Jordan Journal of Mathematics and Statistics (JJMS) 4(1), 2011, pp.7 - 31

GLOBAL STABILITY AND BIFURCATION ANALYSIS OF A HARVESTED STAGE STRUCTURE PREDATOR-PREY SYSTEM WITH LINEAR FUNCTIONAL RESPONSE

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Abstract. The global properties of a harvested stage-structured predator-prey model with linear functional response and constant delay are studied using Lyapunov functions and LaSalle's invariance principle. It is shown that time delay and the harvesting effort can cause a stable equilibrium to become unstable. A condition which leads to the extinction of the predators is indicated. We show also, that the predator coexists with prey permanently if and only if the predator's recruitment rate at the peak of prey abundance is larger than its harvesting rate. By choosing the delay as a bifurcation parameter, we show both analytically and numerically that Hopf bifurcation can occur as the delay crosses some critical value. We, also present results on positivity and boundedness of the solution.

1. Introduction

Time delay are natural components of biological systems and there are numerous reasons for including them in the mathematical models. For example, delays may be included to present resource regeneration times, maturation periods, feeding times, reaction times or to take account of age structure in the population. Incorporating delays into population models can be done either by using discrete delays or

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2000 *Mathematics Subject Classification.* 92D25, 46A45.

Key words and phrases. Stage structure; Globally stable; Hopf bifurcation; Harvesting; Population model; Lyapunov function.

Received: Feb. 11 , 2010 Accepted : Dec. 23 , 2010 .

distributed delays, (for example see [4] , [6], [3], [2]). Many of the models in the literature includes discrete delays. In general, delay differential equations exhibit much more complicated dynamics than ordinary differential equations without delay, since time delay could cause a stable equilibrium to become unstable.

Most of the models in the literature always assumed that all individuals of a single species have largely similar capabilities to hunt or reproduce. However, the life cycle of most, if not all, animals and insects consists of at least two stages, immature and mature. Therefore, it is practical to introduce the stage structure into the competitive or predator-prey models. Stage-structured models have attracted much attention in recent decades. Fundamental work towards a systematic approach to stage-structured model formulation has been made by Gurney et.al. [8] , Nisbet and Gurney [15] and Nisbet et.al. [16]. Further progress has been made by Aiello and Freedman [1], who proposed and studied a single species model with stage structure and discrete delay.

Several predator-prey models, in the literature, based on stage-structure of predator have received considerable attention in recent years. See Wang [18] and Xiao and Chen [20] for global stability and persistence analysis of a stage-structured predator-prey model without delay terms. See also Wang and Chen [17], Wang et al. [19], Georgescu [5] , Liu [14], Kuang [11] and Hasting [10], for stability analysis of staged predator-prey models with time delay.

Recently, Gourley and Kuang [7] formulated a robust stage-structured predator-prey model with the assumption that stage-structured consumer species growth is a combined result of birth and death processes, both of which are closely linked to the dynamical supply of resource. Enlightened by the modeling methods in [7], we consider and study the stage-structured predator-prey model with linear harvesting and the death rate of the mature predator population is of a logistic nature, i.e. it is proportional to square of the population, in order to investigate the effects of stage structure for the predator and the harvesting of both prey and predator on the global dynamics of the linear harvesting predator-prey model. We shall study the system

$$\begin{aligned}
&P'(t) = rP(t)\left(1 - \frac{P(t)}{k}\right) - aM(t)P(t) - h_1P(t),\\
&M'(t) = bae^{-(\gamma+h_3)\tau}M(t-\tau)P(t-\tau) - dM^2(t) - h_2M(t),\\
&I'(t) = baM(t)P(t) - bae^{-(\gamma+h_3)\tau}M(t-\tau)P(t-\tau) - \gamma I(t) - h_3I(t)\\
&P(\theta), M(\theta), I(\theta) \geq 0, \quad \text{are continuous on } -\tau \leq t \leq 0,\\
&P(0), M(0), I(0) > 0.
\end{aligned} \tag{1.1}$$

And for the continuity of the solutions to system (1.1), in this paper, we require

$$I(0) = ba\int_{-\tau}^{0} e^{(\gamma+h_3)s}M(s)P(s)ds, \tag{1.2}$$

System (1.1) has been built based on the following assumptions:

(i) $P(t)$ stands for prey or renewable resource density at time t. The parameters r, k, a, h_1 are positive constants representing the specific growth rate of the prey, carrying capacity, the conversion rate (the coefficient of decrease of prey due to predation), and the harvesting efforts of the prey, respictively. We assume that the prey can be modeled by logistic equation when the consumer is absent.

(ii) As in the work of Aiello and Freedman [1], we assume that the predator population is divided into two distinctive stages: juvenile ($I(t)$) and adults ($M(t)$). And $d, b, \gamma, h_2, h_3 > 0$, which represent, the adult predators' death rate, the adult predators' birth rate, the juvenile predators mortality rate, the harvesting efforts for adult predator, and immature predator, respectively. We assume that the death rate of the mature predator population is of a logistic nature. The constant $\tau \geq 0$ denotes a time delay due to an immature stage. Also, we assume that only adult predators are capable of preying on the prey species. Because for many animals whose babies are raised by their parants or are dependent on the nutrition from the eggs they stay in, the immature are much weaker than the mature, their competition with other individuals of the community can be ignored.

(iii) The expression $e^{-(\gamma+h_3)\tau}$ denotes the fraction of those born at time $t-\tau$ who are still alive now and are not harvested, which accounts for mortality and harvesting during the juvenile phase, follows from the assumption that the death and harvesting of the immature are following a linear law given by $-\gamma I(t)$ and $-h_3 I(t)$.

Now, both r and k of system (1.1) can be easily scaled off by appropriate rescaling of time and the P variable. Therefore, in the following, we will consider the system

$$\begin{aligned}
&P'(t) = P(t)\,(1-P(t)) - aM(t)P(t) - h_1P(t),\\
&M'(t) = bae^{-(\gamma+h_3)\tau}M(t-\tau)P(t-\tau) - dM^2(t) - h_2M(t),\\
&I'(t) = baM(t)P(t) - bae^{-(\gamma+h_3)\tau}M(t-\tau)P(t-\tau) - \gamma I(t) - h_3I(t)\\[1em]
&P(\theta), M(\theta), I(\theta) \geq 0, \text{ are continuous on } -\tau \leq t \leq 0, \qquad (1.3)\\[1em]
&P(0), M(0), I(0) > 0.
\end{aligned}$$

By the third equation of system (1.3), and the initial condition (1.2) we have

$$I(t) = ba\int_{t-\tau}^{t} e^{-(\gamma+h_3)(t-s)}M(s)P(s)ds, \tag{1.4}$$

that is, $I(t)$ is completely determined by $M(t)$ and $P(t)$, and thus the following system can be separated from system (1.1)

$$\begin{aligned} &P'(t) = P(t)\left(1 - P(t)\right) - aM(t)P(t) - h_1P(t), \\ &M'(t) = bae^{-(\gamma+h_3)\tau}M(t-\tau)P(t-\tau) - dM^2(t) - h_2M(t), \\ &P(\theta), M(\theta) \geq 0, \text{ are continuous on } -\tau \leq t \leq 0, \ P(0), M(0) > 0. \end{aligned} \tag{1.5}$$

Before we have the main results, we need to give some propositions which will be used in the next.

