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**STABILITY AND OPTIMAL HARVESTING
OF A PREY-PREDATOR MODEL
WITH STAGE STRUCTURE FOR PREDATOR**

Abstract. The dynamics of a prey-predator system, where predator has two stages, a juvenile stage and a mature stage, is modelled by a system of three ordinary differential equations. Stability and permanence of the system are discussed. Furthermore, we consider the harvesting of prey species and obtain the maximum sustainable yield and the optimal harvesting policy.

1. Introduction. Stage structured models have received much attention in recent years, i.e., models which take into account the fact that individuals in a population may belong to one of two classes, the immature and mature. See, for example, Aiello and Freedman [1990], Aiello *et al.* [1992], Freedman and Wu [1991], Gambell [1985], Landahl and Hanson [1975], Wood *et al.* [1989] and the references therein. In these models, the age of maturity is represented by a time delay. Cannibalism has been observed in a great variety of species, including a number of fish species. Cannibalism models of various types have also been investigated by Cushing [1991], Diekmann *et al.* [1986], Freedman *et al.* [1994], Hastings [1987], Magnusson [1999]. For general models of population growth see Murray [1989]. Recently, papers like Bosch and Gabriel [1997], Kar [2003] and Zhang *et al.* [2000] study the stage structure of species with or without time delays.

The optimal management of renewable resources, which has a direct relationship to sustainable development, has been studied extensively by many authors. Economic and biological aspects of renewable resources management have been considered by Clark [1976] and other authors like Brauer and Soudack [1979, 1981], Dai and Tang [1998], Kar and Chaudhuri [2000, 2003],

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Bhattacharya and Begum [1996], Ragozin and Brown [1985], Mesterton-Gibbons [1988], Leung [1995] and Jerry and Raissi [2001]. From the point of view of ecological managers, it may be desirable for the system to be globally stable or permanent, in order to plan harvesting strategies and keep a sustainable development of the ecosystem.

To facilitate the interpretation of our mathematical findings we assume that the prey or the renewable resource, density of which is denoted by N_1 , can be modelled by a logistic equation when the consumer is absent. We assume that the predators or consumers are divided into two stage groups: juveniles and adults, and their densities are denoted by N_2 and N_3 respectively. Here we also assume that only adult predators are capable of preying on the prey species and that the juvenile predators live on their parents. For example, the Chinese alligator can be regarded as a stage-structured species since the mature is more than 10 years old, and can also be regarded as a predator because almost all aquatic animals are the chief food of the Chinese alligator. Another key and somewhat novel feature of our model is to account for the universally prevalent intra-specific competition in the consumer growth dynamics (Kuang *et al.* [2003]). This intra-specific competition is assumed to induce additional instantaneous deaths only to the adult population and the increased death rate is proportional to the square of the adult population.

With these assumptions, we have the following plausible two-stage prey-predator interaction model:

$$(1.1) \quad \begin{aligned} \frac{dN_1}{dt} &= r_1 N_1 \left(1 - \frac{N_1}{k} \right) - \alpha N_1 N_3, & \frac{dN_2}{dt} &= \beta N_3 - r_2 N_2, \\ \frac{dN_3}{dt} &= -r_3 N_3 + m\alpha N_1 N_3 + \gamma N_2 - \delta N_3^2. \end{aligned}$$

Here r_1 is the specific growth rate of the prey and k is its carrying capacity. α is the predation parameter; m is the conversion factor; r_3 is the death rate of mature predator species; γ is the proportionality constant of transformation of immature to mature predators; $r_2 = \mu + \gamma$, where μ is the death rate; β is the birth rate of the immature populations.

