A delayed predator-prey food chain model with harvesting

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Abstract

This paper deals with a modified version of Leslie-Gower prey-predator food chain model with harvesting where prey grows logistically and predator consumes the prey according to Holling type-II functional form. In deterministic models of prey-predator interaction, it is natural to include a time delay into predator response function. Here we consider a delay into predator response function. The criteria for existence of equilibrium points along with its local stability is discussed. The influence of harvesting on the system is also studied in various cases: (i) only prey species is harvested, (ii) only predator species is harvested and (iii) when both prey and predator species are harvested. Bifurcation analysis is also studied and it is seen that the system undergoes a Hopf bifurcation by the introduction of delay. The qualitative behaviour of the system is verified through numerical simulation.

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1. Introduction

Predator-prey interaction is the fundamental structure in ecosystem. While investigating biological phenomena, one of the familiar nonlinear factors which affect dynamical properties of biological and mathematical models is functional response. In population dynamics, a functional response of the predator to the prey density refers to the change in the density of prey attached per unit time per predator as the prey density changes [19]. Holling C. S. [6] suggested three different kinds of functional response for different kinds of species to model the phenomena of predation, which made the standard Lotka–Volterra system more realistic.

Food chain models are one of the topics of major concern in mathematical ecology and many models have been proposed for instance [8, 12]. The reproduction of predator after the consumption is not instantaneous in general. Some time lag is required for gestation of predators. So, ecologists introduce time delay into the growth equation in modelling various systems. Delayed predator-prey models were first proposed by Volterra [16, 17] in 1925 to study fish population under harvesting. Since then delayed differential equations have been extensively used to model population dynamics, including predator-prey interactions. We refer to the monographs [5, 11, 15] for general delayed biological systems.

The study of population dynamics with harvesting is a subject of mathematical bio-economic and is mainly concerned with the optimal management of renewable resources [2]. Harvesting (catching) is commonly practiced in fisheries, forestry and wild life management. It has a considerable effect on the dynamical evolution of the harvested species, the severity of which depends on the harvesting strategy that can result from rapid depletion to complete preservation of the concerned population. Some works on predator-prey system with harvesting can be found in [3, 7, 14] etc.

The predator–prey food chain model with harvesting is generally described as:

$$\frac{dx}{dt} = rx(t) - p\big(x(t)\big)\,y(t) - H_1(x(t))$$
$$\frac{dy}{dt} = -dy(t) - mp\big(x(t)\big)\,y(t) - H_2(y(t)) \tag{1.1}$$

where r, d, m are positive constants, $p(x)$ is the functional response of the predator $y(t)$, H_1 and H_2 are the harvesting term.

Leslie [9, 10] introduced the following two species Leslie–Gower predator–prey model:

$$\frac{dx}{dt} = (r_1 - b_1 x)x - p(x)y,$$

$$\frac{dy}{dt} = \left(r_2 - \frac{a_2 y}{x}\right)y \tag{1.2}$$

where $x(t)$, $y(t)$ stand for the population (the density) of the prey and the predator at time t, respectively. The parameters r_1 and r_2 are the intrinsic growth rates of the prey and the predator, respectively. b_1 measures the strength of competition among individuals of species x. The value $\frac{r_1}{b_1}$ is the carrying capacity of the prey in the absence of predation. The predator consumes the prey according to the functional response $p(x)$ and grows logistically with growth rate r_2 and carrying capacity $\frac{r_2 x}{a_2}$ proportional to the population size of the prey (or prey abundance). The parameter a_2 is a measure of the food quantity that the prey provides and converted to predator birth. The term y/x is the Leslie–Gower term which measures the loss in the predator population due to rarity (per capita y/x) of its favourite food. The Leslie–Gower formulation is based on the assumption that reduction in a predator population has a reciprocal relationship with per capita availability of its preferred food.

