator functional response in which the feeding rate of the predator increases linearly with the prey density. Kar et al. (2009) further extended the above idea for two prey and one predator system by considering the predator functional response as Holling type I for one prey while for the other prey it is of Holling type II. Kar et al. (2010) further proposed a prey-predator model with non-monotonic functional response and showed the existence of super critical Hopf bifurcation.

In this paper, we extend the two-dimensional model studied by Upadhyay et al. (2010) into a three-dimensional model by considering the fish population as a dynamical variable. We assume that the grazing rate of zooplankton is dependent on the phytoplankton concentration according to a type IV functional response [Upadhyay et al. (2008)] while the predation rate of fish on zooplankton is of type III and on phytoplankton is of type II (Gentleman et al. (2003)). We further assume that the fish population is growing logistically and is harvested according to catch-per-unit-effort (CPUE) hypothesis (Clark (1976)). It may be pointed out here that our model proposed in this paper is much more general than those studied in Kar and Choudhuri (2004) , Kar et al. (2009, 2010) and Upadhyay et al. (2010).

2. The Mathematical Model

Let us consider a habitat consisting of the phytoplankton of density P, zooplankton of density Z and fish population of density F, at any time $T \geq 0$. Keeping the assumptions discussed in the introduction in our mind, and following our previous work [Upadhyay et al. (2010)], the dynamics of the system may be governed by the following system of differential equations:

$$\frac{dP}{dT} = \frac{\xi NP}{H_N + N} - \rho P^2 - \frac{cPZ}{\frac{P^2}{i} + P + a} - \frac{\xi_0 PF}{1 + \xi_0 hP}, \tag{1a}$$

$$\frac{dZ}{dT} = \frac{bcPZ}{\frac{P^2}{i} + P + a} - mZ - \frac{FZ^2}{H_z^2 + Z^2}, \tag{1b}$$

$$\frac{dF}{dT} = s_0 F\left(1 - \frac{F}{K_0}\right) + \frac{\theta_0 FZ^2}{H_z^2 + Z^2} + \frac{\theta_1 \xi_0 PF}{1 + \xi_0 hP} - q_1 EF, \tag{1c}$$

Interactions involved in the minimal model system (1a)-(1b) are pictorially represented in Figure1.

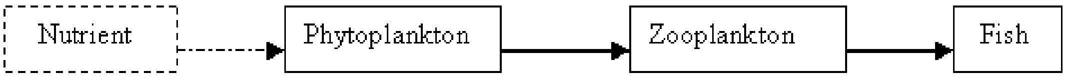

Figure 1. Interactions incorporated in the model system

The interaction part of the model system investigated is depicted by solid arrows. The interaction involving dotted arrows indicates that either of the positive or negative effects involved is considered in the model.

In this model system (1a)-(1c), N is the nutrient level of the system which is assumed to be constant. The nutrient level is increased due to eutrophication. The phytoplankton require both inorganic (phosphorous, nitrogen, iron, silicon, etc.) and organic (vitamins) nutrients for growth. However, excessive nutrients in coastal water can cause excessive growth of phytoplankton, microalgae and macroalgae. An excessive increase in phytoplankton and algae can lead to severe secondary impacts such as – (i) reduction of light which decreases the subaquatic vegetation, (ii) inhibition of the growth of coral reef as nutrient levels favor algae growth over coral larvae, (iii) reduction in the level of dissolved oxygen forming an oxygen-depleted water zone which may cause the ecosystem to collapse. In the present paper, we assume that the phytoplankton grows with a Monod type of nutrient limitation. Growth limitations by different nutrients are same. Instead, it is assumed that there is an overall carrying capacity which is a function of the nutrient level of the system and the phytoplankton do not deplete the nutrient level. ξ is the maximum per capita growth rate of prey population, H_N is the phytoplankton density at which specific growth rate becomes half its saturated value. ρ is the intraspecific interference coefficient of phytoplankton population , c is the rate at which phytoplankton is grazed and it follows Holling Type IV functional response, i is the direct measure of the predator's immunity from or tolerance of the prey, a is the half saturation constant in the absence of any inhibitory effect, b is the conversion coefficient from individuals of phytoplankton into individuals of zooplankton, m is the morality rate of zooplankton.

It is assumed that the zooplankton population is predated by fish which follows Holling Type III functional response and H_z is the zooplankton density at which specific growth rate becomes half its saturation value. It is further assumed that phytoplankton is predated by fish according to type II functional response. The fish population grows logistically with intrinsic growth rate s_0 and carrying capacity K_0 . θ_0 and θ_1 are conversion coefficients ($0<\theta_0,\theta_1<1$) of phytoplankton and zooplankton respectively. The fish population is harvested according to catch-per unit-effort (CPUE) hypothesis and q_1 is the catchability coefficient. Here harvesting effort is a control variable.

We introduce the following substitution and notations to bring the system of equations into non-dimensional form

$$\frac{\xi N}{H_N+N}=r,\ \frac{r}{\rho}=a,\ \alpha=\frac{i}{a},\ \beta=\frac{bc}{r},\ \gamma=\frac{m}{r},\ x=\frac{Fc}{ar^2},\ \eta=\frac{cH_Z}{ar},$$

$$u=\frac{P}{a}\ ,\ v=\frac{cZ}{ar},\ t=rT\,,\alpha_0=\frac{ar\xi_0}{c},\ \alpha_1=a\xi_0 h\,,\ \alpha_2=\frac{\theta_1\xi_0 a}{r},\ s=\frac{s_0}{r},$$

$$K=\frac{cK_0}{ar^2},\ \delta_0=\frac{\theta_0}{r},\ q=\frac{q_1}{r}.$$

Using these parameters, the model system (1a)-(1c) in dimensionless form reduced to

$$\frac{du}{dt} = u\left(1-u\right) - \frac{uv}{\frac{u^2}{\alpha}+u+1} - \frac{\alpha_0 ux}{1+\alpha_1 u}\ , \tag{2a}$$

$$\frac{dv}{dt} = \frac{\beta uv}{\frac{u^2}{\alpha}+u+1} - \gamma v - \frac{xv^2}{v^2+\eta^2}\ , \tag{2b}$$

$$\frac{dx}{dt} = sx\left(1-\frac{x}{K}\right) + \frac{\delta_0 xv^2}{\eta^2+v^2} + \frac{\alpha_2 xu}{1+\alpha_1 u} - qEx, \tag{2c}$$

with initial condition $u(0) > 0,\ v(0) > 0,\ x(0) > 0.$

α is the parameter measuring the ratio of the predator's immunity from or tolerance of the prey to the half-saturation constant in the absence of any inhibitory effect, β is the parameter measuring the ratio of product of conversion coefficient with grazing rate to the product of intensity of competition among individuals of phytoplankton with carrying capacity, γ is the per capita predator death rate.

In the next section, we present the analysis of model (2a)-(2c).

3. Stability Analysis

In the following lemma, we state a region of attraction for the model system (2a)-(2c).

Lemma 1.