Defining

$$N_1 = \frac{kr_2}{r_1} x_1, \quad N_2 = \frac{\beta x_2}{m\alpha}, \quad N_3 = \frac{r_2 x_3}{m\alpha}, \quad t = \frac{\tau}{r_2},$$

we can rewrite (1.1) as

$$(1.2) \quad \begin{aligned} \frac{dx_1}{d\tau} &= ax_1 - x_1^2 - bx_1 x_3, & \frac{dx_2}{d\tau} &= x_3 - x_2, \\ \frac{dx_3}{d\tau} &= -cx_3 + dx_1 x_3 + ex_2 - fx_3^2, \end{aligned}$$

where

$$a = \frac{r_1}{r_2}, \quad b = \frac{1}{m}, \quad c = \frac{r_3}{r_2}, \quad d = \frac{m\alpha k}{r_1}, \quad e = \frac{\gamma\beta}{r_2^2}, \quad f = \frac{\delta}{m\alpha}.$$

In Section 2, we discuss the equilibria and their stability for system (1.2). In Section 3, we consider the harvesting of prey species. Reasonable harvesting policies are indisputably one of the major and interesting problems from the ecological and economical point of view. The exploitation of biological resources and harvests of population species are commonly practised in fishery, forestry and wildlife management. A management of multispecies fisheries is needed to maintain an ecological balance, which is disrupted due to overexploitation of many conventional fish stocks and growing interest in harvesting new kinds of food from the sea. An optimal harvesting policy is studied in Section 4.

2. Equilibria and stability analysis. System (1.2) has to be analyzed with the following initial conditions: $x_1(0) > 0$, $x_2(0) > 0$ and $x_3(0) > 0$. We observe that the right-hand side of (1.2) is a smooth function of the variables (x_1, x_2, x_3) and the parameters, as long as these quantities are non-negative, so local existence and uniqueness properties hold in the positive octant. The state space for system (1.2) is the positive octant, $\{(x_1, x_2, x_3) : x_1 > 0, x_2 > 0 \text{ and } x_3 > 0\}$, which is clearly an invariant set, since the vector field on the boundary does not point to the exterior. Our next result concerns the existence of equilibrium points.

We observe that the possible non-negative equilibria of system (1.2) are $P_0(0, 0, 0)$, $P_1(a, 0, 0)$ and $P_2(x_1^*, x_2^*, x_3^*)$ where

$$x_1^* = \frac{af + bc - be}{db + f} \quad \text{and} \quad x_2^* = x_3^* = \frac{e + da - c}{db + f}.$$

We remark that if $e > c$, then there exists another equilibrium in the absence of prey. But it is not feasible since prey is the only source of food for the predator. So throughout the paper we assume that $c \geq e$ (i.e., the ratio of the death rate of the mature predators to the rate of transformation from immature to mature is greater than or equal to the ratio of the birth rate and enhanced death rate of the immature predators). Therefore, P_2 is feasible if $c < e + ad$.

We are particularly interested in the interior equilibrium point $P_2(x_1^*, x_2^*, x_3^*)$ for its usual importance.

In order to investigate the stability of system (1.2) near P_0 , P_1 and P_2 , we compute the variational matrix which is given by

$$M(x_1, x_2, x_3) = \begin{bmatrix} a - 2x_1 - bx_3 & 0 & -bx_1 \\ 0 & -1 & 1 \\ dx_3 & e & -c + dx_1 - 2fx_3 \end{bmatrix}.$$

Now,

$$M(0, 0, 0) = \begin{bmatrix} a & 0 & 0 \\ 0 & -1 & 1 \\ 0 & e & -c \end{bmatrix}.$$

The characteristic equation of $M(0, 0, 0)$ is $(a - \lambda)\{\lambda^2 + (c + 1)\lambda + c - e\} = 0$. Hence the point $P_0(0, 0, 0)$ is unstable.

Next,

$$M(a, 0, 0) = \begin{bmatrix} -a & 0 & -ba \\ 0 & -1 & 1 \\ 0 & e & -c + ad \end{bmatrix}.$$

The characteristic equation of $M(a, 0, 0)$ is

$$(a + \lambda)\{\lambda^2 - \lambda(ad - c - 1) - (ad + e - c)\} = 0.$$

Therefore $P_1(a, 0, 0)$ is locally asymptotically stable for $c > e + ad$.