Proposition 1.1. *If $P(0), M(0), I(0) > 0$, then every solution $(P(t), M(t), I(t))$ of system (1.3) with initial condition (1.2) is positive for all $t > 0$.*

Proof. Since the right hand side of the equation for P contains a factor of $P(t)$, positivity for $P(t)$ follows by standard arguments. For $M(t)$, if there exists t_0 such that $M(t_0) = 0$, then $t_0 > 0$. Assume that t_0 is the first such time that $M(t) = 0$, that is, $t_0 = \inf\{t > 0 : M(t) = 0\}$, then $M'(t_0) = abe^{-(\gamma+h_3)\tau}M(t_0-\tau)P(t_0-\tau) > 0$. Hence for sufficiently small $\varepsilon > 0$, $M'(t_0 - \varepsilon) > 0$. But by the definition of t_0, $M'(t_0 - \varepsilon) \leq 0$. This contradiction shows that $M(t) > 0$ for all $t > 0$.

Finally, for $I(t)$, since $I(t)$ is strictly positive on some $[0, \varepsilon)$, as it starts with strictly positive $I(0)$, then, using (1.4), I is the integral of a continuous function which is strictly positive at least on $[0, t]$.

Now we prove the following proposition.

Proposition 1.2. *System (1.3) is always dissipative in the first quadrant.*

Proof. By positivity of solutions

$$P'(t) \leq P(t)(1 - P(t)).$$

Thus we have

$$\limsup_{t\to\infty} P(t) \leq 1. \tag{1.6}$$

Choose the function

$$W(t) = be^{-(\gamma+h_3)\tau}P(t) + M(t+\tau),$$

and calculating the derivative of $W(t)$ along the solution of (1.3), we have

$$\begin{aligned} W'(t) &= be^{-(\gamma+h_3)\tau}P(t)(1-P(t)) - bh_1e^{-(\gamma+h_3)\tau}P(t) - dM^2(t+\tau) - h_2M(t+\tau) \\ &\leq be^{-(\gamma+h_3)\tau}P(t)(1-P(t)) - bh_1e^{-(\gamma+h_3)\tau}P(t) - h_2M(t+\tau) \\ &= -h_2W(t) + h_2be^{-(\gamma+h_3)\tau}P(t) + be^{-(\gamma+h_3)\tau}P(t)(1-P(t)) \\ &\quad -bh_1e^{-(\gamma+h_3)\tau}P(t). \end{aligned}$$

By (1.6), there exist some positive constants B and T, such that

$$W'(t) \leq B - h_2W(t), \quad \text{for all } t \geq T.$$

Thus

$$\limsup_{t\to\infty} W(t) \leq \frac{B}{h_2},$$

and consequently $P(t)$ and $M(t)$ are ultimately bounded. Using (1.4), we also have that $I(t)$ is ultimately bounded, proving the proposition.

2. The Feasibility and Local Stability of the Equilibria

The equilibria of our model are determined by setting $P' = M' = I' = 0$ in system (1.3) and solving the resulting algebraic equations. It is clear that if $h_1 > 1$, the origin $E_0 = (0, 0, 0)$ is the only nonnegative equilibrium of system (1.3). Also, if $h_1 < 1$, then system (1.3) has the boundary equilibrium $E_1 = (1 - h_1, 0, 0)$ and the interior equilibrium $E_2 = (\hat{P}, \hat{M}, \hat{I})$, where

$$\begin{aligned} \hat{P} &= \frac{d(1-h_1) + ah_2}{ba^2 e^{-(\gamma+h_3)\tau} + d}, \\ \hat{M} &= \frac{ba(1-h_1)e^{-(\gamma+h_3)\tau} - h_2}{ba^2 e^{-(\gamma+h_3)\tau} + d}, \\ \hat{I} &= \frac{ba(1-e^{-(\gamma+h_3)\tau})\left[(ba(1-h_1)e^{-(\gamma+h_3)\tau} - h_2)(d(1-h_1)+ah_2)\right]}{(\gamma+h_3)(ba^2 e^{-(\gamma+h_3)\tau} + d)}. \end{aligned} \tag{2.1}$$

Obviously, the interior equilibrium will exist if and only if

$$bae^{-(\gamma+h_3)\tau}(1-h_1) > h_2, \tag{2.2}$$

which means that whether the interior equilibrium is feasible or not depends on the values of the parameters. Note that, condition (2.2) can only possibly be satisfied for τ up to a certain finit value on the interval $[0, \tau^*)$, where

$$\tau^* = \frac{1}{\gamma + h_3} \ln\left(\frac{ba(1-h_1)}{h_2}\right).$$

Increasing τ in $[0, \tau^*)$ causing the coincidence of E_2 with E_1 at the finite value τ^*, that is, as τ approaches τ^*, then $\hat{P}$ approaches $1 - h_1$ and $\hat{M}$ approaches 0. Also, we may observe that the interior equilibrium does not exist if the immature populations have a high death rate. On the other hand, the harvesting efforts h_1, h_2, and h_3 also affect the existence of the positive equilibrium since they are involved in (2.2). We see how the harvesting rate affect the dynamics of system (1.3), for example, the more a prey population is harvested, the lower is the number of predators at the equilibrium, and the less a prey population is harvested, the higher is the number of predators at the equilibrium.