The set

$$\Omega = \left\{(u,v,x) : 0 \le \beta u(t) + v(t) \le \frac{2\beta}{\delta_1}, 0 \le x(t) \le L\right\} \tag{3}$$

is a region of attraction of all solutions initiating in the interior of positive octant Ω, where

$$\delta_1 = \min(1,\gamma),$$
$$L = \frac{K}{s}\left(s + \frac{\alpha_2}{1+\alpha_1} + \frac{4\beta^2\delta_0^2}{4\beta^2+\delta_1^{\,2}\eta^2}\right).$$

The above lemma shows that all solutions of the model (2a)-(2c) are non-negative and bounded, which shows that the model is biologically well-behaved.

Proof:

The proof of this lemma is similar to Freedman and So (1985), Shukla and Dubey (1997), hence omitted.

Now, we discuss the equilibrium analysis of the model. The model (2a)-(2c) has six non-negative equilibrium points, viz,

$$P_0(0,0,0),\ P_1(1,0,0),\ P_2(0,0,\bar{\bar{x}}),\ P_3(\bar{u},\bar{v},0),\ P_4(\hat{u},0,\hat{x}) \text{ and } P(u^*,v^*,x^*).$$

It may be noted here that the equilibrium points P_0, and P_1 always exist.

For the point P_2, $\bar{\bar{x}}$ is given by $\bar{\bar{x}} = \frac{K}{s}(s-qE)$ and it exists iff $s > qE$.

In the equilibrium point P_3, $\bar{u}$ and $\bar{v}$ are the positive solutions of the following equations:

$$(1-u) - \frac{v}{\left(\frac{u^2}{\alpha}+u+1\right)} = 0, \tag{4a}$$

$$\frac{\beta u}{\left(\frac{u^2}{\alpha}+u+1\right)} - \gamma = 0. \tag{4b}$$

From (4a) and (4b) we get

$$v = (1-u)\left(\frac{u^2}{\alpha}+u+1\right), \tag{4c}$$

and

$$\gamma u^2 - \alpha(\beta-\gamma)u + \alpha\gamma = 0\ . \tag{4d}$$

From (4d), we note the following:

i) When $\beta - \gamma = \frac{2\gamma}{\sqrt{\alpha}}$, then equation (4d) has a unique root, namely,

$$u = \bar{u}_1 = \frac{\alpha(\beta-\gamma)}{2\gamma} = \sqrt{\alpha}\ .$$

In such case, equilibrium $P_3^1(\bar{u}_1, \bar{v}_1, 0)$ exists, where

$$\bar{u}_1 = \frac{\alpha(\beta-\gamma)}{2\gamma} = \sqrt{\alpha},$$
$$v_1 = \bar{v}_1 = (1-\bar{u}_1)\left(\frac{\bar{u}_1^2}{\alpha} + \bar{u}_1 + 1\right),$$

under the condition $0 < \sqrt{\alpha} < 1$.

ii) When $\beta - \gamma > \frac{2\gamma}{\sqrt{\alpha}}$ *i.e.* $\frac{\beta}{\gamma} > 1 + \frac{2\gamma}{\sqrt{\alpha}}$,

then equation (4d) has two distinct positive real roots, namely,

$$\bar{u}_2 = \frac{\alpha}{2\gamma}\left[(\beta-\gamma) + \sqrt{(\beta-\gamma)^2 - \left(\frac{2\gamma}{\sqrt{\alpha}}\right)^2}\right],$$

$$\bar{u}_3 = \frac{\alpha}{2\gamma}\left[(\beta-\gamma) - \sqrt{(\beta-\gamma)^2 - \left(\frac{2\gamma}{\sqrt{\alpha}}\right)^2}\right].$$

Thus, in this case we have two equilibrium points $P_3^2(\bar{u}_2, \bar{v}_2, 0)$ and $P_3^3(\bar{u}_3, \bar{v}_3, 0)$, where $\bar{v}_2$ and $\bar{v}_3$ are calculated from equation (4c).

Now, to show the existence of the equilibrium point $P_4(\hat{u}, 0, \hat{x})$, we note that $\hat{u}$ and $\hat{x}$ are the positive solutions of the two equations:

$$(1-u) - \frac{\alpha_0 x}{1+\alpha_1 u} = 0, \tag{5a}$$

and

$$s\left(1 - \frac{x}{K}\right) + \frac{\alpha_2 u}{1+\alpha_1 u} - qE = 0. \tag{5b}$$

From (5a),

$$x = \frac{1}{\alpha_0}(1-u)(1+\alpha_1 u), \tag{5c}$$

Clearly, $x > 0$ if $u < 1$. (5d)

Substituting the value of x from (5c) into (5b), we get

$$a_1 u^3 + a_2 u^2 + a_3 u + a_4 = 0, \tag{5e}$$

where

$$a_1 = s\alpha_1^2, \;\; a_2 = s\alpha_1(2-\alpha_1),$$
$$a_3 = (s\alpha_0\alpha_1 K - 2\alpha_1 s + s + \alpha_0\alpha_2 K - q\alpha_0\alpha_1 KE), \;\; a_4 = s\alpha_0 K - s - q\alpha_0 KE.$$

Using the Decarte's rule of sign, it may be noted that equation (5e) has a positive real root if

$$\frac{\alpha_0 K}{s}(s - qE) < 1. \tag{5f}$$

This shows that $P_4(\hat{u}, 0, \hat{x})$ exists under conditions (5d) and (5f).

Existence of interior equilibrium point $P^*(u^*, v^*, x^*)$: in this case u^*, v^* and x^* are the positive solutions of following three equations:

$$(1-u) - \frac{v}{\frac{u^2}{\alpha} + u + 1} - \frac{\alpha_0 x}{1+\alpha_1 u} = 0, \tag{6a}$$

$$\frac{\beta u}{\frac{u^2}{\alpha} + u + 1} - \gamma - \frac{xv}{\eta^2 + v^2} = 0, \tag{6b}$$

$$s\left(1 - \frac{x}{K}\right) + \frac{\delta_0 v^2}{\eta^2 + v^2} + \frac{\alpha_2 u}{1+\alpha_1 u} - qE = 0. \tag{6c}$$

From equation (6a), we get

$$v = \left[(1-u) - \frac{\alpha_0 x}{1+\alpha_1 u}\right]\left(\frac{u^2}{\alpha} + u + 1\right) \; . \tag{6d}$$

Clearly,

$$v > 0 \text{ if } (1-u)(1+\alpha_1 u) > \alpha_0 x, \tag{6e}$$

Putting the value of v from (6d) into equations (6b and 6c) we get two equation in u and x.