Finally,

$$M(x_1^*, x_2^*, x_3^*) = \begin{bmatrix} -x_1^* & 0 & -bx_1^* \\ 0 & -1 & 1 \\ dx_3^* & e & -c - 2fx_3^* + dx_1^* \end{bmatrix}.$$

The characteristic equation of $M(x_1^*, x_2^*, x_3^*)$ is $\lambda^3 + A\lambda^2 + B\lambda + C = 0$ where

$$A = 1 + e + x_1^* + fx_3^* > 0,$$

$$B = fx_3^* + x_1^* + x_1^*(fx_3^* + e) + bdx_1^*x_3^*,$$

$$C = (f + bd)x_1^*x_3^* > 0.$$

Obviously, $AB - C > 0$. According to the Routh-Hurwitz criterion, $P_2(x_1^*, x_2^*, x_3^*)$ is locally asymptotically stable if $c < e + ad$.

Now we shall discuss the condition of global stability, permanence and extinction for system (1.2). First, we set

$$\mathbb{R}_+^3 = \{x = (x_1, x_2, x_3) \in \mathbb{R}^3 : x_i \geq 0\},$$

$$\text{Int } \mathbb{R}_+^3 = \{x = (x_1, x_2, x_3) \in \mathbb{R}^3 : x_i > 0\}.$$

DEFINITION 2.1. An equilibrium point $P(x_1, x_2, x_3)$ is said to be *globally asymptotically stable* in \mathbb{R}_+^3 if it is locally asymptotically stable and all trajectories in \mathbb{R}_+^3 converge to $P(x_1, x_2, x_3)$.

LEMMA 2.1. (i) *If $c \geq e + ad$, then the equilibrium $P_1(a, 0, 0)$ is globally asymptotically stable in \mathbb{R}_+^3 .*

(ii) *If $c < e + ad$, then the unique interior equilibrium point $P_2(x_1^*, x_2^*, x_3^*)$ is globally asymptotically stable in $\text{Int } \mathbb{R}_+^3$.*

Proof. (i) We construct the Lyapunov function

$$V_1 = \alpha_1 \left(x_1 - a - a \ln \frac{x_1}{a} \right) + \alpha_2 x_2 + \alpha_3 x_3$$

where $\alpha_i, i = 1, 2, 3$, are positive constants to be determined below. Calculating the derivative of V_1 along each solution of (1.2), we have

$$\begin{aligned} \frac{dV_1}{d\tau} &= \alpha_1 \left(\frac{x_1 - a}{x_1} \right) \frac{dx_1}{d\tau} + \alpha_2 \frac{dx_2}{d\tau} + \alpha_3 \frac{dx_3}{d\tau} \\ &= -\alpha_1(x_1 - a)^2 - \alpha_1 b(x_1 - a)x_3 + (\alpha_2 x_3 - c\alpha_3 x_3) \\ &\quad - \alpha_2 x_2 + \alpha_3 e x_2 + \alpha_3 d x_1 x_3 - \alpha_3 f x_3^2. \end{aligned}$$

Let $\alpha_1 = d/b, \alpha_2 = e$ and $\alpha_3 = 1$. Then

$$\frac{dV_1}{d\tau} = -\frac{d}{b}(x_1 - a)^2 - (c - e - ad)x_3 - f x_3^2 < 0 \text{ in Int } \mathbb{R}_+^3 \quad \text{for } c \geq e + ad.$$

Therefore, by Lyapunov-LaSalle (Hale [1969]), it follows that P_1 is locally asymptotically stable and all trajectories starting in $\text{Int } \mathbb{R}_+^3$ approach P_1 as t goes to infinity. This establishes the global asymptotic stability.