2.1. **Local Stability Analysis.** We will now study the local stability of equilibria E_0, E_1, and E_2. We shall linearise system (1.3) to determine whether trajectories that start sufficiently close to an equilibrium point are drawn towards or repelled away from that point. To do so, and for convenience, let

$$x(t) = col\left(P(t) - P^*, M(t) - M^*, I(t) - I^*\right), x \in \mathbf{R}^3, t > 0,$$

where (P^*, M^*, I^*) is any arbitrary equilibrium point of system (1.3). Then, system (1.3) can be written as

$$\frac{d}{dt}\mathbf{X}(t) = F(x(t), x(t-\tau),$$

where $F : \mathbf{C}([-\tau, 0], \mathbf{R}^3) \to \mathbf{R}^3$ is continuously differentiable function. Hence, define the matrices $A, B \in \mathbf{R}^{3\times3}$

$$A = \left[\frac{\partial F}{\partial x(t)}\right]_{x^*}; B = \left[\frac{\partial F}{\partial x(t-\tau)}\right]_{x^*}.$$

System (1.3), linearised around x^*, takes the form

$$\frac{dx(t)}{dt} = Ax(t) + Bx(t-\tau),$$

and the corresponding characteristic equation is

$$det\left[A + Be^{-\lambda\tau} - \lambda I\right] = 0,$$

where λ are the corresponding characteristic roots.

It is easy to check that the linearised system of (1.3) will be

$$P'(t) = (1 - 2P^* - aM^* - h_1)\, P(t) - aP^* M(t)$$

$$M'(t) = baM^* e^{-(\gamma+h_3)\tau} P(t-\tau) + baP^* e^{-(\gamma+h_3)\tau} M(t-\tau) - 2dM^* M(t) - h_2 M(t)$$

$$I'(t) = baP^* M(t) + baM^* P(t) - bae^{-(\gamma+h_3)\tau} P^* M(t-\tau) - bae^{-(\gamma+h_3)\tau} M^* P(t-\tau)$$

$$-\gamma I(t) - h_3 I(t).$$

The characteristic equation resulting from the linearised system at (P^*, M^*, I^*) is

$$(\lambda + \gamma + h_3)\,[(\lambda - A)(\lambda + B) + C] = 0, \tag{2.3}$$

where

$$\begin{aligned} A &= 1 - 2P^* - aM^* - h_1 \\ B &= 2dM^* + h_2 - baP^* e^{-(\gamma+h_3+\lambda)\tau} \\ C &= ba^2 P^* M^* e^{-(\gamma+h_3+\lambda)\tau}. \end{aligned}$$

We will begin by investigating the linearised stability of each equilibrium. Starting with $E_0 = (0, 0, 0)$, it is clear that the characteristic equation (2.3) reduces to

$$(\lambda + \gamma + h_3)(\lambda - (1 - h_1))(\lambda + h_2) = 0$$

Clearly, $\lambda = -(\gamma + h_3), \lambda = -h_2$ and $\lambda = 1 - h_1$ are always negative eigenvalues, therefore $E_0 = (0, 0, 0)$ is locally asymptotically stable for $h_1 > 1$.

For the equilibrium $E_1 = (1 - h_1, 0, 0)$ the characteristic equation can be found by setting $(P^*, M^*, I^*) = (1 - h_1, 0, 0)$ in (2.3) for $h_1 < 1$ to obtain

$$(\lambda + \gamma + h_3)(\lambda - (h_1 - 1))\left(\lambda + h_2 - ba(1 - h_1)e^{-(\gamma+h_3+\lambda)\tau}\right) = 0.$$

Hence, if condition (2.2) holds, then the boundary equilibrium $E_1 = (1 - h_1, 0, 0)$ is locally unstable. However, if $bae^{-(\gamma+h_3)\tau}(1 - h_1) < h_2$, then $E_1 = (1 - h_1, 0, 0)$ is linearly stable, because it can be shown under this condition that the equation

$$\lambda + h_2 = ba(1-h_1)e^{-(\gamma+h_3+\lambda)\tau},$$

does not have roots with $Re\lambda \geq 0$. In fact we will prove in the next section that $E_1 = (1-h_1, 0, 0)$ is globally asymptotically stable in this case.
For the equilibrium $E_2 = (\hat{P}, \hat{M}, \hat{I})$ the characteristic equation takes the form

$$(\lambda + d + h_3)\left(\lambda^2 + a_1\lambda + a_2 + (a_3\lambda + a_4)e^{-\lambda\tau}\right) = 0, \tag{2.4}$$

where

$$\begin{aligned} a_1 &= 2d\hat{M} + h_2 + \hat{P}, \\ a_2 &= \hat{P}(2d\hat{M} + h_2) \\ a_3 &= -(d\hat{M} + h_2) \\ a_4 &= (d\hat{M} + h_2)(a\hat{M} - \hat{P}). \end{aligned}$$

One eigenvalue is $\lambda = -(d + h_3) < 0$. The remaining eigenvalues are the roots of

$$\lambda^2 + a_1\lambda + a_2 + (a_3\lambda + a_4)e^{-\lambda\tau} = 0. \tag{2.5}$$

We will try to understand the situation by finding conditions for stability when $\tau = 0$. In the absence of delay ($\tau = 0$) equation (2.5) is of the form

$$\lambda^2 + (a_1 + a_3) + a_2 + a_4 = 0, \tag{2.6}$$

where, in this case $\hat{P} = \dfrac{d(1-h_1) + ah_2}{ba^2 + d}$, $\hat{M} = \dfrac{ba(1-h_1) - h_2}{ba^2 + d}$ and $\hat{I} = 0$. We can see that (2.6) has negative roots if and only if $a_1 + a_3 > 0$ and $a_2 + a_4 > 0$. But it is easy to show that

$$a_1 + a_3 = d\hat{M} + \hat{P} > 0.$$

Also

$$a_2 + a_4 = \hat{M}(d\hat{P} + ad\hat{M} + ah_2) > 0.$$

Therefore, the equilibrium $E_2 = (\hat{P}, \hat{M}, \hat{I})$ is locally asymptotically stable for $\tau = 0$. In the following, we shall discuss the global properties of nonnegative equilibria.