These two functions are given below:

$$\frac{\beta u}{\left(\frac{u^2}{\alpha}+u+1\right)} - \gamma - \frac{x\left(\frac{u^2}{\alpha}+u+1\right)\left\{(1-u)-\frac{\alpha_0 x}{1+\alpha_1 u}\right\}}{\eta^2 + \left(\frac{u^2}{\alpha}+u+1\right)^2 \left\{(1-u)-\frac{\alpha_0 x}{1+\alpha_1 u}\right\}^2} = 0 = F_1(u,x), \quad \text{(say)} \tag{7a}$$

$$s\left(1-\frac{x}{K}\right) + \frac{\delta_0 \left(\frac{u^2}{\alpha}+u+1\right)^2 \left\{(1-u)-\frac{\alpha_0 x}{1+\alpha_1 u}\right\}^2}{\eta^2 + \left(\frac{u^2}{\alpha}+u+1\right)^2 \left\{(1-u)-\frac{\alpha_0 x}{1+\alpha_1 u}\right\}^2} + \frac{\alpha_2 u}{1+\alpha_1 u} - qE = 0 = F_2(u,x), \text{(say)}. \tag{7b}$$

From (7a), we note the following:

i) when $u = 0$, $F_1(0,x) = 0$ has a real root x_a which is given by

$$x_a = \frac{(2\alpha_0\gamma - 1) - \sqrt{1+4\alpha_0\gamma\eta^2(1-\alpha_0\gamma)}}{2\alpha_0(\alpha_0\gamma - 1)}.$$

We note that $x_a > 0$ if $\alpha_0\gamma < 1$. (8a)

ii) When $x = 0$, then $F_1(u,0) = 0$ has a real root u_a which is given by

$$u_a = \frac{\alpha}{2\gamma}\left[(\beta-\gamma) + \sqrt{(\beta-\gamma)^2 - \left(\frac{2\gamma}{\sqrt{\alpha}}\right)^2}\right].$$

We note that $u_a > 0$ if $\frac{\beta}{\gamma} > 1 + \frac{2}{\sqrt{\alpha}}$. (8b)

Let F_{1x} and F_{1u} be the partial derivatives of F_1 with respect to x and u, respectively. Then, let

$$\frac{du}{dx} = -\frac{F_{1x}}{F_{1u}}, \text{ where } F_{1u} \neq 0.$$

It may be noted that

$$\frac{du}{dx} < 0, \text{ if } \left.\begin{array}{l}\text{either } i)\ F_{1x} > 0 \text{ and } F_{1u} > 0, \\ \text{or, } \quad ii) F_{1x} < 0 \text{ and } F_{1u} < 0.\end{array}\right\} \tag{8c}$$

From (7b), we note the following:

i) When $u = 0$, $F_2(0, x) = 0$ has a positive real root x_b if $(qE - s)(\eta^2 + 1) < \delta_0$, (9a)

ii) $\dfrac{du}{dx} = -\dfrac{F_{2x}}{F_{2u}}$.

Clearly,

$$\frac{du}{dx} > 0, \text{ if } \left.\begin{array}{l}\text{either } i)\ F_{2x} > 0 \text{ and } F_{2u} < 0, \\ \text{or, } \quad ii) F_{2x} < 0 \text{ and } F_{2u} > 0,\end{array}\right\} \text{ holds.} \tag{9b}$$

From the above analysis, we note that the isoclines (7a) and (7b) intersect at a unique point (u^*, x^*), if in addition to conditions (8a)-(9b), the following condition

$$x_b < x_a \ . \tag{9c}$$

This completes the existence of interior equilibrium $P^*(u^*, v^*, x^*)$.

Now we discuss the local and global stability behavior of these equilibrium points. For local stability analysis, first we find the variational matrices with respect to each equilibrium point. Then, by using eigenvalue method and the Routh-Hurwitz criteria, we get the following results.

i) The point $P_0(0,0,0)$ is always a saddle point. In fact, P_0 has a unstable manifold in the $u-$direction and stable manifold in the $v-$direction. P_0 is stable or unstable in the x-direction according as $(s - qE)$ is negative or positive.

ii) The point $P_1(1,0,0)$ is locally asymptotically stable if $\gamma > \dfrac{\alpha\beta}{2\alpha + 1}$ and $qE > s + \dfrac{\alpha_2}{1 + \alpha_1}$, otherwise it is a saddle point. It may be noted that P_1 has always stable manifold in the $u-$direction.

iii) The point P_2, whenever it exists, is locally asymptotically stable if $K > \dfrac{s}{\alpha_0(s - qE)}$. If $K < \dfrac{s}{\alpha_0(s - qE)}$, then P_2 is a saddle point with stable manifold in the $v - x$ plane and unstable manifold in the u-direction.

iv) If the following inequalities hold:

a) $\frac{1}{2} < \sqrt{\alpha} < 1$,

b) $qE > s + \frac{\delta_0 \overline{v}_1^2}{\overline{v}_1^2 + \eta^2} + \frac{\alpha_2 \overline{u}_1}{1 + \alpha_1 \overline{u}_1}$,

where $u_1 = \sqrt{\alpha}$, $v_1 = (1 - \sqrt{\alpha})(2 + \sqrt{\alpha})$, then the point $P_3^1(\overline{u}_1, \overline{v}_1, 0)$ is locally asymptotically stable. Otherwise, $P_3^1(\overline{u}_1, \overline{v}_1, 0)$ is a saddle point with stable manifold in the v – direction and unstable manifold in the ux – plane.

v) If the following inequalities hold:

a) $$s + \delta_0 \frac{(1-\overline{u}_i)^2 \left(\frac{\overline{u}_i^2}{\alpha} + \overline{u}_i + 1 \right)^2}{\eta^2 + (1-\overline{u}_i)^2 \left(\frac{\overline{u}_i^2}{\alpha} + \overline{u}_i + 1 \right)^2} + \alpha_2 \frac{\overline{u}_i}{1 + \alpha_1 \overline{u}_i} - qE < 0,$$

b) $\overline{u}_i^2 < \alpha < 1$,

c) $\overline{u}_i > \frac{2}{3}(1 - \alpha)$,

where $i = 2, 3$, then $P_3^i(\overline{u}_i, \overline{v}_i, 0)$ is locally asymptotically stable.

vi) The point $P_4(\hat{u}, 0, \hat{x})$ is locally asymptotically stable if $\beta \hat{u} < \gamma(\frac{\hat{u}^2}{\alpha} + \hat{u} + 1)$.

If $\beta \hat{u} > \gamma(\frac{\hat{u}^2}{\alpha} + \hat{u} + 1)$, then P_4 is a saddle point with stable manifold in the ux -plane and unstable manifold in the v -direction.

The stability behavior of the interior equilibrium point P^* is not obvious from the variational matrix. However, with the help of Liapunov's direct method, we are able to find sufficient conditions for P^* to be locally asymptotically stable. We state these results in the following theorem.

We use the following notations:

$$L_1 = \frac{v^*}{\left(\frac{u^{*2}}{\alpha}+u^*+1\right)^2}\left(1+\frac{2u^*}{\alpha}\right)+\frac{\alpha_0\alpha_1 x^*}{(1+\alpha_1 u^*)^2}\ , \tag{10a}$$

$$L_2 = \left[\frac{v^*(u^*+\alpha+1)}{\alpha\left(\frac{u^{*2}}{\alpha}+u^*+1\right)}+\frac{\alpha_0\alpha_1 x^*}{(1+\alpha_1 u^*)}\right], \tag{10b}$$

$$c_1 = \frac{2\alpha_0\delta_0\eta^2 u^*(1+\alpha_1 u^*)}{\alpha_2 v^*(\eta^2+v^{*2})},\ c_2 = \frac{\alpha_0 u^*(1+\alpha_1 u^*)}{\alpha_2 x^*}\ , \tag{10c}$$

$$d_1 = \left(\frac{2K\alpha_0\delta_0^2(1+\alpha_1 u^*)}{s\alpha_2 x^*(\eta^2+v^{*2})}\right)\left(\frac{\left(\frac{2\beta}{\delta_0}+v^*\right)^2\left(\eta^2+\frac{4\beta^2}{\delta_0^2}\right)}{\left(\eta^2-\frac{2\beta v^*}{\delta_0}\right)}\right),\quad d_2 = \frac{\alpha_0(1+\alpha_1 u^*)}{\alpha_2}\ . \tag{10d}$$

Theorem 1.