As in the case of severe scarcity, the predator can switch over to other populations but its growth will be limited by the fact that its most favourite food is not available in abundance. In order to solve such deficiency in the above system, Aziz-Alaoui and Daher [1] proposed and studied the following predator–prey model with modified Leslie–Gower and Holling-type II schemes:

$$\frac{dx}{dt} = \left(r_1 - b_1 x - \frac{a_1 y}{x+k_1}\right)x,$$
$$\frac{dy}{dt} = \left(r_2 - \frac{a_2 y}{x+k_2}\right)y \tag{1.3}$$

where r_1, b_1, r_2, a_2 have the same meaning as before. a_1 is the maximum value which per capita reduction rate of x can attain; k_1 and k_2 measure the extent to which environment provides protection to prey x and to predator y respectively. Many researchers considered system (1.3) and its non-autonomous versions by incorporating delay, impulses, harvesting, stochastic perturbation Alee effect and so on [4, 13, 18, 20].

In this paper we consider the predator-prey model with time delay and harvesting as

$$\frac{dx}{dt} = r_1 x - b_1 x^2 - \frac{a_1 xy}{x+k_1} - \frac{h_1 x}{c_1 + x}$$
$$\frac{dy}{dt} = \left[r_2 - \frac{a_2 y(t-\tau)}{x(t-\tau)+k_2}\right]y - \frac{h_2 y}{c_2 + y} \tag{1.4}$$

with initial conditions: $x(\theta)$, $y(\theta) \geq 0$, $\theta \in [-\tau, 0)$ and $x(0) > 0$, $y(0) > 0$ where x and y represent the population densities at time t; b_1, r_i, a_i, k_i, h_i, c_i ($i = 1,2$) are model parameters assuming only positive values, r_1 is the growth rate of prey x, b_1 measures the strength of competition among individuals of species x, a_1 is the maximum value which per capita reduction rate of x can attain, k_1 (respectively, k_2) measures the extent to which environment provides protection to prey x (respectively, to predator y), r_2 describes the growth rates of y, and a_2 has a similar meaning to a_1, h_1, h_2 are maximum harvesting rate and c_1, c_2 are the half saturation value of harvesting respectively.

The system (1.4) has six equilibrium points. They are: (i) trivial equilibrium $P_0(0,0)$, (ii) prey extinction equilibrium $P_1(0, y^+)$ and $P_2(0, y^-)$ where $y^\pm = \frac{(r_2 k_2 - a_2 c_2) \pm \sqrt{(r_2 k_2 - a_2 c_2)^2 - 4k_2(h_2 - r_2 c_2)}}{2a_2}$ (iii) predator free equilibrium $P_3(x^+, 0)$ and $P_4(x^-, 0)$ where $x^\pm = \frac{(r_1 - b_1 c_1) \pm \sqrt{(r_1 - b_1 c_1)^2 - 4b_1(h_1 - r_1 c_1)}}{2b_1}$ and (iv) interior equilibrium $P^*(x^*, y^*)$ which is the coexistence of predator and prey where x^*, y^* satisfy the simultaneous equations:

$$r_1 - b_1 x^* - \frac{a_1 y^*}{x^* + k_1} - \frac{h_1}{c_1 + x^*} = 0,$$

$$r_2 - \frac{a_2 y^*}{x^* + k_2} - \frac{h_2}{c_2 + y^*} = 0 \tag{1.5}$$
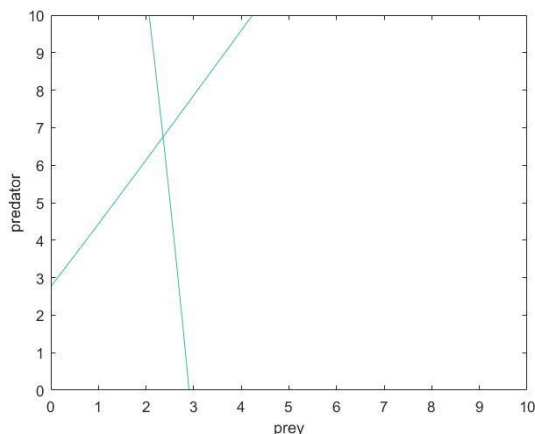

Fig.1 An interior equilibrium point exists for the following parametric values
$$r_1 = 9, r_2 = 7, b_1 = 3, a_1 = 2, a_2 = 4, k_1 = 6, k_2 = 2, h_1 = 2, h_2 = 7, c_1 = 4, c_2 = 2$$

2. Existence and Stability

(i)   If $h_2 - r_2 c_2 < 0$, then $y^+ > 0$ and $y^- < 0$. So, there exists single prey extinction positive equilibrium $P_1(0, y^+)$.