Theorem 2.1. (i) *If $h_1 > 1$, then the trivial equilibrium $E_0 = (0,0,0)$ (i.e., the case in which all species tend to extinction) of the system (1.3) is globally asymptotically stable.*

(ii) *If $h_1 < 1$, and $b < \dfrac{h_2}{a(1-h_1)}$, then the boundary equilibrium $E_1 = (1-h_1, 0, 0)$ (i.e., the case in which the predator classes tend to extinction) of the system (1.3) is globally asymptotically stable.*

(iii) *If $ba(1-h_1) > h_2$, $\tau = 0$, then the interior equilibrium $E_2 = (\hat{P}, \hat{M}, \hat{I})$ (i.e., the case in which the coexistence of both species is assured for all future time) of the system (1.3) is globally asymptotically stable.*

Proof: (i) Let us consider the Liapunov function, defined by

$$V_1 = bP(t) + M(t) + I(t).$$

Note that $V_1(P,M,I) \geq 0$ and $V_1(P,M,I) = 0$ if and only if $P = 0$, $M = 0$, $I = 0$. We now calculate the derivative of V_1 along the solution of system (1.3). We have

$$\begin{aligned} \frac{dV_1}{dt} &= bP(t)\left(1-P(t)\right) - baM(t)P(t) - bh_1P(t) + bae^{-(\gamma+h_3)\tau}M(t-\tau)P(t-\tau) \\ &\quad -dM^2(t) - h_2M(t) + baM(t)P(t) - bae^{-(\gamma+h_3)\tau}M(t-\tau)P(t-\tau) \\ &\quad -\gamma I(t) - h_3I(t) \\ &= bP(t)(1-h_1) - bP^2(t) - dM^2(t) - h_2M(t) - \gamma I(t) - h_3I(t) \leq 0. \end{aligned}$$

Set

$$D_1 = \left\{(P,M,I) \in \mathbf{R}^3_+ : V'(t) = 0\right\} = \left\{(P,M,I) \in \mathbf{R}^3_+ : P = M = I = 0\right\} = E_0.$$

According to LaSalle Theorem ([12]), E_0 is globally asymptotically stable for $h_1 > 1$.

(ii) We construct the Liapunov function V_2, defined by

$$V_2 = \left[P(t) + h_1 - 1 - (1-h_1)\ln\left(\frac{P(t)}{1-h_1}\right)\right] + \lambda(M(t) + I(t)).$$

Calculating the derivative of V_2 along each solution of (1.3), we have

$$\begin{aligned}
V_2' &= \left(P'(t) - (1-h_1)\frac{P'(t)}{P(t)}\right) + \lambda(M'(t) + I'(t)) \\
&= (P(t) - (1-h_1))(1 - P(t) - h_1) + (1-h_1)aM(t) - aP(t)M(t) \\
&\quad -\lambda dM^2(t) - \lambda h_2 M(t) + \lambda baM(t)P(t) - \lambda\gamma I(t) - \lambda h_3 I(t) \\
&= -\left(P(t) - (1-h_1)\right)^2 - \lambda dM^2 - \left(\lambda h_2 - (1-h_1)a\right)M(t) \\
&\quad -\left(a - \lambda ba\right)P(t)M(t) - \lambda\left(\gamma + h_3\right)I(t).
\end{aligned}$$

Therefore, $V_2' \leq 0$ and $V_2' = 0$ if and only if (P, M, I) coincides with E_1 provided that the arbitrary positive constant λ in V_2 can be chosen in such a way that

$$\frac{(1-h_1)a}{h_2} \leq \lambda \leq \frac{1}{b}. \tag{2.7}$$

Hence (2.7) becomes a sufficient condition for the global asymptotic stability of $E_1 = (1-h_1, 0, 0)$. But (2.7) reduces to $b < \dfrac{h_2}{a(1-h_1)}$, this completes the proof of (ii).

(iii) We make use of the general Liapunov function V_3, defined by

$$\begin{aligned}
V_3 &= b\left[P(t) - \hat{P} - \hat{P}\ln\left(\frac{P(t)}{\hat{P}}\right)\right] + \left[M(t) - \hat{M} - \hat{M}\ln\left(\frac{M(t)}{\hat{M}}\right)\right] \\
&+ I(t).
\end{aligned}$$

Now calculating the derivative of V_3 along each solution of system (1.3), with $\tau = 0$, we have

$$\begin{aligned}
V_3' &= b\left(P'(t) - \hat{P}\frac{P'(t)}{P(t)}\right) + \left(M'(t) - \hat{M}\frac{M'(t)}{M(t)}\right) + I'(t) \\
&= b\Big[P(t) - P^2(t) - aM(t)P(t) - h_1P(t) - \hat{P}\left(1 - P(t) - aM(t) - h_1\right)\Big] \\
&\quad + \Big[baM(t)P(t) - dM^2(t) - h_2M(t) - \hat{M}\left(baP(t) - dM(t) - h_2\right)\Big] \\
&\quad -(\gamma + h_3)I(t) \\
&= b\left(P(t) - \hat{P}\right)\left[1 - P(t) - aM(t) - h_1\right] + \left(M(t) - \hat{M}\right)\left[baP(t) - dM(t) - h_2\right] \\
&\quad -(\gamma + h_3)I(t) \\
&= b(P(t) - \hat{P}) - b(P(t) - \hat{P})^2 - b\hat{P}(P(t) - \hat{P}) \\
&\quad -ab(P(t) - \hat{P})\hat{M} - bh_1(P(t) - \hat{P}) + ab(M(t) - \hat{M})\hat{P} \\
&\quad -d(M(t) - \hat{M})^2 - d(M(t) - \hat{M})\hat{M} - h_2(M(t) - \hat{M}) \\
&= b(P - \hat{P})\Big[1 - \hat{P} - a\hat{M} - h_1\Big] - b(P(t) - \hat{P})^2 \\
&\quad +(M(t) - \hat{M})\Big[ab\hat{P} - d\hat{M} - h_2\Big] - (M(t) - \hat{M})^2 \\
&= -b(P(t) - \hat{P})^2 - (M(t) - \hat{M})^2 \leq 0,
\end{aligned}$$

where we have used

$$1 - \hat{P} - a\hat{M} - h_1 = 0, \text{ and } ab\hat{P} - d\hat{M} - h_2 = 0,$$

when $\tau = 0$.

Now, set

$$D_2 = \left\{(P, M, I) \in \mathbf{R}^3 : V_3' = 0\right\} = \Big\{(P, M, I) \in \mathbf{R}^3 : P = \hat{P}, M = \hat{M}, I = \hat{I}\Big\} = E_2$$

Hence, according to LaSalle theorem [12], $E_2 = (\hat{P}, \hat{M}, \hat{I})$ is globally asymptotically stable for $bp(1 - h_1) > h_2$ and $\tau = 0$.

3. Hopf Bifurcation of the Positive Equilibrium

In this section, we focus on investigating the existence of Hopf bifurcation at the positive equilibrium $E_2 = (\hat{P}, \hat{M}, \hat{I})$ of system (1.3) by using the time delay as a parameter of bifurcation.