(ii) Let us take the Lyapunov function

$$V_2(x_1, x_2, x_3) = \sum \alpha_i \left(x_i - x_i^* - x_i^* \ln \frac{x_i}{x_i^*} \right)$$

where $\alpha_i, i = 1, 2, 3$, are positive constants to be determined below. Calculating the derivative along each solution of (1.2), we have

$$\begin{aligned} \frac{dV_2}{d\tau} &= \sum \alpha_i \left(\frac{x_i - x_i^*}{x_i} \right) \frac{dx_i}{d\tau} \\ &= -\alpha_1(x_1 - x_1^*)^2 - b\alpha_1(x_1 - x_1^*)(x_3 - x_3^*) + \alpha_2(x_2 - x_3^*) \left(\frac{x_3}{x_2} - \frac{x_3^*}{x_2^*} \right) \\ &\quad + \alpha_3 d(x_3 - x_3^*)(x_1 - x_1^*) + e\alpha_3(x_3 - x_3^*) \left(\frac{x_2}{x_3} - \frac{x_2^*}{x_3^*} \right) \\ &\quad - f\alpha_3(x_3 - x_3^*)^2. \end{aligned}$$

Let $\alpha_1 = d/b, \alpha_2 = e$ and $\alpha_3 = 1$. Then

$$\begin{aligned} \frac{dV_2}{d\tau} &= -\frac{d}{b}(x_1 - x_1^*)^2 - f(x_3 - x_3^*)^2 - e \left(\frac{x_3}{x_2 x_2^*} \right) (x_2 - x_2^*)^2 \\ &\quad - e \left(\frac{x_2}{x_3 x_3^*} \right) (x_3 - x_3^*)^2 + \frac{2e}{x_2^*} (x_2 - x_2^*)(x_3 - x_3^*) \\ &= -\frac{d}{b}(x_1 - x_1^*)^2 - f(x_3 - x_3^*)^2 \\ &\quad - e x_2^* \left[\sqrt{\frac{x_3}{x_2}} (x_2 - x_2^*)^2 - \sqrt{\frac{x_2}{x_3}} (x_3 - x_3^*) \right]^2 < 0. \end{aligned}$$

By similar arguments to those used for P_1 , we conclude that $P_2(x_1^*, x_2^*, x_3^*)$ is globally asymptotically stable if $c < e + ad$.

DEFINITION 2.2. System (1.2) is said to be *permanent* if there are positive constants m and M such that each positive solution $x(t, x_0)$ of (1.2) with initial condition $x_0 \in \text{Int } \mathbb{R}_+^3$ satisfies

$$m \leq \liminf_{t \rightarrow \infty} x_i(t, x_0) \leq \limsup_{t \rightarrow \infty} x_i(t, x_0) \leq M, \quad i = 1, 2, 3.$$

DEFINITION 2.3. The i th species of system (1.2) is said to be *extinctive* if each positive solution $x(t, x_0)$ of (1.2) with initial condition $x_0 \in \text{Int } \mathbb{R}_+^3$ satisfies

$$\lim_{t \rightarrow \infty} x_i(t, x_0) = 0, \quad i = 1, 2, 3.$$

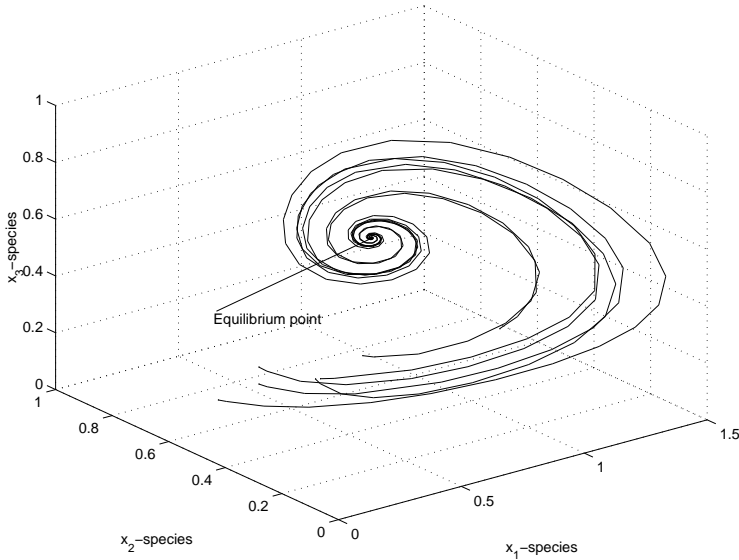


Fig. 1. Phase space trajectories of system (1.2) beginning with different initial levels. It is seen that $P_2(0.77, 0.56, 0.56)$ is a global attractor, where $a = 3.0, f = 0.04, b = 4, c = 2.5, e = 0.2, d = 3.0$.