(ii)   If $h_2 - r_2 c_2 > 0$ and $\Delta_2 > 0$ and $r_2 k_2 - a_2 c_2 > 0$, then there exist two positive prey extinction equilibria $P_1(0, y^+)$ and $P_2(0, y^-)$ where $\Delta_2 = (r_2 k_2 - a_2 c_2)^2 - 4k_2(h_2 - r_2 c_2)$.

(iii) If $h_2 - r_2 c_2 = 0$ and $r_2 k_2 - a_2 c_2 > 0$, then $y^- = 0, y^+ > 0$. So there exists unique prey extinction equilibrium $\left(0, \frac{r_2 k_2 - a_2 c_2}{a_2}\right)$.

(iv)   If $h_1 - r_1 c_1 < 0$, then $x^+ > 0$ and $x^- < 0$. So, there exists a single predator free equilibrium $P_3(x^+, 0)$.

(v)   If $h_1 - r_1 c_1 > 0$ and $\Delta_1 > 0$ and $r_1 - b_1 c_1 > 0$, then there exist two positive predator free equilibrium $P_3(x^+, 0)$ and $P_4(x^-, 0)$ where $\Delta_1 = (r_1 - b_1 c_1)^2 - 4b_1(h_1 - r_1 c_1)$.

(vi)   If $h_1 - r_1 c_1 = 0$ and $r_1 - b_1 c_1 > 0$, then $x^- = 0, x^+ > 0$. So, there exists a unique predator free equilibrium $\left(\frac{r_1 - b_1 c_1}{b_1}, 0\right)$.

Since we are interested in the coexistence of predator and prey, we study stability analysis only for the interior equilibrium point $P^*(x^*, y^*)$.

Case1. $\tau = 0$

Introducing perturbations $x(t) = X(t) + x^*$, $y(t) = Y(t) + y^*$ in (1.4) and neglecting 2nd and higher order products of $X(t)$ and $Y(t)$, still denoting $X(t)$ and $Y(t)$ by $x(t)$ and $y(t)$ respectively, we get

$$\frac{dx}{dt} = \alpha\, x(t) + \beta\, y(t)$$
$$\frac{dy}{dt} = \gamma\, x(t) + \delta\, y(t) \tag{2.1}$$

Where

$$\alpha = -b_1 x^* + \frac{a_1 x^* y^*}{(x^* + k_1)^2} + \frac{h_1 x^*}{(c_1 + x^*)^2}, \quad \beta = -\frac{a_1 x^*}{x^* + k_1}, \quad \gamma = \frac{a_2 y^{*2}}{(x^* + k_2)^2}, \quad \delta = \frac{-a_2 y^*}{x^* + k_2} + \frac{h_2 y^*}{(c_2 + y^*)^2}. \tag{2.2}$$

Hence the Jacobian matrix at $P^*(x^*, y^*)$ for the linearized system (2.1) is

$$J(x^*, y^*) = \begin{pmatrix} \alpha & \beta \\ \gamma & \delta \end{pmatrix}$$

The characteristic equation of the linearized system (2.1) is given by

$$\lambda^2 - p\lambda + q = 0, \tag{2.3}$$

where
$$p = trace\, J(x^*, y^*) = \alpha + \delta,$$

$$q = detJ(x^*, y^*) = \alpha\delta - \beta\gamma. \tag{2.4}$$

The stability of the interior equilibrium point $P^*(x^*, y^*)$ depends on the sign of the trace and the determinant of the Jacobian matrix $J(x^*, y^*)$. Here are the different cases:

Case(a): If $trace\ J < 0$ and $detJ > 0$, then $P^*(x^*, y^*)$ is a stable node or a stable spiral.