According to Theorem 2.1 the positive equilibrium E_2 is asymptotically stable at $\tau = 0$. Stability switches for increasing τ in $[0, \tau^*)$ may occur only with a pair of roots $\lambda = \pm\omega(\tau)i$, $\omega(\tau)$ real positive, that cross the imaginary axis. To determine the stability switch delay values we proceed as follows.

For $\tau > 0$, assume $\lambda = \omega(\tau)i$ $(\omega(\tau) > 0)$ is a root of

$$\lambda^2 + a_1\lambda + a_2 + (a_3\lambda + a_4)e^{-\lambda\tau} = 0, \tag{3.1}$$

where

$$\begin{aligned} a_1 &= 2d\hat{M} + h_2 + \hat{P}, \\ a_2 &= \hat{P}(2d\hat{M} + h_2) \\ a_3 &= -(d\hat{M} + h_2) \\ a_4 &= (d\hat{M} + h_2)(a\hat{M} - \hat{P}). \end{aligned}$$

then we have

$$-\omega^2(\tau) + ia_1\omega(\tau) + a_2 + (ia_3\omega(\tau) + a_4)e^{-i\omega(\tau)\tau} = 0.$$

Separating the real and imaginary parts, we have

$$\begin{aligned} -\omega^2(\tau) + a_2 + a_4\cos\omega(\tau)\tau + a_3\omega(\tau)\sin\omega(\tau)\tau &= 0 \qquad (3.2) \\ a_1\omega(\tau) + a_3\omega(\tau)\cos\omega(\tau)\tau - a_4\sin\omega(\tau)\tau &= 0. \end{aligned}$$

Squaring both sides and adding them, we obtain the following fourth degree polynomial

$$F(\omega(\tau), \tau) = \omega^4(\tau) + (a_1^2 - a_3^2 - 2a_2)\omega^2(\tau) + a_2^2 - a_4^2 = 0. \tag{3.3}$$

Depending on the sign of $a_1^2 - a_3^2 - 2a_2$ and $a_2^2 - a_4^2$, the system may have no positive real roots, or the root

$$\omega_+(\tau) = \frac{1}{\sqrt{2}} \left\{ a_3^2 - a_1^2 + 2a_2 + \sqrt{(a_3^2 - a_1^2 + 2a_2)^2 - 4(a_2^2 - a_4^2)} \right\}^{\frac{1}{2}}, \tag{3.4}$$

or otherwise the root

$$\omega_-(\tau) = \frac{1}{\sqrt{2}} \left\{ a_3^2 - a_1^2 + 2a_2 - \sqrt{(a_3^2 - a_1^2 + 2a_2)^2 - 4(a_2^2 - a_4^2)} \right\}^{\frac{1}{2}}, \tag{3.5}$$

or, as a last case, both the roots $\omega_+(\tau)$ and $\omega_-(\tau)$. Note that if (3.3) has no positive roots $\omega(\tau)$ in $[0, \tau^*)$, then no stability switches can occur. But its easy to show that

$$a_1^2 - a_3^2 - 2a_2 = 3d^2\hat{M}^2 + 2dh_2\hat{M} + \hat{P}^2 > 0.$$

Thus $F(\omega, \tau) \neq 0$ for all $\tau \in [0, \tau^*)$ if $a_2^2 > a_4^2$, this means that, no stability switches occur as we increase $\tau \in [0, \tau^*)$.
Summarizing the above, we have the following theorem.

Theorem 3.1. *If $a_2^2 > a_4^2$, then the positive equilibrium $E_2 = (\hat{P}, \hat{M}, \hat{I})$ of system (1.3) is asymptotically stable for all $\tau \in [0, \tau^*)$.*

Next, we want to find the τ values of the stability switches that require for each positive root $\omega(\tau)$ of (3.3). These values can be found by substituting ω_+ into system (3.3) and solving for τ, we obtain

$$\tau_j^+ = \frac{1}{\omega_+} \cos^{-1} \left\{ \frac{\omega_+ a_4 - a_2 a_4 - a_1 a_3 \omega_+}{a_4^2 + a_3^2 \omega_+^2} \right\} + \frac{2\pi j}{\omega_+}, j = 0, 1, 2, \ldots \tag{3.6}$$

where $\tau_j^+ < \tau^*$.
To see if bifurcations occur, we need to verify the transversality condition

$$\frac{d}{d\tau} Re\lambda(\tau_0^+) > 0.$$

This will signify that there exists at least one eigenvalue with positive real part for $\tau > \tau_0^+$, that is, if a root of 3.1, crosses the imaginary axis while τ increases, it must cross from left to right. Moreover, the conditions for the existence of a Hopf bifurcation ([9]) are then satisfied yielding a periodic solution. Differentiating equation (3.1) with respect to τ we obtain

$$\left(2\lambda + a_1 - \tau(a_3\lambda + a_4)e^{-\lambda\tau} + a_3 e^{-\lambda\tau}\right)\frac{d\lambda}{d\tau} = \lambda(a_3\lambda + a_4)e^{-\lambda\tau}.$$

Hence,

$$\left(\frac{d\lambda}{d\tau}\right)^{-1} = \frac{(2\lambda + a_1)e^{\lambda\tau}}{\lambda(a_3\lambda + a_4)} + \frac{a_3}{\lambda(a_3\lambda + a_4)} - \frac{\tau}{\lambda}.$$

Notice that at $\lambda = i\omega_+$,

$$\begin{aligned}
sign &= sign\left\{Re\left[\frac{(2\lambda + a_1)e^{\lambda\tau}}{\lambda(a_3\lambda + a_4)}\right] + Re\left[\frac{a_3}{\lambda(a_3\lambda + a_4)}\right]\right\} \\
&= sign\left\{Re\left[\frac{a_1\cos\omega_+\tau_j - 2\omega_+\sin\omega_+\tau_j + (2\omega_+\cos\omega_+\tau_j + a_1\sin\omega_+\tau_j)}{-a_3\omega_+^2 + ia_4\omega_+}\right]\right. \\
&\quad \left. + Re\left[\frac{a_3}{-a_3\omega_+^2 + ia_4\omega_+}\right]\right\} \\
&= sign\left\{\frac{1}{\Lambda}\left[-a_3\omega_+^2\left(a_1\cos\omega_+\tau_j - 2\omega_+\sin\omega_+\tau_j\right)\right.\right. \\
&\quad \left.\left. + a_4\omega_+(2\omega_+\cos\omega_+\tau_j + a_1\sin\omega_+\tau_j) - a_3^2\omega_+^2\right]\right\} \\
&= sign\left\{\frac{1}{\Lambda}\left[a_1\omega_+(a_4\sin\omega_+\tau_j - a_3\omega_+\cos\omega_+\tau_j)\right.\right. \\
&\quad \left.\left. + 2\omega_+^2(a_4\cos\omega_+\tau_j + a_3\omega_+\sin\omega_+\tau_j) - a_3^2\omega_+^2\right]\right\} \\
&= sign\left\{\frac{1}{\Lambda}\left[a_1^2\omega_+^2 + 2\omega_+^4 - 2a_2\omega_+^2 - a_3^2\omega_+^2\right]\right\} \\
&= sign\left\{\frac{\omega_+^2}{\Lambda}\left[2\omega_+^2 + a_1^2 - 2a_2 - a_3^2\right]\right\} \\
&= sign\left\{\frac{\omega_+^2}{\Lambda}\left[\sqrt{(a_3^2 + 2a_2 - a_1^2)^2 - 4(a_2^2 - a_4^2)}\right]\right\} > 0.
\end{aligned}$$