REMARK. We have $c \geq e + ad \Leftrightarrow r_3 \geq m\alpha k + \gamma\beta/r_2$.

We have the following theorem.

THEOREM 2.1. (i) *The predator species of system (1.2) is extinctive and the prey species is not extinctive if and only if $c \geq e + ad$.*

(ii) *Both prey and predator species are permanent if and only if $c < e + ad$.*

Proof. This follows easily from Definitions 2.1 and 2.2, and Lemma 2.1.

3. Harvesting of prey species. In order to study the effect of harvesting on system (1.2), let us consider the following system:

$$(3.1) \quad \begin{aligned} \frac{dx_1}{d\tau} &= ax_1 - x_1^2 - bx_1x_3 - qEx_1, \\ \frac{dx_2}{d\tau} &= x_3 - x_2, \\ \frac{dx_3}{d\tau} &= -cx_3 + dx_1x_3 + ex_2 - fx_3^2. \end{aligned}$$

Here qEx_1 is based on the catch-per-unit-effort hypothesis (Clark [1976]), where q is the catchability coefficient and E is the harvesting effort.

The possible non-negative equilibria of system (3.1) are $Q_0(0, 0, 0)$, $Q_1(a - qE, 0, 0)$ and $Q_2(\bar{x}_1, \bar{x}_2, \bar{x}_3)$ where

$$\bar{x}_1 = \frac{(a - qE)f + bc - be}{db + f}, \quad \bar{x}_2 = \bar{x}_3 = \frac{e - c + d(a - qE)}{db + f}.$$

Similar to the previous section, we have the following theorem.

- THEOREM 3.1.** (i) *The predator species of system (3.1) is extinctive and the prey species is not extinctive if and only if $c + qEd \geq e + ad$.*
 (ii) *System (3.1) is permanent if and only if $c + qEd < e + ad$.*
 (iii) *Both prey and predator species of system (3.1) are extinctive if and only if $a < qE$.*

In the following we shall consider the maximum sustainable yield of system (3.1).

Maximum sustainable yield. The maximum sustainable yield (MSY) of a biological resource population is the maximum rate at which it can be harvested even after maintaining the population at a constant level.

THEOREM 3.2. *The maximum sustainable yield of system (3.1) is equal to*

$$\frac{(af + bc - be)^2}{4(db + f)f}$$

and occurs at the effort level

$$E_{\text{MSY}} = \frac{af + bc - be}{2qf}.$$

Proof. Corresponding to a given effort E , the sustainable yield is given by

$$h(E) = qE\bar{x}_1 = qE \frac{(a - qE)f + bc - be}{db + f}.$$

Then

$$\frac{dh}{dE} = \frac{q}{db + f} [(a - qE)f + bc - be] - \frac{q^2Ef}{db + f}$$

and $dh/dE = 0$ gives

$$\bar{E} = \frac{af + bc - be}{2qf}.$$

Now

$$\frac{d^2h}{dE^2} = -\frac{2q^2f}{db + f} < 0.$$

Therefore, $h(E)$ is maximum when $E = \bar{E}$. Hence,

$$\text{MSY} = q\bar{E}\bar{x}_1 = \frac{(af + bc - be)^2}{4(db + f)f}.$$

Thus the MSY occurs at the effort level $E_{\text{MSY}} = \bar{E}$ and for any value of $E > E_{\text{MSY}}$, the yield $h(E)$ monotonically decreases with E towards zero (see Figure 2). If the effort level exceeds its MSY level, biologists call it a case of biological overexploitation. It is observed that at E_{MSY} , Q_2 is globally asymptotically stable.