Case(b): If $trace\ J > 0$ and $detJ > 0$, then $P^*(x^*, y^*)$ is an unstable node or an unstable spiral.

Case(c): If $detJ < 0$, then $P^*(x^*, y^*)$ is a saddle point.

Case(d): If $trace\ J = 0$, $detJ > 0$ then there are some limit cycles around $P^*(x^*, y^*)$.

In case(d) the system (1) goes to a Hopf bifurcation. We take c_1 or c_2 as bifurcation parameter.

For our model, we see that the expression for $trace\ J$ and $detJ$ are not explicitly depends on c_1 and c_2 and it is impossible to derive some conditions depending on c_1 and c_2. So alternatively, we can show the sign of $trace\ J$ and $detJ$ by taking some numerical values of the parameters and draw the graphs of $traceJ$ and $detJ$ in the plane of $c_1 - c_2$.
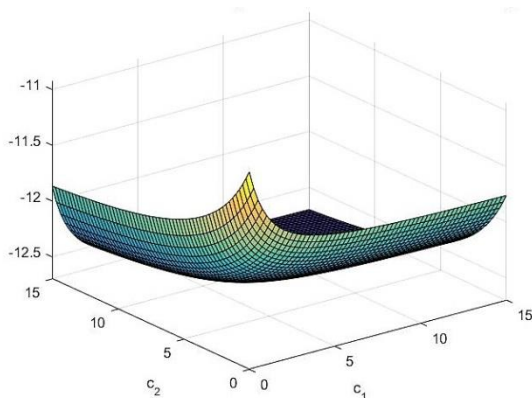

Fig.2 Plot of $trace\ J$ in $c_1 - c_2$ plane.

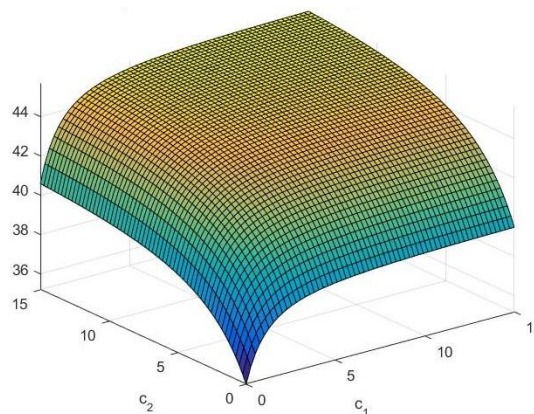**Fig.3** Plot of $det\ J$ in $c_1 - c_2$ plane.

In figure 2 and 3, we see that the values of trJ and $detJ$ can be both positive and negative when c_1 and c_2 vary. Thus, the cases we consider above are tenable.

Case 2. $\tau \neq 0$.

Let us consider the linearized system (1.4) with delay as

$$\frac{dx}{dt} = \alpha\ x(t) + \beta\ y(t)$$
$$\frac{dy}{dt} = \gamma\ x(t - \tau) + \delta\ y(t - \tau) \tag{2.5}$$

where $\alpha, \beta, \gamma, \delta$ are given by (2.2). The characteristic equation of (2.5) is

$$\lambda^2 + A\lambda + (B + C\lambda)e^{-\lambda\tau} = 0 \tag{2.6}$$

Where $A = -\alpha$, $B = \alpha\delta - \beta\gamma$, $C = -\delta$. \qquad (2.7)

Substituting $\lambda = \mu(\tau) + i\omega(\tau)$ in (2.6) and separating real and imaginary parts, we get

$$\mu^2 - \omega^2 + A\mu + (B + C\mu)e^{-\mu\tau}\cos\omega\tau + C\omega e^{-\mu\tau}\sin\omega\tau = 0$$

$$2\mu\omega + A\omega - (B + C\mu)e^{-\mu\tau}\sin\omega\tau + C\omega e^{-\mu\tau}\cos\omega\tau = 0 \tag{2.8}$$