where, $\Lambda = a_3^2\omega_+^4 + a_4^2\omega_+^2$.

We summarize the above results in the following theorem.

Theorem 3.2. *If* τ_j^+ *satisfy (3.6) and* $a_2^2 < a_4^2$ *then the equilibrium* E_2 *of system (1.3) is asymptotically stable for* $\tau < \tau_0^+$ *and unstable for* $\tau > \tau_0^+$*. The system undergoes a Hopf bifurcation at* $\tau = \tau_0^+$ *and generates a periodic solution.*

4. **Global Attractiveness**

In this section, we consider the global stability of the interior equilibrium E_2 in system (1.5). But before we have the next result, we need the following lemma which will be used in the proof of the next theorem.

Lemma 4.1. *(see (*[13]*)). Given the equation*

$$u'(t) = au(t-\tau) - cu^2(t) - bu(t),$$

where a,b,c, and $\tau > 0$ *and* $u(t) > 0$ *for* $-\tau \leq t \leq 0$*, then*
(i) If $a > b$*, then* $\lim_{t\to\infty} u(t) = \frac{a-b}{c}$*. (ii) If* $a < b$*, then* $\lim_{t\to\infty} u(t) = 0$.

Theorem 4.1. *If* $bae^{-(\gamma+h_3)\tau}(1-h_1) > h_2$ *and* $a^2be^{-(\gamma+h_3)\tau} < d$ *hold, then the positive equilibrium* E_2 *in system (1.5) is globally atractive.*

Proof: By the first equation of system (1.5) and the boundedness of $P(t)$, for sufficiently small $\varepsilon > 0$, there is a $T_1 > 0$ such that $P(t) < 1 - h_1 + \varepsilon = \overline{P_1}$ for $t \geq T_1$. Replacing this inequality into the second equation of (1.5), we have

$$M'(t) < bae^{-(\gamma+h_3)\tau}\,\overline{P}_1 M(t-\tau) - dM^2(t) - h_2 M(t),\ t \geq T_1 + \tau.$$

Consider the system

$$v'(t) = bae^{-(\gamma+h_3)\tau}\,\overline{P_1} v(t-\tau) - dv^2(t) - h_2 v(t),\ t \geq T_1 + \tau,$$

$$v(t) = M(t), \quad t \in [T_1, T_1 + \tau].$$

Noting that, from (2.2) $bae^{-(\gamma+h_3)\tau}\overline{P_1} - h_2 > bae^{-(\gamma+h_3)\tau}(1-h_1) - h_2 > 0$. Thus by lemma 1, we have

$$\lim_{t\to\infty} v(t) = \frac{bae^{-(\gamma+h_3)\tau}\overline{P_1} - h_2}{d} > 0.$$

By the comparison theorem, we have $M(t) \leq v(t)$, $t \geq T_1 + \tau$. Then for sufficiently small $\varepsilon > 0$, there exists $T_2 > T_1 + \tau$ such that

$$M(t) < \frac{bae^{-(\gamma+h_3)\tau}\overline{P_1} - h_2}{d} + \varepsilon = \overline{M_1},\ t \geq T_2.$$

Replacing the last inequality into the first equation of (1.5), we have

$$P'(t) > P(t)(1 - P(t)) - aP(t)\overline{M_1} - h_1 P(t),\ \ t \geq T_2.$$

Using the comparison theorem, for sufficiently small $\varepsilon > 0$, there is a $T_3 > T_2$ such that

$$P(t) > \Psi - \varepsilon = \underline{P_1},\ \ t \geq T_3,$$

where $\Psi = 1 - a\overline{M_1} - h_1$ is the positive solution of

$$P(t)(1 - P(t)) - aP(t)\overline{M_1} - h_1 P(t) = 0.$$

Replacing $\underline{P_1}$ into the second equation of (1.5), we have

$$M'(t) > bae^{-(\gamma+h_3)\tau}\underline{P_1}M(t-\tau) - dM^2(t) - h_2 M(t),\ t \geq T_3 + \tau.$$

Since $bae^{-(\gamma+h_3)\tau}\underline{P_1} > h_2$, for sufficiently small ε, then by lemma 1 and similar arguments to $\overline{M_1}$, for the above selected $\varepsilon > 0$, there exists $T_4 > T_3 + \tau$ such that

$$M(t) > \frac{bae^{-(\gamma+h_3)\tau}\underline{P_1} - h_2}{d} - \varepsilon = \underline{M_1} > 0,\ t \geq T_4.$$

Therefore, we have that

$$\underline{P_1} < P(t) < \overline{P_1},\ \ \underline{M_1} < M(t) < \overline{M_1},$$

hold for system (1.5).

Replacing $\underline{M_1}$ into the first equation of (1.5), we have

$$P'(t) > P(t)(1 - P(t)) - aP(t)\underline{M_1} - h_1 P(t),\ \ t \geq T_4.$$

By comparison theorem, for sufficiently small $\varepsilon > 0$, there is a $T_5 > T_4$ such that

$$P(t) < \Psi_1 + \varepsilon = \overline{P_2} > 0,$$

where $\Psi_1 = 1 - a\underline{M_1} - h_1$.

Replacing $\overline{P_2}$ into the second equation of (1.5), we have

$$M'(t) < bae^{-(\gamma+h_3)\tau}\overline{P_2}M(t-\tau) - dM^2(t) - h_2M(t),\ t \geq T_5 + \tau.$$

Since $\overline{P_2} > \underline{P_1}$, then $bae^{-(\gamma+h_3)\tau}\overline{P_2} > h_2$. Thus using arguments similar to above, for sufficiently small $\varepsilon > 0$, there is a $T_6 > T_5 + \tau$ such that

$$M(t) < \frac{bae^{-(\gamma+h_3)\tau}\overline{P_2} - h_2}{d} + \varepsilon = \overline{M_2},\ t \geq T_6,$$

by the definition of $\overline{M_2}$ and $\overline{M_1}$ we get $\overline{M_2} < \overline{M_1}$.

