HARVESTING IN A TWO-PREY ONE-PREDATOR FISHERY: A BIOECONOMIC MODEL

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Abstract

A multispecies harvesting model with interference is proposed. The model is based on Lotka-Volterra dynamics with two competing species which are affected not only by harvesting but also by the presence of a predator, the third species. In order to understand the dynamics of this complicated system, we choose to model the simplest possible predator response function in which the feeding rate of the predator increases linearly with prey density. We derive the conditions for global stability of the system using a Lyapunov function. The possibility of existence of a bioeconomic equilibrium is discussed. The optimal harvest policy is studied and the solution is derived in the equilibrium case using Pontryagin's maximal principle. Finally, some numerical examples are discussed.

1. Introduction

Bioeconomic modelling of the exploitation of biological resources such as fisheries and forestries has gained importance in recent years. The techniques and issues associated with the bioeconomic exploitation of these resources have been discussed in detail by Clark [5, 6]. Since most marine fisheries are essentially multispecies in nature, exploitation of mixed-species fisheries has started to draw attention from researchers. Although numerous models on single species fisheries have so far appeared in the fishery literature, no fully adequate studies on multispecies fisheries appear to exist. It is very difficult to construct a realistic model of a multispecies community. Even if we succeed in formulating such a model, it is quite likely that the model may not be analytically tractable. Not every part of the catch is edible and harvesting harms some of the marine species which live on the other species in the sea. Thus the predator species are likely to become extinct with an indiscrete increase in the harvesting of prey

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species. Therefore, how best to harvest ecologically or economically interdependent populations in the sense of maximising the present value of a stream of revenues from them, while maintaining ecological balance, is an important optimal control problem for fisheries. Clark [5] discussed an optimal equilibrium policy for the combined harvesting of two ecologically independent species. Chaudhuri [1, 2] formulated an optimal control problem for the combined harvesting of two competing species. Models on the combined harvesting of a two-species prey-predator fishery have been discussed by Chaudhuri and Saha Ray [4], Mesterton-Gibbons [7], Ragozin and Brown [3] *etc*. Most of the mathematical models on the harvesting of a multispecies fishery have so far assumed that the species are affected by harvesting only. To the authors' knowledge, no attempt has yet been made to study a harvesting model of two competing species in the presence of a predator, the third species which is not harvested.

In this paper, we study the problem of harvesting two competing species in the presence of a predator species which feeds on both the competing species. A combined harvesting effort is devoted to the exploitation of the first two (prey) species while the third (predator) species is not harvested. The problem is clearly stated in the next section. We have analysed the existence and stability of the equilibria of the system. We derive conditions for *global* stability of the system. Taking simple economic considerations into account, we discuss the possibilities of the existence of a *bioeconomic equilibrium*. The optimal policy of exploitation is derived using Pontryagin's maximal principle. Last, some numerical illustrations are given.

2. Formulation of the problem

The ecological system is as follows. There are two fish species which compete with each other for the use of a common resource and both of them are subjected to continuous harvesting. There is a predator (for example a *whale*) feeding on both of them. It is assumed that the predator population is not harvested (for example *whale harvesting has been prohibited*). Thus the interaction between the harvesting agency and the predator is through the third party, namely, the prey. Since we are not making a case study in respect of a specific prey-predator community, we have opted for the logistic growth function for both the prey species (that is, the population density of each prey is resource limited) and for simplicity, the feeding rate of the predator species is assumed to increase linearly with prey density.

The governing equations of the system can be written as

$$
\begin{aligned}
dx_1/dt &= x_1[\lambda_1(1 - x_1/k_1) - \alpha_{12}x_2 - \alpha_{13}x_3] - q_1Ex_1, \\
dx_2/dt &= x_2[\lambda_2(1 - x_2/k_2) - \alpha_{21}x_1 - \alpha_{23}x_3] - q_2Ex_2, \\
dx_3/dt &= x_3[\alpha_{31}x_1 + \alpha_{32}x_2 - x_3],
\end{aligned}
\tag{2.1}
$$

where $\lambda_1, \lambda_2, k_1, k_2, \alpha_{12}, \alpha_{13}, \alpha_{21}, \alpha_{23}, \alpha_{31}$ and α_{32} are positive rate constants. Specifically λ_1, λ_2 are the *biotic potentials* and k_1, k_2 are the environmental *carrying capacities* of the two prey species; α_{12}, α_{21} are the coefficients of *interspecific competition* between the two prey species; α_{13}, α_{23} are the predation coefficients; α_{31}, α_{32} are the conversion parameters; E is the harvesting effort; q_1, q_2 are the *catchability coefficients* of x_1 and x_2 respectively. The catch-rate functions $q_1 E x_1$ and $q_2 E x_2$ are based on the CPUE (catch-per-unit-effort) hypothesis [5].