Let the following inequalities hold:

$$L_1 < 1, \tag{11a}$$

$$v^* < \eta\,, \tag{11b}$$

$$\left(\frac{u^*}{\left(\frac{u^{*2}}{\alpha}+u^*+1\right)}+c_1\frac{\beta v^*\left(1-\frac{u^{*2}}{\alpha}\right)}{\left(\frac{u^{*2}}{\alpha}+u^*+1\right)^2}\right)^2 < c_1 u^* L_1\left(\frac{v^* x^*(\eta^2-v^{*2})}{(\eta^2+v^{*2})^2}\right), \tag{11c}$$

then P^* is locally asymptotically stable.

Proof:

Proof of this theorem is given in Appendix-A.

Theorem 2.

Let the following inequalities hold in Ω:

$$L_2 < 1, \tag{12a}$$

$$2\beta v^* < \delta_0 \eta^2, \tag{12b}$$

$$\left(d_1\beta + 1 + \frac{d_1\beta u^*(u^* + \alpha + 1)}{\alpha\left(\frac{u^{*2}}{\alpha} + u^* + 1\right)} \right)^2 < (1 - L_2)\left(\frac{d_1 x^*}{\left(\eta^* + \frac{4\beta^2}{\delta_0^2}\right)(\eta^2 + v^{*2})} \left(\frac{\delta_0\eta^2 - 2\beta v^*}{\delta_0} \right) \right), \tag{12c}$$

then P^* is globally asymptotically stable with respect to all solutions initiating in the interior of the positive octant Ω.

Proof:

Proof of this theorem is given in Appendix-B.

4. Numerical Simulation Results

For the numerical integration of the model system, we have used the Runge-Kutta fourth order procedure on the MATLAB 7.0 platform. The dynamics of the model system (2) is studied with the help of numerical simulation. We choose the following set of values of parameters:

$$\begin{aligned} &\alpha_0 = 0.2,\ \alpha_1 = 0.001,\ \beta = 3.33,\ \gamma = 0.25,\ \eta = 2.5,\ s = 1.9,\ K = 150,\ \delta_0 = 4.1, \\ &\alpha_2 = 5.5,\ qE = 3.9,\ \alpha = 0.17. \end{aligned} \tag{13a}$$

These parameter values are selected on the basis of values given by Letellier and Aziz-Alaoui (2002). It is observed that model system (2) has a chaotic solution for the above set of parameter values (see Figure 2). The time series for these populations are presented in Figure 3. The chaotic nature of the model system is confirmed by SIC test and is presented in Figure 4a and 4b.

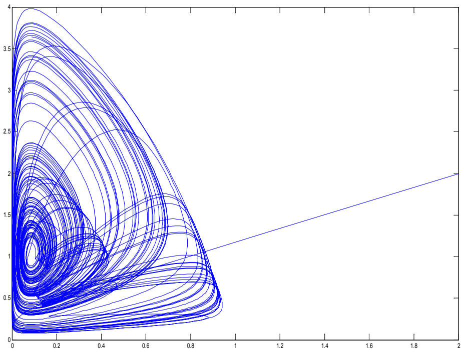

Figure 2. Chaotic attractor for the parameter values given in (13a)

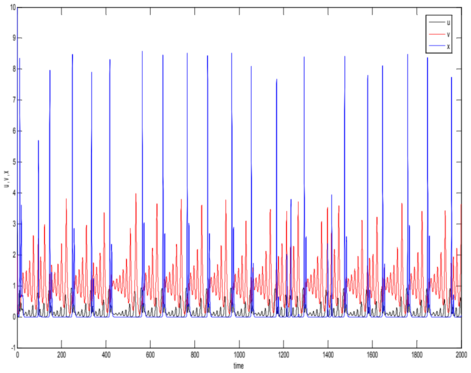

Figure 3. Time series for *u, v, x* species

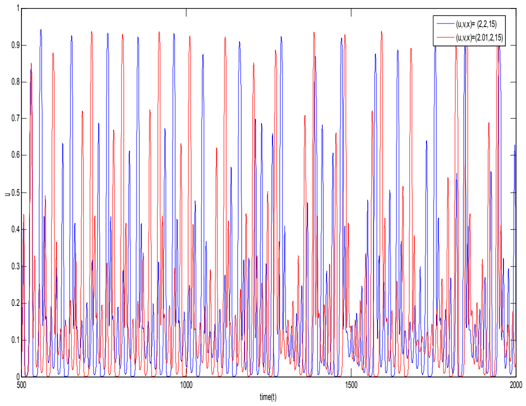

Figure 4a. SIC in species *u*

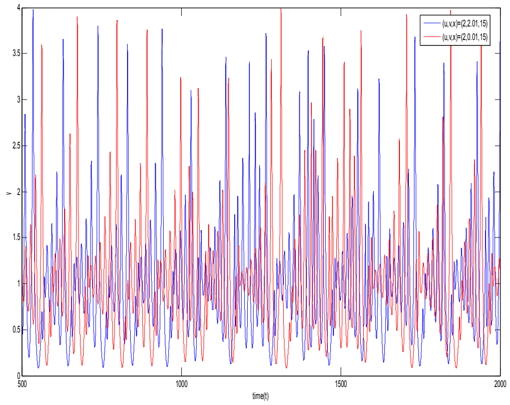

Figure 4b. SIC in species *v*

The stable focus is obtained [see Figure 5] for the following set of parameter values

$$\alpha = 1.8,\ \alpha_0 = 0.25,\ \alpha_1 = 0.001,\ \beta = 4.93,\ \gamma = 0.25,\ \eta = 2.5,\ s = 3.2,\ K = 150,\ \delta_0 = 5.2,\ \alpha_2 = 5.5,\ qE = 3.8. \tag{13b}$$

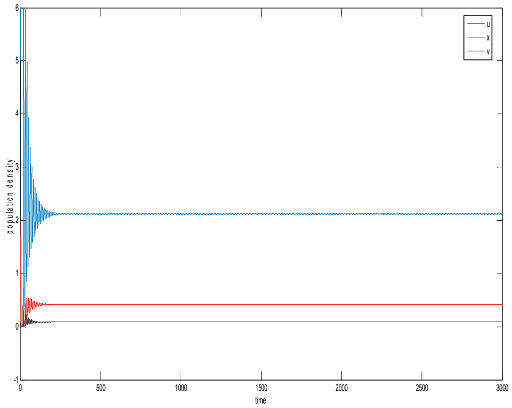

Figure 5. Time series for u, v, x species showing the stable focus for the parameter values given in (13b)

A bifurcation diagram of model system (2) is plotted in Figure 6 and the blow-up bifurcation diagram is presented in Figure 7 and 8 in the different ranges for the control parameter, α, measuring the ratio of the predator's immunity from or tolerance of the prey to the half-saturation constant in the absence of any inhibitory effect. This figure exhibits the transition from chaos to order through a sequence of period halving bifurcations. The blow-up bifurcation diagrams show that the model system possesses a rich variety of dynamical behavior including KAM tori for bifurcation parameter α in the ranges [0.34, 0.36] and [0.33, 0.35]. Closed curve in this diagram correspond to invariant KAM tori in the phase space. Later on, theses curves break and give rise to chaotic dynamics. The chaotic behavior of the system is not continuing further, as the unstable period-3 orbits which originate at the time of saddle-node bifurcation do not allow it to move further. The bifurcation diagram are plotted with the help of software – "Dynamics: Numerical exploration" developed by Nusse and Yorke (1994).