Replacing $\overline{M_2}$ into the first equation of (1.5) we have

$$P'(t) > P(t)(1 - P(t)) - aP(t)\overline{M_2} - h_1P(t),\ \ t \geq T_6.$$

Then we have

$$P(t) > \Psi_2 - \varepsilon = \underline{P_2} > 0,\ \ t \geq T_7,$$

with $\Psi_2 = 1 - a\overline{M_2} - h_1$. By the definition of $\underline{P_2}$, we have $\underline{P_2} > \underline{P_1}$.

Replacing $\underline{P_2}$ into the second equation of (1.5), then by arguments similar to those for $\overline{M_2}$, we get that there exists a $T_8 > T_7 + \tau$ such that

$$M(t) > \frac{bae^{-(\gamma+h_3)\tau}\underline{P_2} - h_2}{d} - \varepsilon = \underline{M_2},\ t \geq T_8,$$

and we get $\underline{M_2} > \underline{M_1}$.

Therefore, we have

$$\begin{aligned} 0 &< \underline{P_1} < \underline{P_2} < P(t) < \overline{P_2} < \overline{P_1}, \\ 0 &< \underline{M_1} < \underline{M_2} < M(t) < \overline{M_2} < \overline{M_1},\ \ t \geq T_8. \end{aligned}$$

By repeating the above arguments, we get four sequences $\left\{\overline{P_n}\right\}_{n=1}^{n=\infty}$, $\left\{\underline{P_n}\right\}_{n=1}^{n=\infty}$, $\left\{\overline{M_n}\right\}_{n=1}^{n=\infty}$, $\left\{\underline{M_n}\right\}_{n=1}^{n=\infty}$ with

$$\begin{aligned} 0 &< \underline{P_1} < \cdots < \underline{P_n} < P(t) < \overline{P_n} < \cdots < \overline{P_1}, \\ 0 &< \underline{M_1} < \cdots < \underline{M_n} < M(t) < \overline{M_n} < \cdots < \overline{M_1}, \ \ t \geq T_{4n}. \end{aligned} \tag{4.1}$$

From (4.1) follows that the limit of each sequence in $\left\{\overline{P_n}\right\}_{n=1}^{n=\infty}$, $\left\{\underline{P_n}\right\}_{n=1}^{n=\infty}$, $\left\{\overline{M_n}\right\}_{n=1}^{n=\infty}$, $\left\{\underline{M_n}\right\}_{n=1}^{n=\infty}$ exists. Denote

$$\overline{P} = \lim_{n\to\infty} \overline{P_n}, \ \ \overline{M} = \lim_{n\to\infty} \overline{M_n}, \ \ \underline{P} = \lim_{n\to\infty} \underline{P_n}, \ \ \underline{M} = \lim_{n\to\infty} \underline{M_n};$$

thus we get $\overline{P} \geq \underline{P}$, $\overline{M} \geq \underline{M}$. To complete the proof, it suffices to prove $\overline{P} = \underline{P}$, $\overline{M} = \underline{M}$.

By the definition of $\overline{M_n}$, $\underline{M_n}$ we have

$$\overline{M_n} = \frac{bae^{-(\gamma+h_3)\tau}\overline{P_n} - h_2}{d} + \varepsilon, \ \ \underline{M_n} = \frac{bae^{-(\gamma+h_3)\tau}\underline{P_n} - h_2}{d} - \varepsilon,$$

then we have

$$\overline{M_n} - \underline{M_n} = \frac{bae^{-(\gamma+h_3)\tau}}{d}\left(\overline{P_n} - \underline{P_n}\right) + 2\varepsilon. \tag{4.2}$$

By the definition of $\overline{P_n}$, $\underline{P_n}$ and using (4.2), we have

$$\begin{aligned} \overline{P_n} - \underline{P_n} &= (1 - a\underline{M_{n-1}} - h_1) - (1 - a\overline{M_n} - h_1) + 2\varepsilon \\ &= a(\overline{M_n} - \underline{M_{n-1}}) + 2\varepsilon \\ &= \frac{a^2be^{-(\gamma+h_3)\tau}}{d}(\overline{P_n} - \underline{P_{n-1}}) + 2\varepsilon(a+1). \end{aligned}$$

Let $n \to \infty$, then we have

$$\overline{P} - \underline{P} \leq \frac{a^2be^{-(\gamma+h_3)\tau}}{d}(\overline{P} - \underline{P}) + 2\varepsilon(a+1),$$

thus

$$\left\{1 - \frac{a^2be^{-(\gamma+h_3)\tau}}{d}\right\}(\overline{P} - \underline{P}) \leq 2\varepsilon(a+1).$$

By $0 < \frac{a^2 b e^{-(\gamma+h_3)\tau}}{d} < 1$, we have $1 - \frac{a^2 b e^{-(\gamma+h_3)\tau}}{d} > 0$, and noting that ε can be arbitrarily small, then we have $\overline{P} = \underline{P}$. By (4.2) and let $n \to \infty$, we get $\overline{M} = \underline{M}$. This proves the theorem.

5. **Interpretation of the Theoretical Results**

In this section, we present a numerical analysis on model (1.5) to illustrate the applicability of our main results. We shall first confirme numerically the result in section 3, Theorem 3.1 for certain values of the parameters, that when $a_2^2 > a_4^2$ then E_2 is always stable regardles of the value of the delay, see Figure 1.
Then in Figure 2 we carried out several simulation, for another combination of parameter values. For the parameter values used (see caption) the interior equilibrium loses stability and then regains stability at a larger τ, befor the equilibrium itself finally disappears at $\tau^* \approx 5$.
Figure 3, shows numerical simulation in the unlikely case that juveniles do not suffer any mortality ($\gamma = 0$). Unlike the result in [7] , where their simulation indicates that, the stability of the interior equilibrium is permanently lost and oscillatory dynamics will persist and gain complexity when τ is increased, our results, in this case, shows that for lower τ the equilibrium E_2 is stable, then loses stability and then regains it as τ is increased.