Here λ, μ, ω are functions of τ. Now we will examine the change of stability of $P^*(x^*, y^*)$ which occurs at the values of τ for which $\mu(\tau) = 0$ and $\omega(\tau) \neq 0$. Let for $\tau = \tau_0$, $\mu(\tau_0) = 0$ and $\omega(\tau_0) = \omega_0 \neq 0$, then (2.8) becomes

$$B\cos\omega_0\tau_0 + C\omega_0\sin\omega_0\tau_0 - \omega_0^2 = 0,$$

$$C\omega_0\cos\omega_0\tau_0 - B\sin\omega_0\tau_0 + A\omega_0 = 0. \tag{2.9}$$

Squaring and adding the above two equations, we get

$$\omega_0^4 + (A^2 - C^2)\omega_0^2 - B^2 = 0. \tag{2.10}$$

Positive root of the equation (2.10) is given by

$$\omega_0^2 = \frac{1}{2}\left[(\delta^2 - \alpha^2) + \sqrt{(\delta^2 - \alpha^2)^2 + 4(\alpha\delta - \beta\gamma)^2}\right]$$

(2.11)

Again from (2.9), we get

$$\tan\omega_0\tau_0 = \frac{C\omega_0^2 + AB}{(B - AC)\omega_0}$$

(2.12)

Solving for τ_0, we get

$$\tau_{0n} = \frac{1}{\omega_0}\arctan\left[\frac{C\omega_0^2 + AB}{(B - AC)\omega_0}\right] + \frac{2n\pi}{\omega_0}$$

(2.13)

where $n = 0, 1, 2, 3, \ldots$.

The smallest τ_0, is obtained by choosing $n = 0$ (denoting $\tau_{00} = \tau_0$), then from (2.13), we get

$$\tau_0 = \frac{1}{\omega_0}\arctan\left[\frac{C\omega_0^2 + AB}{(B - AC)\omega_0}\right] = \frac{1}{\omega_0}\arctan\left[\frac{\delta\omega_0^2 + \alpha(\alpha\delta - \beta\gamma)}{\beta\gamma\omega_0}\right]$$

(2.14)

We now show that

$$\left.\frac{d\mu(\tau)}{d\tau}\right|_{\tau=\tau_0} > 0$$

(2.15)

This will signify that there will be at least one eigen value with positive real part for $\tau > \tau_0$. Moreover, the condition for Hopf bifurcation is then satisfied yielding the required periodic solution. Now differentiating (2.6) with respect to τ, we get

$$\left(\frac{d\lambda}{d\tau}\right)^{-1} = -\frac{2\lambda + A}{\lambda(\lambda^2 + A\lambda)} + \frac{C}{\lambda(B + C\lambda)} - \frac{\tau}{\lambda}$$

Thus sign of

$$\left[\frac{d(\operatorname{Re}\lambda)}{d\tau}\right]_{\lambda=i\omega_0} = \text{sign of } \left[\operatorname{Re}\left(\frac{d\lambda}{d\tau}\right)^{-1}\right]_{\lambda=i\omega_0}$$

Now,

$$\operatorname{Re}\left(\frac{d\lambda}{d\tau}\right)^{-1} = \operatorname{Re}\left[-\frac{2i\omega_0 + A}{i\omega_0(-\omega_0^2 + iA\omega_0)} + \frac{C}{i\omega_0(B + Ci\omega_0)} - \frac{\tau}{i\omega_0}\right]$$

$$= \frac{2\omega_0^2 + A^2}{\omega_0^2(\omega_0^2 + A^2)} - \frac{C^2}{B^2 + C^2\omega_0^2}$$

$$= \frac{C^2\omega_0^4 + 2B^2\omega_0^2 + A^2B^2}{\omega_0^2(\omega_0^2 + A^2)(B^2 + C^2\omega_0^2)}$$

(2.16)

Therefore

$$\left[\frac{d(\operatorname{Re}\lambda)}{d\tau}\right]_{\lambda=i\omega_0} = \left.\frac{d\mu(\tau)}{d\tau}\right|_{\tau=\tau_0} > 0$$

(2.17)

Therefore, the transversality condition holds, hence Hopf bifurcation occurs at $\omega = \omega_0$, $\tau = \tau_0$.