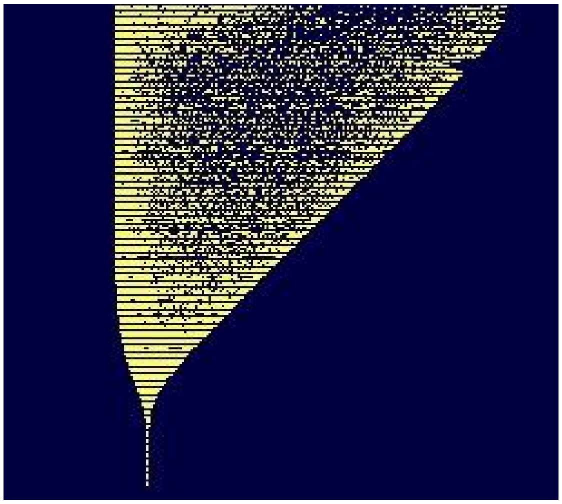

Figure 6. Bifurcation diagram in the ranges $u \in [-2,2]$, $\alpha \in [0.1,3]$.

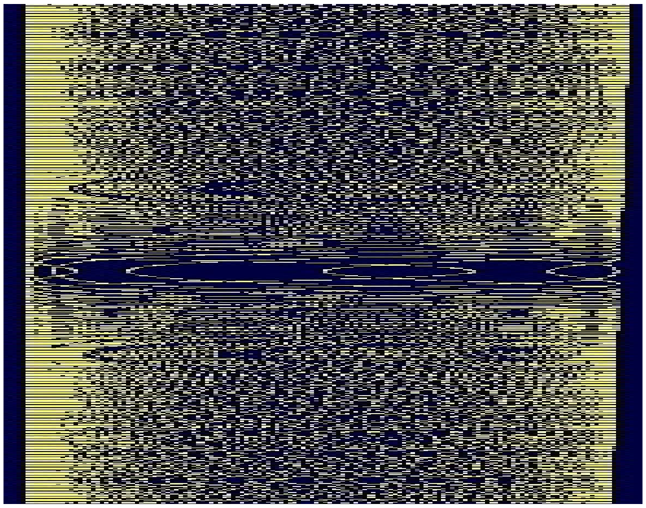

Figure 7. Magnified bifurcation diagram in the ranges $u \in [-2,2]$, $\alpha \in [0.34,0.36]$

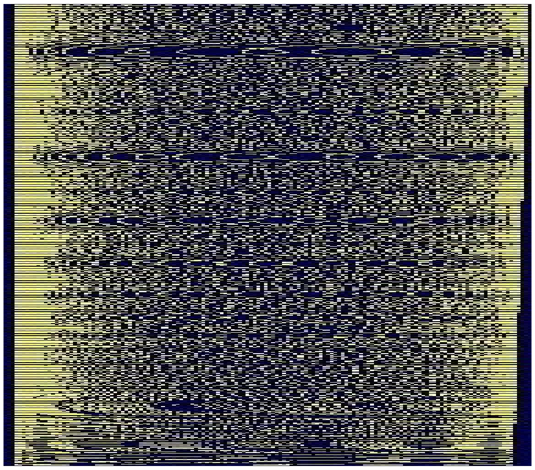

Figure 8. Magnified bifurcation diagram in the ranges $u \in [-2,2]$, $\alpha \in [0.33,0.35]$

5. Bionomical Equilibrium

The net economic revenue at time t is given by

$$\pi(x,E,t) = (pqx - c)E, \tag{14a}$$

p is the price per unit harvested fish and c is the cost per unit effort. The bionomical equilibrium is $P_\infty(u_\infty, v_\infty, x_\infty, E_\infty)$, where $u_\infty, v_\infty, x_\infty$ and E_∞ are positive solutions of

$$\dot{u} = \dot{v} = \dot{x} = \pi = 0\,. \tag{14b}$$

Solving (14a) we get $x_\infty = \dfrac{c}{pq}$, substituting this value in (6a) & (6b), these equations reduce to

$$1-u_\infty-\frac{v_\infty}{\frac{u_\infty^2}{\alpha}+u_\infty+1}-\frac{\alpha_0 c}{pq(1+\alpha_1 u_\infty)}=0, \tag{14c}$$

$$\frac{\beta u_\infty}{\frac{u_\infty^2}{\alpha}+u_\infty+1}-\gamma-\frac{c v_\infty}{pq(\eta^2+v_\infty^2)}=0. \tag{14d}$$

We show that the above two isoclines (14c) and (14d) intersect at a unique point in the interior of the positive quadrant. For this purpose we note the following from (14c):

i) When $u_\infty = 0$, then $v_\infty = 1-\frac{\alpha_0 c}{pq} = v_{1\infty}$ (say),

$v_{1\infty} > 0$ if $\alpha_0 c < pq$.

ii) When $v_\infty = 0$, then $u_\infty = u_{1\infty}$ is given by

$$u_{1\infty}=\frac{-pq(1-\alpha_1)+\sqrt{p^2q^2(1-\alpha_1)^2-4\alpha_1 pq(\alpha_0 c-pq)}}{2\alpha_1 pq}>0,$$

iii) Assume that $\frac{dv_\infty}{du_\infty}<0$.

Now from equation (14d), we note the following:

iv) When $u_\infty = 0$, then $v_\infty = v_{2\infty}$ is given by

$$v_{2\infty}=\frac{-c\pm\sqrt{c^2-4\gamma^2p^2q^2\eta^2}}{2\gamma pq}.$$

We note that $v_{2\infty}$ is always real and negative if $c > 2\gamma pq\eta$.

v) When $v_\infty = 0$, then $u_\infty = u_{2\infty}$ is given by

$$u_{2\infty}=\frac{\alpha}{2\gamma}\left[(\beta-\gamma)\pm\sqrt{(\beta-\gamma)^2-\left(\frac{2\gamma}{\sqrt{\alpha}}\right)^2}\right].$$

If $\beta > \gamma(1+\frac{2}{\sqrt{\alpha}})$, then $u_{2\infty}$ is always positive.

vi) Assume that $\frac{dv_\infty}{du_\infty} > 0.$

The above analysis shows that the two isoclines (14c) and (14d) intersect at a unique point (u_∞, v_∞) if in addition to assumptions (i-vi), the following holds:

$$u_{2\infty} < u_{1\infty}.$$

After knowing the values of u_∞ and v_∞, we may calculate E_∞ from (6c), that is,

$$E_\infty = \frac{s}{q}\left(1-\frac{c}{pqK}\right)+\frac{\delta_0 v_\infty^2}{\eta^2+v_\infty^2}+\frac{\alpha_2 u_\infty}{1+\alpha_1 u_\infty}.$$

It is clear that $E_\infty > 0$ if $pqK > c$.