6. **Discussion**

In this paper, we study the stage-structured predator-prey model with linear functional response, and continuous harvesting on prey and predator populations.
We give the conditions which are sufficient for the coexistence and extinction of system (1.3). Our results suggest that the predator coexists with prey permanently if and only if (2.2) holds true, i.e., predator's recruitment rate ($bae^{-(\gamma+h_3)\tau}$) at the peak of prey abundance is larger than its harvesting rate (h_2), and that if it takes too

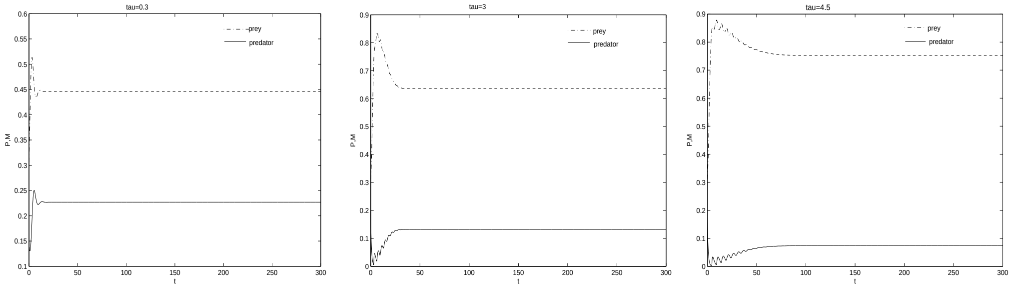

FIGURE 1. A solution of model (1.5) illustrating a situation in which both the prey and predator converges to the equilibrium values for all values of $\tau \in [0, 6.4]$, where $a = 2.0$, $b = 2.0$, $\gamma = 0.1$, $d = 3$, $h_1 = h_3 = 0.1$, $h_2 = 1$. Note that, for all values of τ, $a_2^2 > a_4^2$.

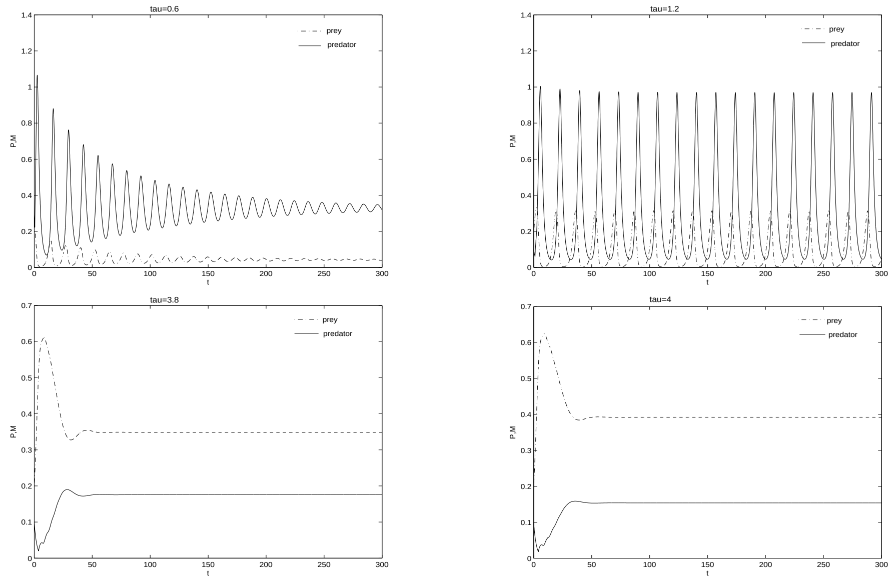

FIGURE 2. A solution of model (1.5), where $a = 2.0$, $b = 10$, $\gamma = 0.5$, $d = 0.5$, $h_1 = 0.3$, $h_3 = 0.2$, $h_2 = 0.4$ and $\tau \in [0, 5]$. Note that, at $\tau = 1.2$ system (1.5) generates a periodic solution since $a_2 < a_4$

much for the immature predator to mature, or the through-stage death rate of the immature predator is high (that is, the recruitment rate is small compared to h_2),

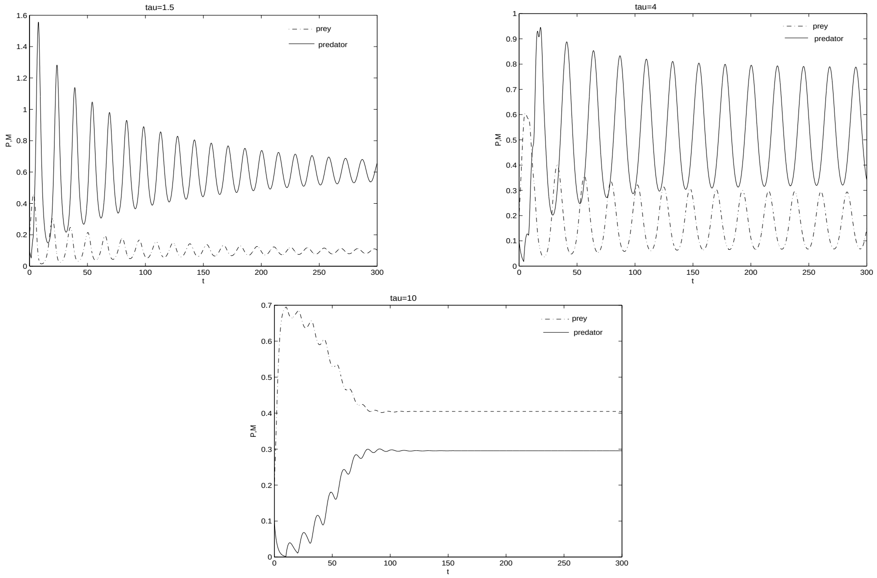

FIGURE 3. A solution of model (1.5), where $a = 1.0$, $b = 10$, $\gamma = 0$ (i.e. no juvenile mortality), $d = 0.5$, $h_1 = 0.3$, $h_3 = 0.2$, $h_2 = 0.4$ and $\tau \in [0, 14.3]$.

then the total number of production during the adult stage will not be enough to compensate the total loss of immature predators and the predator classes will tend to extinction. Also, if the harvesting rate of the immature population is increased, it may be responsible for the extinction of predators.

We also find the stability switches of the interior equilibrium E_2 due to the increase of time delay τ: as τ increases, we see that oscillatory dynamics may appear and further increas of τ will return the oscillatory dynamics to the steady state form.

Finally, we proved that the three equilibria are globally asymptotically stable. The results show that the behavior of harvesting on prey and predator populations affect the dynamical behavior of system (1.3). That is, it can prevent the predator from dying out.

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