3. The steady states

The steady states of the system (2.1) are $P_0(0, 0, 0)$, $P_1(0, \bar{x}_2, \bar{x}_3)$, $P_2(\bar{\bar{x}}_1, 0, \bar{\bar{x}}_3)$ and $P_3(x_1^*, x_2^*, x_3^*)$, where

$$\bar{x}_2 = \frac{\lambda_2 - q_2 E}{\lambda_2/k_2 + \alpha_{32}\alpha_{23}}, \qquad \bar{x}_3 = \frac{\alpha_{32}(\lambda_2 - q_2 E)}{\lambda_2/k_2 + \alpha_{32}\alpha_{23}},$$

$$\bar{\bar{x}}_1 = \frac{\lambda_1 - q_1 E}{\lambda_1/k_1 + \alpha_{31}\alpha_{13}}, \qquad \bar{\bar{x}}_3 = \frac{\alpha_{31}(\lambda_1 - q_1 E)}{\lambda_1/k_1 + \alpha_{31}\alpha_{13}}.$$

We assume here that the interior equilibrium point (x_1^*, x_2^*, x_3^*) exists. There are also three other equilibria in the $x_1 x_2$-plane ($x_3 = 0$). But we are not interested in these equilibria, since for $x_3 = 0$, this is a two-species competitive model which has been studied in depth by Chaudhuri [1].

The equilibrium point P_1 exists if $E < \lambda_2/q_2$, that is, if $E < \text{BTP}_{x_2}$ and P_2 exists if $E < \lambda_1/q_1$, that is, if $E < \text{BTP}_{x_1}$. The ratio (λ/q) of the biotic potential (λ) to the catchability coefficient (q) is known as the *Biotechnical Productivity* (BTP) of the species [5].

4. Local stability

The eigenvalues of the variational matrix $V(0, 0, 0)$ are 0, $\lambda_1 - q_1 E$ and $\lambda_2 - q_2 E$ (see Appendix A). Hence the integral curves terminate in a plane corresponding to the steady state.

One of the eigenvalues of the variational matrix $V(0, \bar{x}_2, \bar{x}_3)$ is $\lambda_1 - \alpha_{12}\bar{x}_2 - \alpha_{13}\bar{x}_3 - q_1 E$ (see Appendix B). This eigenvalue is negative or positive according to whether λ_1/q_1 is less or greater than $(\alpha_{12}\bar{x}_2 + \alpha_{13}\bar{x}_3)/q_1 + E$.

The other two eigenvalues are given by the roots of the following quadratic equation

$$\mu^2 + \mu(\lambda_2 \bar{x}_2/k_2 + \bar{x}_3) + (\lambda_2/k_2 + \alpha_{23}\alpha_{32})\bar{x}_2\bar{x}_3 = 0. \tag{4.1}$$

In (4.1), the sum of the roots $= -(\lambda_2 \bar{x}_2/k_2 + \bar{x}_3)$, which is always negative and the product of the roots $= (\lambda_2/k_2 + \alpha_{23}\alpha_{32})\bar{x}_2\bar{x}_3$, which is always positive.

Therefore the roots of (4.1) are real and negative or complex conjugates having negative real parts. Thus P_1 is asymptotically stable only if

$$\lambda_1/q_1 < (\alpha_{12}\bar{x}_2 + \alpha_{13}\bar{x}_3)/q_1 + E.$$

We have already found that the steady state P_1 exists if $E < \lambda_2/q_2$. Hence the condition for asymptotic stability of P_1 becomes

$$\frac{\lambda_1}{q_1} - \frac{\alpha_{12}\bar{x}_2 + \alpha_{13}\bar{x}_3}{q_1} < E < \frac{\lambda_2}{q_2}.$$

This defines a range in which the fishing effort must lie to ensure a stable equilibrium P_1.

One of the eigenvalues of the variational matrix $V(\bar{\bar{x}}_1, 0, \bar{\bar{x}}_3)$ is $\lambda_2 - \alpha_{21}\bar{\bar{x}}_1 - \alpha_{23}\bar{\bar{x}}_3 - q_2E$ (see Appendix C). This eigenvalue is negative or positive according to whether λ_2/q_2 is less or greater than $(\alpha_{21}\bar{\bar{x}}_1 + \alpha_{23}\bar{\bar{x}}_3)/q_2 + E$. The other two eigenvalues are given by the roots of the quadratic equation

$$\mu^2 + (\lambda_1\bar{\bar{x}}_1/k_1 + \bar{\bar{x}}_3)\mu + (\lambda_1/k_1 + \alpha_{31}\alpha_{13})\bar{\bar{x}}_1\bar{\bar{x}}_3 = 0. \tag{4.2}$$

In (4.2), the sum of the roots $= -(\lambda_1\bar{\bar{x}}_1/k_1 + \bar{\bar{x}}_3)$, which is always negative and the product of the roots $= (\lambda_1/k_1 + \alpha_{31}\alpha_{13})\bar{\bar{x}}_1\bar{\bar{x}}_3$, which is always positive.