This shows that bionomical equilibrium $P_\infty(u_\infty, v_\infty, x_\infty, E_\infty)$ exists.

6. Maximum Sustainable Yield

It is well known [Clark (1976)] that the value of Maximum sustainable yield (MSY) in absence of any alternative resource is

$$h_{MSY}^0 = \frac{sK}{4} .$$

In the present case when the fish population depends on phytoplankton and zooplankton both, then we have

$$h = qEx^* = sx^*\left(1-\frac{x^*}{K}\right)+\frac{\delta_0 v^{*2} x^*}{\eta^{*2}+v^{*2}}+\frac{\alpha_2 u^* x^*}{1+\alpha_1 u^*}.$$

We note that $\frac{\partial h}{\partial x^*} = 0$ yields

$$x^* = \frac{K}{2}\left\{1+\frac{1}{s}\left(\frac{\delta_0 v^{*2}}{\eta^2+v^{*2}}+\frac{\alpha_2 u^*}{1+\alpha_1 u^*}\right)\right\} \text{ and } \frac{\partial^2 h}{\partial x^{*2}} < 0 .$$

Thus, we have

$$h_{MSY} = \frac{sK}{4}\left\{1 + \frac{1}{s}\left(\frac{\delta_0 v^{*2}}{\eta^2 + v^{*2}} + \frac{\alpha_2 u^*}{1 + \alpha_1 u^*}\right)\right\}^2 .$$

From the above equations, if $u^* = v^* = 0$, then $h_{MSY} = \frac{sK}{4} = h^0_{MSY}$. This result matches with the result of Clark (1976). Thus, $h > h_{MSY}$, then it denotes the overexploitation of fish population and if $h < h_{MSY}$, then the fish population is under exploitation.

7. Optimal Harvesting Policy

In this section, we explain the optimal harvesting policy to be adopted by a regulatory agency. The net economic revenue to the fisherman

= revenues obtained by selling the fishes – cost of harvesting,

$$= pqx(t)E(t) - cE(t) = (pqx(t) - c)E(t).$$

Now, our objective is to solve the following optimization problem:

$$\max J,$$

subject to the state equation (6a)-(6c) and to the control constraints $0 < E < E_{\max}$, where

$$J = \int_0^\infty e^{-\delta t}(pqx(t) - c)E(t)\, dt$$

is the continuous time-stream of revenues and δ is instantaneous rate of annual discount.

Now to find the optimal level of equilibrium we use Pontryagins's Maximum Principle. The associated Hamiltonian function is given by

$$\begin{aligned} H &= e^{-\delta t}(pqx(t) - c)E \\ &\quad + \lambda_1(t)\left[u(1-u) - \frac{uv}{\frac{u^2}{\alpha} + u + 1} - \frac{\alpha_0 ux}{1 + \alpha_1 u}\right] + \lambda_2(t)\left[\frac{\beta uv}{\frac{u^2}{\alpha} + u + 1} - \gamma v - \frac{xv^2}{\eta^2 + v^2}\right] \\ &\quad + \lambda_3(t)\left[sx\left(1 - \frac{x}{K}\right) + \delta_0 \frac{xv^2}{\eta^2 + v^2} + \alpha_2 \frac{ux}{1 + \alpha_1 u} - qEx\right], \end{aligned} \tag{15}$$

where λ_1, λ_2 and λ_3 are adjoint variables, $\sigma(t) = e^{-\delta t}(pqx - c) - \lambda_3 qx$ is the switching function.

The optimal control $E(t)$ which maximizes H must satisfy the condition

$$E(t) = \begin{cases} E_{\max}, & \sigma(t) > 0 \text{ i.e. } \lambda_3 e^{\delta t} < p - \dfrac{c}{qx}, \\ 0, & \sigma(t) < 0 \text{ i.e. } \lambda_3 e^{\delta t} > p - \dfrac{c}{qx}. \end{cases}$$

Now the usual shadow price is $\lambda_3 e^{\delta t}$ and the net economic revenue on a unit harvest is $p - \dfrac{c}{qx}$. Thus, if the shadow price is less than the net economic revenue on a unit harvest, then $E = E_{\max}$, the shadow price is greater than the net economic revenue on a unit harvest, then $E = 0$ and when shadow price equals the net economic revenue on a unit harvest, i.e., $\sigma(t) = 0$, then the Hamiltonian becomes independent of the control variable $E(t)$ i.e., $\dfrac{\partial H}{\partial E} = 0$.

This is necessary condition for singular control $E^*(t)$ to be optimal over control set

$$0 < E^* < E_{\max}.$$

Hence, the optimal harvesting policy is

$$E(t) = \begin{cases} E_{\max}, & \sigma(t) > 0, \\ 0, & \sigma(t) < 0, \\ E^*(t), & \sigma(t) = 0. \end{cases} \tag{16}$$

For the singular control to be optimal, we must have $\dfrac{\partial H}{\partial E} = \sigma(t) = 0$. This gives

$$\lambda_3 = e^{-\delta t}\left(p - \frac{c}{qx}\right). \tag{17}$$

According to this principle, the adjoint equations are

$$\frac{d\lambda_1}{dt} = -\frac{\partial H}{\partial u}, \quad \frac{d\lambda_2}{dt} = -\frac{\partial H}{\partial v}, \quad \frac{d\lambda_3}{dt} = -\frac{\partial H}{\partial x}. \tag{18}$$

From the first adjoint equation, we have

$$\frac{d\lambda_1}{dt}=-\lambda_1\left[(1-2u)-\frac{v-\dfrac{u^2v}{\alpha}}{\left(\dfrac{u^2}{\alpha}+u+1\right)^2}-\frac{\alpha_0 x}{(1+\alpha_1 u)^2}\right]-\lambda_2\left[\frac{\beta v-\dfrac{\beta u^2 v}{\alpha}}{\left(\dfrac{u^2}{\alpha}+u+1\right)^2}\right]-\lambda_3\frac{\alpha_2 x}{(1+\alpha_1 u)^2}.$$

Using equation (6a), this equation becomes

$$\frac{d\lambda_1}{dt}=-\lambda_1\left[-u+\frac{uv\left(1+\dfrac{2u}{\alpha}\right)}{\left(\dfrac{u^2}{\alpha}+u+1\right)^2}+\frac{\alpha_0\alpha_1 ux}{(1+\alpha_1 u)^2}\right]-\lambda_2\left[\frac{\beta v\left(1-\dfrac{u^2}{\alpha}\right)}{\left(\dfrac{u^2}{\alpha}+u+1\right)^2}\right]-\lambda_3\frac{\alpha_2 x}{(1+\alpha_1 u)^2}. \qquad (19)$$

The second adjoint equation can be written as

$$\frac{d\lambda_2}{dt}=\lambda_1\frac{u}{\left(\dfrac{u^2}{\alpha}+u+1\right)}-\lambda_2\left[\frac{\beta u}{\left(\dfrac{u^2}{\alpha}+u+1\right)}-\gamma-\frac{2vx\eta^2}{(\eta^2+v^2)^2}\right]-\lambda_3\frac{2\delta_0\eta^2 vx}{(\eta^2+v^2)^2}.$$