Thus, the Hopf bifurcating periodic solution arising at the parametric relation $\tau = \tau_0$.

3. The influence of harvesting

Now we discuss the influence of harvesting on the system (1.4), which we describe in three aspects.

Case1: Only prey species is harvested. Here we consider $h_2 = 0$.

Case2: Only predator species is harvested. Here we consider $h_1 = 0$.

Case3: When both prey and predator species are harvested.

Here we consider for simplicity that $h_1 = h_2 = h$. This is called non-selective harvesting.

Since the analytical solution for this model cannot be determined explicitly, we are going through numerical simulation.

4. Results based on numerical simulation

Using numeric analysis instead of real world data, which of course would be of great interest, has many advantages. It may also be noted that the simulation presented in this paper should be considered from a qualitative rather than a quantitative point of view. However, numerous scenarios covering the breadth of the biological feasible parameter space were conducted and the results display the gamut of dynamical results collected from all the scenarios tested.

(i) Let us take $r_1 = 9, r_2 = 7, b_1 = 3, a_1 = 2, a_2 = 4, k_1 = 6, k_2 = 2, h_1 = 2, h_2 = 7, c_1 = 4, c_2 = 2$ then the system (1.3) has a positive interior equilibrium $P^*(x^*, y^*) \approx (2.3564, 6.7524)$. when $\tau = 0$, the interior equilibrium point $P^*(x^*, y^*) \approx (2.3564, 6.7524)$ is globally asymptotically stable [see fig. 4, 5].

(ii) For the harvesting of only prey species, we take $h_2 = 0$. Then for the parametric values $r_1 = 9, r_2 = 7, b_1 = 3, a_1 = 2, a_2 = 4, k_1 = 6, k_2 = 2, c_1 = 4, c_2 = 2$, we see that both the prey and predator population decrease when h_1 increases [see fig.6].

When only predator species is harvested, we take $h_1 = 0$. Then for the parametric values $r_1 = 9, r_2 = 7, b_1 = 3, a_1 = 2, a_2 = 4, k_1 = 6, k_2 = 2, c_1 = 4, c_2 = 2$, we see that increasing the value of h_2, prey population increase and predator population decrease [see fig.7].

Lastly when we consider the case $h_1 = h_2 = h$, see that for the parametric values $r_1 = 9, r_2 = 7, b_1 = 3, a_1 = 2, a_2 = 4, k_1 = 6, k_2 = 2, c_1 = 4, c_2 = 4$, both the prey and predator population decrease for the increase of h [see fig.8].

(iii) When $\tau \neq 0$, we get $\omega_0 = 6.044748581$ and $\tau_0 = 0.2598$. The positive interior equilibrium point $P^*(x^*, y^*) \approx (2.3564, 6.7524)$ is asymptotically stable when $0 \leq \tau < \tau_0$ [see fig. 9] more over the system becomes unstable when $\tau > \tau_0$ and these bifurcating periodic solutions from $P^*(x^*, y^*) \approx (2.3564, 6.7524)$ at τ_0 are stable [see fig.10, 11].
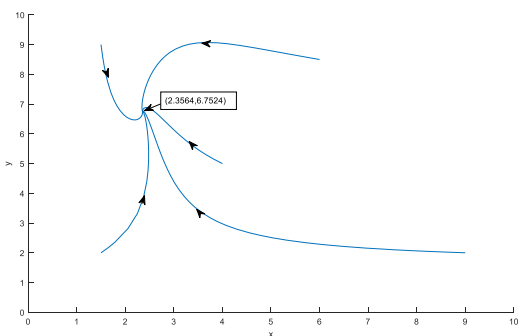