For simulation let us take $a = 3.0$, $f = 0.7$, $b = 4.0$, $c = 0.62$, $d = 3.0$, $e = 0.25$, $q = 0.5$. For these values we get $E_{\text{MSY}} = 4.95$ and $\text{MSY} = 0.38$.

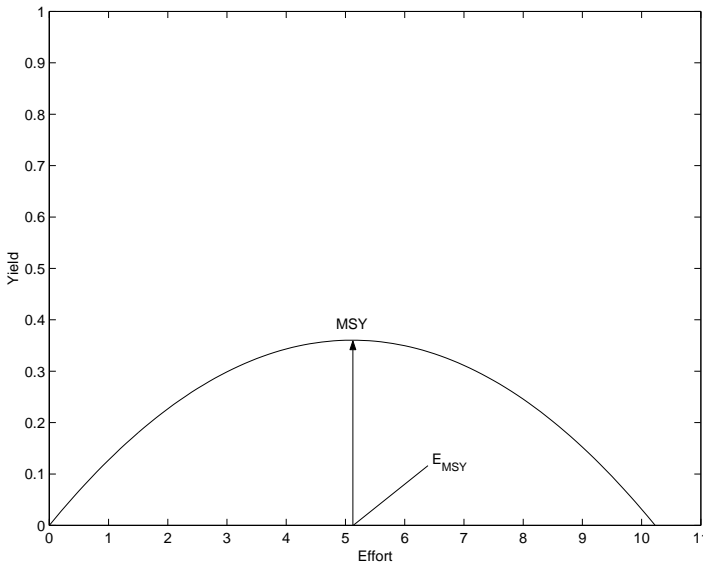


Fig. 2. Yield-effort curve. The curve shows that when $E > E_{\text{MSY}}$, yield monotonically decreases with effort E towards zero.

4. Optimal harvesting policy. The MSY is a simple way to manage resources taking into consideration that overexploiting resources leads to a loss in productivity. Therefore, the aim is to determine how much we can harvest without altering dangerously the harvested population. The main

problem of the MSY is economical irrelevance. It is so since it takes into consideration the benefits of resource exploitation, but completely disregards its costs. For example, it ignores the fact that if a species is harvested in such a way that its population decreases to a certain level, then the cost of harvesting can become exorbitant because finding the desirable resource becomes more consuming. This might lead to a situation where the cost of harvesting is higher than the benefit. Confronted with the inadequacy of the MSY, people tried to replace it by the “optimal sustainable yield”, which is based on the standard cost benefit criterion used to maximize the revenues. Our objective is to solve the following optimization problem:

$$(4.1) \quad \max \int_0^{\infty} e^{-\theta\tau} (pqx_1 - c)E(\tau) d\tau$$

subject to the state equations of (3.1) and the control constraint $0 \leq E(\tau) \leq E_{\max}$, where θ is the instantaneous annual discount rate.

In order to solve the above optimization problem, we employ Pontryagin's Maximal Principle (Pontryagin *et al.* [1964]).

The associated Hamiltonian function is given by

$$H = e^{-\theta\tau} (pqx_1 - c)E + \lambda_1 [ax_1 - x_1^2 - bx_1x_3 - qEx_1] + \lambda_2 [x_3 - x_2] + \lambda_3 [-cx_3 + dx_1x_3 + ex_2 - fx_3^2]$$

where λ_1, λ_2 and λ_3 are adjoint variables and

$$\phi(\tau) = e^{-\theta\tau} (pqx_1 - c) - \lambda_1 qx_1$$

is called the *switching function*.