Using equation (6b), this equation becomes

$$\frac{d\lambda_2}{dt}=\lambda_1\frac{u}{\left(\dfrac{u^2}{\alpha}+u+1\right)}-\lambda_2\frac{vx(v^2-\eta^2)}{(\eta^2+v^2)^2}-\lambda_3\frac{2\delta_0\eta^2 vx}{(\eta^2+v^2)^2}. \qquad (20)$$

The third adjoint equation can be written as

$$\frac{d\lambda_3}{dt}=-e^{-\delta t}pqE+\lambda_1\frac{\alpha_0 u}{(1+\alpha_1 u)}+\lambda_2\frac{v^2}{\eta^2+v^2}-\lambda_3\left[s\left(1-\frac{2x}{K}\right)+\frac{\delta_0 v^2}{\eta^2+v^2}+\frac{\alpha_2 u}{(1+\alpha_1 u)}-qE\right].$$

Using equation (6c), this equation becomes

$$\frac{d\lambda_3}{dt}=-e^{-\delta t}pqE+\lambda_1\frac{\alpha_0 u}{(1+\alpha_1 u)}+\lambda_2\frac{v^2}{\eta^2+v^2}+\lambda_3\frac{sx}{K}. \qquad (21)$$

From (17), differentiating with respect to t, we have

$$\frac{d\lambda_3}{dt}=-\delta\lambda_3, \qquad (22)$$

with the help of (22), equation (21) reduces to

$$\lambda_1 \frac{\alpha_0 u}{1+\alpha_1 u} = -\lambda_2 \frac{v^2}{\eta^2 + v^2} - e^{-\delta t}\left\{-pqE + \left(\delta + \frac{sx}{K}\right)\left(p - \frac{c}{qx}\right)\right\}. \tag{23}$$

Putting the values of λ_1 in (20), we get

$$\frac{d\lambda_2}{dt} - A_1\lambda_2 = -A_2 e^{-\delta t}, \tag{24}$$

where

$$A_1 = -\left\{\frac{1+\alpha_1 u}{\alpha_0\left(\dfrac{u^2}{\alpha} + u + 1\right)}\frac{v^2}{(\eta^2+v^2)} + \frac{xv(v^2-\eta^2)}{(\eta^2+v^2)^2}\right\},$$

$$A_2 = \frac{1+\alpha_1 u}{\alpha_0\left(\dfrac{u^2}{\alpha} + u + 1\right)}\left\{-pqE + \left(\delta + \frac{sx}{K}\right)\left(p - \frac{c}{qx}\right)\right\} + \left(p - \frac{c}{qx}\right)\frac{2\delta_0\eta^2 xv}{(\eta^2+v^2)^2}.$$

Solving (24), we get $\lambda_2 = \dfrac{A_2}{A_1+\delta}e^{-\delta t} + k_0 e^{A_1 t}$.

We note that when $t \to \infty$, then shadow price $\lambda_2 e^{\delta t}$ is bounded if $k_0 = 0$. Thus,

$$\lambda_2 = \frac{A_2 e^{-\delta t}}{A_1 + \delta}. \tag{25}$$

Putting the values of λ_2 and λ_3 in equation (19), we get

$$\frac{d\lambda_1}{dt} - B_1\lambda_1 = -B_2 e^{-\delta t}, \tag{26}$$

where

$$B_1 = -\left[-u + \frac{uv\left(1+\frac{2u}{\alpha}\right)}{\left(\frac{u^2}{\alpha}+u+1\right)^2} + \frac{\alpha_0\alpha_1 ux}{(1+\alpha_1 u)^2} \right],$$

$$B_2 = \left[\frac{A_2}{A_1+\delta} \frac{\beta v\left(1-\frac{u^2}{\alpha}\right)}{\left(\frac{u^2}{\alpha}+u+1\right)^2} + \left(p-\frac{c}{qx}\right)\frac{\alpha_2 x}{(1+\alpha_1 u)^2} \right].$$

Solving (26), we get

$$\lambda_1 = \frac{B_2 e^{-\delta t}}{B_1+\delta} + k_1 e^{B_1 t}.$$

We note that when $t \to \infty$, then shadow price $\lambda_1 e^{\delta t}$ is bounded if and only if $k_1 = 0$. Thus we have

$$\lambda_1 = \frac{B_2 e^{-\delta t}}{B_1+\delta}. \tag{27}$$

After knowing the values of λ_1, λ_2 and λ_3, the value of E can be calculated from equation (21), and it is given by

$$E = E_\delta = \frac{1}{pq}\left[\left(p-\frac{c}{qx}\right)\left(\delta+\frac{sx}{K}\right) + \frac{B_2}{(B_1+\delta)}\frac{\alpha_0 u}{(1+\alpha_1 u)} + \frac{A_2}{(A_1+\delta)}\frac{v^2}{(v^2+\eta^2)}\right], \tag{28}$$

where E_δ =optimal level of effort. Hence, solving the equation (6a)-(6c) with the help of (28), we get an optimal solution $(u_\delta, v_\delta, x_\delta)$ and the optimal harvesting effort $E = E_\delta$.

8. Conclusion

In this paper, a mathematical model to study the dynamics of phytoplankton, zooplankton, fish population has been proposed and analyzed in which functional responses are considered to be of Holling type II, III and IV. The fish population is harvested according to CPUE hypothesis and harvesting effort is a control variable. The existence of equilibrium points and their stability analysis have been discussed with the help of stability theory of ordinary differential equations. The positive equilibrium point is locally and globally asymptotically stable under a fixed region of attraction when certain conditions are satisfied. We have observed that model system (2) has a chaotic solution for the chosen set of parameter values. For the different values α, measuring the ratio of the predator's immunity from or tolerance of the prey to the half saturation constant in the absence of any inhibitory effect, the system exhibits bifurcation phenomena. The bifurcation and blow-up bifurcation diagrams exhibit the transition from chaos to order through a sequence of periods having bifurcation. The blow-up bifurcation diagram shows that the model system possesses a rich variety of dynamical behavior. The chaotic behavior of the system is not continuing further, as the unstable period-3 orbits which originate at the time of saddle-node bifurcation do not allow it to move further. Birge (1897) observed the marine habitat to be highly heterogeneous in factors such as light, nutrients, temperature and oxygen. In lakes, both the medium (e.g. water and sediments) and the organisms are highly dynamic; currents, wave action and turbulence render spatial patterns highly ephemeral (Downing (1991)). It becomes clear early in the study of temperate aquatic habitats that they varied in composition spatially and temporally. The most important temporal variations were perceived to be seasonal developments of pelagic communities mediated by annual cycles of temperature (Downing (1991)).

We have discussed the bionomical equilibrium of the model and found the sustainable yield (h) and maximum sustainable yield (h_{MSY}). It has been shown that if $h > h_{\text{MSY}}$, then the over-exploitation of fish population takes place and if $h < h_{\text{MSY}}$, then the fish population is under exploitation. By constructing an appropriate Hamiltonian function and using Pontryagin's Maximum Principal, the optimal harvesting policy has been discussed. We also found an optimal equilibrium solution. The idea contained in the paper provides a better understanding of the relative role of different factors; e.g., different predation rate of phytoplankton and zooplankton by fish population and intensity of interference among individual of predator.