Fig.4 Phase plane trajectory shows that the system is globally asymptotically stable for the parametric values $r_1 = 9, r_2 = 7, b_1 = 3, a_1 = 2, a_2 = 4, k_1 = 6, k_2 = 2, h_1 = 2, h_2 = 7, c_1 = 4, c_2 = 2$
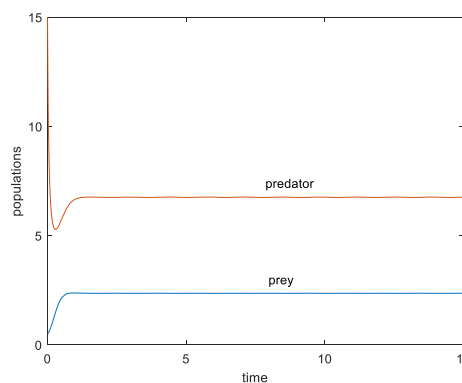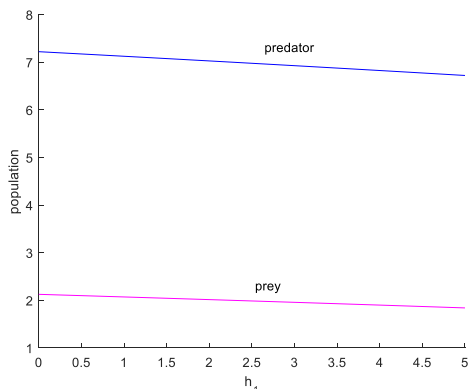

Fig.5 The system is globally asymptotically stable for the parametric values $r_1 = 9, r_2 = 7, b_1 = 3, a_1 = 2, a_2 = 4, k_1 = 6, k_2 = 2, h_1 = 2, h_2 = 7, c_1 = 4, c_2 = 2$

Fig6. This figure shows that when $h_2 = 0$, then for the ascending values of h_1 and for the parametric values $r_1 = 9, r_2 = 7, b_1 = 3, a_1 = 2, a_2 = 4, k_1 = 6, k_2 = 2, c_1 = 4, c_2 = 2$ both prey and predator population decrease.
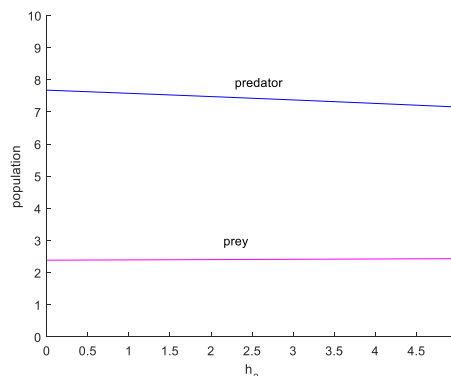

Fig.7 This figure shows that when $h_1 = 0$, then for the ascending values of h_2 and for the parametric values $r_1 = 9, r_2 = 7, b_1 = 3, a_1 = 2, a_2 = 4, k_1 = 6, k_2 = 2, c_1 = 4, c_2 = 2$ Prey population increase
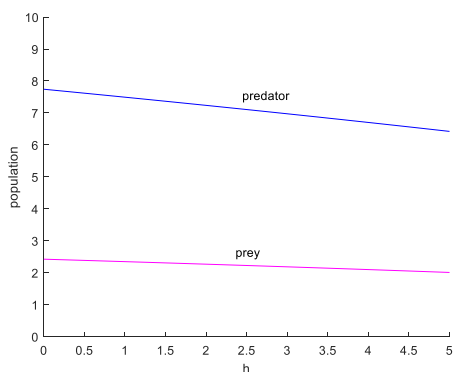
and predator population decrease.