Since H is linear in the control variable, the optimal control will be a combination of the extreme control and the singular control. The optimal control $E(\tau)$ which maximizes H must satisfy the following conditions:

$$E = \begin{cases} E_{\max} & \text{when } \phi(\tau) > 0, \text{ i.e. when } \lambda_1(\tau)e^{\theta\tau} < p - c/qx_1, \\ 0 & \text{when } \phi(\tau) < 0, \text{ i.e., when } \lambda_1(\tau)e^{\theta\tau} > p - c/qx_1. \end{cases}$$

$\lambda_1(\tau)e^{\theta\tau}$ is the usual shadow price and $p - c/qx_1$ is the net economic revenue on a unit harvest. This shows that $E = E_{\max}$ or zero according as the shadow price is less than or greater than the net economic revenue on a unit harvest. Economically, the first condition implies that if the profit after paying all the expenses is positive, then it is beneficial to harvest up to the limit of available effort. The second condition implies that when the shadow price exceeds the fisherman's net economic revenue on a unit harvest, then the fisherman will not exert any effort.

When $\phi(\tau) = 0$, i.e. when the shadow price equals the net economic revenue on a unit harvest, then the Hamiltonian H becomes independent of the control variable $E(\tau)$, i.e., $\partial H/\partial E = 0$. This is the necessary and

sufficient condition for the singular control $E^*(\tau)$ to be optimal over the control set $0 < E^* < E_{\max}$.

Thus the optimal harvest policy is

$$(4.2) \quad E(\tau) = \begin{cases} E_{\max}, & \phi(\tau) > 0, \\ 0, & \phi(\tau) < 0, \\ E^*, & \phi(\tau) = 0. \end{cases}$$

When $\phi(\tau) = 0$, it follows that

$$(4.3) \quad \lambda_1 = e^{-\theta\tau}(pqx_1 - c)/qx_1.$$

Now the adjoint equations are

$$(4.4) \quad \frac{d\lambda_1}{d\tau} = -\frac{\partial H}{\partial x_1} = -[e^{-\theta\tau}pqE + \lambda_1(a - 2x_1 - bx_3 - qE) + \lambda_3(dx_3)],$$

$$(4.5) \quad \frac{d\lambda_2}{d\tau} = -\frac{\partial H}{\partial x_2} = -[-\lambda_2 + \lambda_3e],$$

$$(4.6) \quad \frac{d\lambda_3}{d\tau} = -\frac{\partial H}{\partial x_3} = -[\lambda_1(-bx_1) + \lambda_2 + \lambda_3(-c + dx_1 - 2fx_3)].$$

To obtain an optimal equilibrium solution, we shall use

$$(4.7) \quad \begin{cases} a - x_1 - bx_3 - qE = 0, \\ x_3 - x_2 = 0, \\ -cx_3 + dx_1x_3 + ex_2 - fx_3^2 = 0, \end{cases}$$

and x_1, x_2, x_3 and E can be treated as constants.

By using (4.7), equations (4.4), (4.5) and (4.6) take the form

$$(4.8) \quad \begin{cases} (D - x_1)\lambda_1 + (dx_3)\lambda_3 = e^{-\theta\tau}pqE, \\ (D - 1)\lambda_2 + e\lambda_3 = 0, \\ (D + (-c + dx_1 - 2fx_3))\lambda_3 + \lambda_2 - bx_1\lambda_1 = 0, \end{cases}$$

where $D \equiv d/d\tau$. By eliminating λ_1, λ_2 from the above differential equations we get

$$(4.9) \quad \begin{aligned} (A_2D^2 + A_1D + A_0)\lambda_3 &= Me^{-\theta\tau}, \\ A_2 &= 1, \\ A_1 &= -c + dx_1 - 2fx_3 - 1, \\ A_0 &= -(-c + dx_1 - 2fx_3) - e, \\ M &= -\frac{b}{q}(pqx_1 - c)(\theta + 1). \end{aligned}$$

Therefore, the solution of (4.9) is

$$(4.10) \quad \lambda_3 = B_1e^{m_1\tau} + B_2e^{m_2\tau} + \frac{M}{N}e^{-\theta\tau}$$

where B_i , $i = 1, 2$, are arbitrary constants and the m_i , $i = 1, 2$, are the roots of the characteristic equation of (4.9) and $N = A_2\theta^2 - A_1\theta + A_0 \neq 0$.