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APPENDIX A

Proof of Theorem 1:

First of all, we linearize the model system (2a)-(2c) by using the following transformation:

$$u = u^* + U,\ v = v^* + V,\ x = x^* + X,$$

where (U, V, X) are small perturbations about the interior equilibrium (u^*, v^*, x^*).
Then the model system (2a)-(2c) can be written as

$$\left.\begin{aligned} \frac{dU}{dt} &= -M_{11}U + M_{12}V + M_{13}X \\ \frac{dV}{dt} &= M_{21}U - M_{22}V + M_{23}X \\ \frac{dX}{dt} &= M_{31}U + M_{32}V - M_{33}X \end{aligned}\right\}, \tag{A1}$$

where

$$M_{11} = u^*\left[1 - \frac{v^*\left(1 + \frac{2u^*}{\alpha}\right)}{\left(\frac{u^{*2}}{\alpha} + u^* + 1\right)^2} - \frac{\alpha_0\alpha_1 x^*}{(1+\alpha_1 u^*)^2}\right],\ M_{12} = -\frac{u^*}{\left(\frac{u^{*2}}{\alpha} + u^* + 1\right)},\ M_{13} = -\frac{\alpha_0 u^*}{1+\alpha_1 u^*},$$

$$M_{21} = \frac{\beta v^*\left(1 - \frac{u^{*2}}{\alpha}\right)}{\left(\frac{u^{*2}}{\alpha} + u^* + 1\right)^2},\ M_{22} = \frac{x^* v^*(\eta^2 - v^{*2})}{(v^{*2}+\eta^2)^2},\ M_{23} = -\frac{v^{*2}}{\left(v^{*2}+\eta^2\right)}, \tag{A2}$$

$$M_{31} = \frac{\alpha_2 x^*}{(1+\alpha_1 u^*)^2},\ M_{32} = \frac{2\delta_0 x^* v^* \eta^2}{(v^{*2}+\eta^2)^2},\ M_{33} = \frac{s x^*}{K}.$$

Let

$$W = \frac{1}{2}U^2 + c_1\frac{1}{2}V^2 + c_2\frac{1}{2}X^2$$

be a positive definite function, where $c_1 \& c_2$ are positive constants as chosen in (10c). Differentiating W with respect to time along the solution of model (A1), a little algebraic manipulation yields

$$\begin{aligned}\frac{dW}{dt} &= -\frac{1}{2}M_{11}U^2 + (M_{12} + c_1 M_{21})UV - \frac{1}{2}c_1 M_{22}V^2 \\ &\quad -\frac{1}{2}M_{11}U^2 + (M_{13} + c_2 M_{31})UX - \frac{1}{2}c_2 M_{33}X^2 \\ &\quad -\frac{1}{2}c_1 M_{22}V^2 + (c_1 M_{23} + c_2 M_{32})VX - \frac{1}{2}c_2 M_{33}X^2.\end{aligned} \tag{A3}$$

Sufficient conditions for $\frac{dW}{dt}$ to be negative definite are that the following inequalities hold:

$$M_{ii} > 0, \quad i = 1, 2. \tag{A4}$$

$$\left(M_{12} + c_1 M_{21}\right)^2 < c_1 M_{11} M_{22}, \tag{A5}$$

$$\left(M_{13} + c_2 M_{31}\right)^2 < c_2 M_{11} M_{33}, \tag{A6}$$

$$\left(c_1 M_{23} + c_2 M_{32}\right)^2 < c_1 c_2 M_{22} M_{33}. \tag{A7}$$

For the values of $c_1 \& c_2$, as given in equation (10c),we note that condition (A6) and (A7) are satisfied, and (11a) implies $M_{11} > 0$ and (11b) implies $M_{22} > 0$. Thus (A4) holds true. Again (11c) implies (A5). This shows that $\frac{dW}{dt}$ is negative definite under conditions stated in Theorem 1. This completes the proof of theorem.

APPENDIX B

Proof of Theorem 2:

Let us choose a positive definite function

$$W_1 = \left(u - u^* - u^* \ln\frac{u}{u^*}\right) + d_1\left(v - v^* - v^* \ln\frac{v}{v^*}\right) + d_2\left(x - x^* - x^* \ln\frac{x}{x^*}\right), \tag{B1}$$

where d_1 and d_2 are some positive constant as given in equation (10d).

Differentiating W_1 with respect to time along the solution of model (2a)-(2c), a little algebraic manipulation yields

$$\begin{aligned}\frac{dW_1}{dt} &= -\frac{1}{2}a_{11}(u-u^*)^2 + a_{12}(u-u^*)(v-v^*) - \frac{1}{2}a_{22}(v-v^*)^2 \\ &\quad -\frac{1}{2}a_{11}(u-u^*)^2 + a_{13}(u-u^*)(x-x^*) - \frac{1}{2}a_{33}(x-x^*)^2 \\ &\quad -\frac{1}{2}a_{22}(v-v^*)^2 + a_{23}(v-v^*)(x-x^*) - \frac{1}{2}a_{33}(x-x^*)^2,\end{aligned} \tag{B2}$$

where

$$a_{11} = 1 - \frac{v^*(u+u^*+\alpha)}{\alpha\left(\dfrac{u^2}{\alpha}+u+1\right)\left(\dfrac{u^{*2}}{\alpha}+u^*+1\right)} - \frac{\alpha_0\alpha_1 x^*}{(1+\alpha_1 u)(1+\alpha_1 u^*)},$$

$$a_{22} = \frac{d_1 x^*(\eta^2 - vv^*)}{(\eta^2+v^2)(\eta^2+v^{*2})}, \quad a_{33} = \frac{d_2 s}{K},$$

$$a_{12} = \frac{d_1\beta - 1}{\left(\dfrac{u^2}{\alpha}+u+1\right)} - \frac{d_1\beta u^*(\alpha+u+u^*)}{\alpha\left(\dfrac{u^2}{\alpha}+u+1\right)\left(\dfrac{u^{*2}}{\alpha}+u^*+1\right)},$$

$$a_{13} = \frac{1}{(1+\alpha_1 u)(1+\alpha_1 u^*)}[\alpha_2 d_2 - \alpha_0 - \alpha_0\alpha_1 u^*],$$

$$a_{23} = -\frac{d_1 v}{\left(\eta^2+v^2\right)} + \frac{d_2\delta_0\eta^2(v+v^*)}{(\eta^2+v^2)(\eta^2+v^{*2})}.$$

Sufficient conditions for $\frac{dW_1}{dt}$ to be negative definite is that the following inequalities hold:

$$a_{ii} > 0, \qquad i = 1, 2. \tag{B3}$$

$$a_{12}^2 < a_{11}a_{22}, \tag{B4}$$

$$a_{13}^2 < a_{11}a_{33}, \tag{B5}$$

$$a_{23}^2 < a_{22}a_{33}. \tag{B6}$$

For the chosen values of d_1 & d_2 (see eq. (10d)), condition (B5) and (B6) are satisfied. We further note that (12a) implies $a_{11} > 0$ and (12b) implies $a_{22} > 0$. After substituting the values of a_{ij} in Equation (B4), we maximize the LHS and minimize the RHS using Lemma 1. Then we note that (12c) implies (B4). Thus W_1 is a Liapunov function for all solutions initiating in the interior of the positive constant whose domain contains the region of attraction Ω, proving the theorem.