Fig.8 This figure shows that when $h_1 = h_2 = h$, then for the ascending values of h and for the parametric values $r_1 = 9, r_2 = 7$, $b_1 = 3, a_1 = 2$, $a_2 = 4, k_1 = 6, k_2 = 2, c_1 = 4, c_2 = 4$, both prey and predator population decrease.
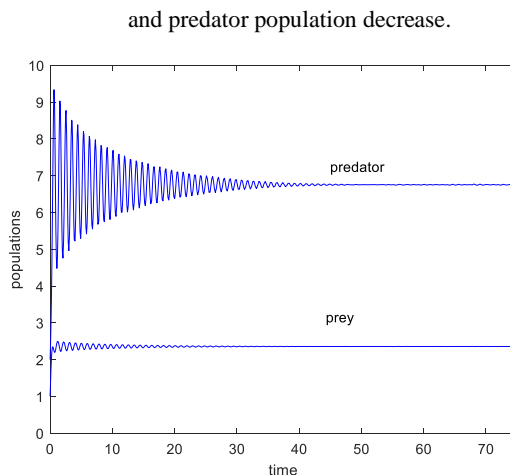

Fig.9 This figure shows that for the parametric values $r_1 = 9, r_2 = 7, b_1 = 3, a_1 = 2, a_2 = 4, k_1 = 6, k_2 = 2$, $h_1 = 2, h_2 = 7, c_1 = 4, c_2 = 2$ and $\tau = 0.21 < \tau_0 = 0.2598$ the system is stable.

Fig.10 This figure shows that for the parametric values $r_1 = 9, r_2 = 7, b_1 = 3, a_1 = 2, a_2 = 4, k_1 = 6$, $k_2 = 2, h_1 = 2, h_2 = 7, c_1 = 4, c_2 = 2$ and $\tau = 0.27 > \tau_0 = 0.2598$, the system is unstable.
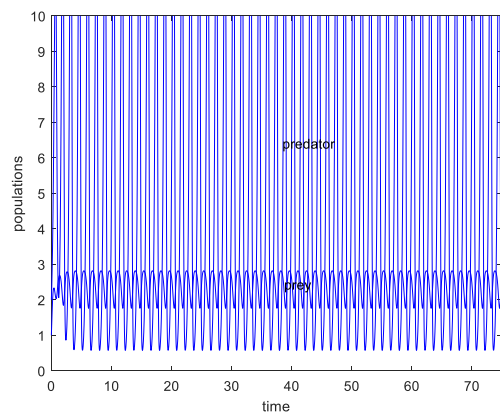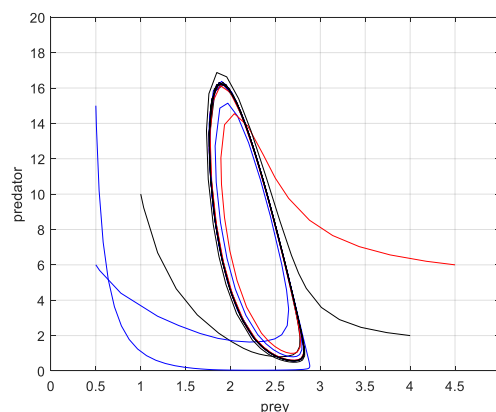

Fig.11 This figure shows that for the parametric values $r_1 = 9, r_2 = 7, b_1 = 3, a_1 = 2$, $a_2 = 4, k_1 = 6, k_2 = 2, h_1 = 2, h_2 = 7, c_1 = 4$, $c_2 = 2$ and for $\tau = 0.27 > \tau_0 = 0.2598$. The solution of the system (1.4) shows a limit cyclic behavior.

5. Conclusion

In this work we consider a delayed predator prey model which is a modified version of the Leslie-Gower scheme and on the Holling-type II scheme. Since harvesting has a strong impact on the dynamics of a system, we have considered the catch-rate function for both prey and predator based on Holling type-II functional form. Here we are not deriving the optimal harvesting policy [14]; instead we are giving some effects of harvesting on the system. The above observations show that the harvesting of either species plays an important role to shape the dynamical behaviour of the system.

In most of the ecosystems, population of one species does not respond instantaneously to the interactions with other species. To incorporate this idea in modelling approach, the time delay models have been developed. We introduce time delay into the growth equation of predator and taking delay as bifurcation parameter. We see that a Hopf bifurcation occurs whenever delay increases a critical value.

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