It is clear from (4.10) that λ_3 is bounded if and only if $m_i < 0$, $i = 1, 2$, or the B_i , $i = 1, 2$, are identically equal to zero. For robust calculations we ignore the case $m_i < 0$, $i = 1, 2$, and take $B_i = 0$, $i = 1, 2$. Then we have

$$(4.11) \quad \lambda_3 = \frac{M}{N} e^{-\theta\tau}.$$

Now substituting λ_3 from (4.11) and λ_1 from (4.3) into the first equation of (4.8) we get the singular path

$$(4.12) \quad \frac{pqx_1 - c}{qx_1} (\theta + x_1) - dx_3 \frac{M}{N} + p(a - x_1 - bx_3) = 0.$$

Equation (4.12) together with (4.7) gives the optimal equilibrium population (x_1^*, x_2^*, x_3^*) and the corresponding optimal harvesting effort E^* .

5. Concluding remarks. In this paper, we have considered a prey-predator model with stage-structure for predator. We have first discussed the existence of possible steady states and then local as well as global stability. An important and interesting question in mathematical ecology is permanence, which ensures the survival of biological species and excludes extinction of species for all positive initial conditions. The question of permanence of biological species is of particular interest to fishery, forestry and wildlife managers. If it is known that a system exhibits such a permanent behaviour, then ecological planning based on a fixed eventual population can be carried out. Analyzing the problem we have obtained conditions for permanence of the solutions of our system.

We have also studied the dynamical behaviour of the system when prey species are subjected to harvesting. Our study indicates a practical danger in the ecological reality. More care should be exercised in setting harvesting rates, since the maximum sustainable yields of the harvesting rates may be far less than what we assumed for the existence of feasible equilibria. Next the optimal harvesting policy is discussed using bang-bang controls and singular controls.

The dynamics exhibited by the system shows good consistence with the observation in biological reality. If the unharvested system is permanent, then a sufficiently small harvesting rate will not change drastically the qualitative behaviour of the system, but the region of coexistence shrinks as the harvesting rate increases. The result provides a theoretical support for safe harvesting in biological resource management.

Before ending this article, we would like to mention that there is still tremendous amount of work to do in this model. For example,

- (i) One can consider the stage-structure of prey population.
- (ii) The effort level E may be taken as dynamic, i.e. time dependent.

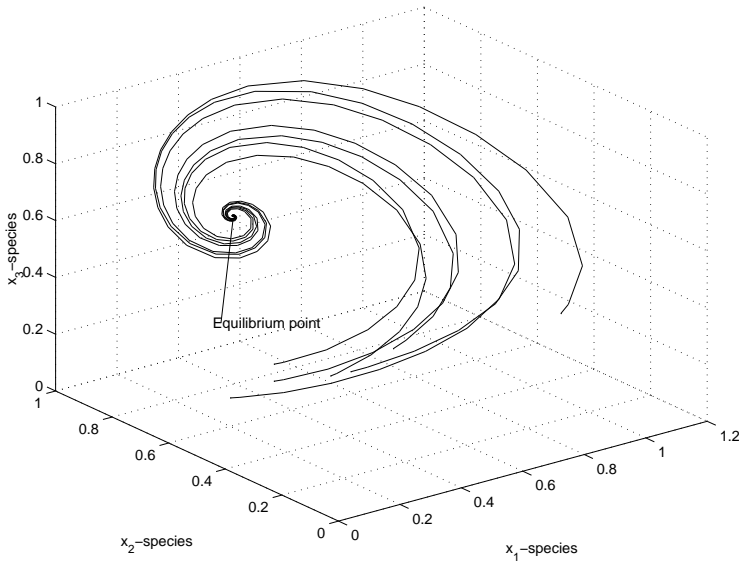


Fig. 3. Phase space trajectories of system (3.1) for $E = E_{MSY}$. It is seen that the corresponding equilibrium point $(0.16, 0.13, 0.13)$ is a global attractor.

- (iii) Gestation period for predator is also an important characteristic to be considered. We leave it for future considerations.

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