Therefore the roots of (4.2) are real and negative or complex conjugates having negative real parts. Thus P_2 is asymptotically stable only if

$$\lambda_2/q_2 < (\alpha_{21}\bar{\bar{x}}_1 + \alpha_{23}\bar{\bar{x}}_3)/q_2 + E.$$

Since P_2 exists only if $E < \lambda_1/q_1$, the condition for asymptotic stability of P_2 becomes

$$\lambda_2/q_2 - (\alpha_{21}\bar{\bar{x}}_1 + \alpha_{23}\bar{\bar{x}}_3)/q_2 < E < \lambda_1/q_1.$$

The effort level must lie within this range for the existence of a stable steady state P_2. The characteristic equation for the variational matrix $V(x_1^*, x_2^*, x_3^*)$ is $b_3\mu^3 + b_2\mu^2 + b_1\mu + b_0 = 0$ (see Appendix D).

Using the Routh-Hurwitz criteria [8], it can be shown that P_3 is stable if

(i) $\lambda_1/k_1 > \alpha_{12}\alpha_{31}/\alpha_{32}$ and
(ii) $\lambda_2/k_2 > \alpha_{21}\alpha_{32}/\alpha_{31}$.

5. Global stability

In this section, we shall prove the global stability of the system (2.1) by constructing a suitable Lyapunov function.

THEOREM 1. *The interior equilibrium point P_3 is globally asymptotically stable if*

(i) $\alpha_{13} = \alpha_{31}$, $\alpha_{23} = \alpha_{32}$ *and*
(ii) $(4\lambda_1\lambda_2)/(k_1k_2) > (\alpha_{12} + \alpha_{21})^2$.

PROOF. Let us consider a suitable Lyapunov function

$$v(x_1, x_2, x_3) = (x_1 - x_1^*) - x_1^* \log(x_1/x_1^*) + (x_2 - x_2^*) - x_2^* \log(x_2/x_2^*)$$
$$+ (x_3 - x_3^*) - x_3^* \log(x_3/x_3^*).$$

Obviously v is positive definite.

The time derivative of v along the solutions of (2.1), after a little simplification, is given by

$$\frac{dv}{dt} = -\Big[\lambda_1(x_1 - x_1^*)^2/k_1 + (x_1 - x_1^*)(x_2 - x_2^*)(\alpha_{12} + \alpha_{21})$$
$$+ \lambda_2(x_2 - x_2^*)^2/k_2 + (x_2 - x_2^*)(x_3 - x_3^*)(\alpha_{23} - \alpha_{32})$$
$$+ (x_3 - x_3^*)^2 + (x_3 - x_3^*)(x_1 - x_1^*)(\alpha_{13} - \alpha_{31})\Big]. \tag{5.1}$$

The right-hand side of (5.1) can be written as $-X^T A X$, where

$$X^T = \big[(x_1 - x_1^*), (x_2 - x_2^*), (x_3 - x_3^*)\big]$$

and

$$A = \begin{bmatrix} \lambda_1/k_1 & (\alpha_{12} + \alpha_{21})/2 & (\alpha_{13} - \alpha_{31})/2 \\ (\alpha_{12} + \alpha_{21})/2 & \lambda_2/k_2 & (\alpha_{23} - \alpha_{32})/2 \\ (\alpha_{13} - \alpha_{31})/2 & (\alpha_{23} - \alpha_{32})/2 & 1 \end{bmatrix}.$$

Therefore $dv/dt < 0$ if A is positive definite. The matrix A is positive definite if the hypotheses of Theorem 1 are satisfied.

6. Bionomic equilibrium

The term bionomic equilibrium is an amalgamation of the concepts of biological equilibrium as well as economic equilibrium. As we already saw, a biological equilibrium is given by $\dot{x}_1 = 0$, $\dot{x}_2 = 0$, $\dot{x}_3 = 0$. The economic equilibrium is said to be achieved when TR (the total revenue obtained by selling the harvested biomass) equals TC (the total cost for the effort devoted to harvesting).

Let $C = $ constant fishing cost per unit effort, $p_1 = $ constant price per unit biomass of the first species, and $p_2 = $ constant price per unit biomass of the second species.

The economic rent (net revenue) at any time is given by

$$\pi(x_1, x_2, x_3, E) = \text{TR} - \text{TC} = (p_1 q_1 x_1 + p_2 q_2 x_2 - C)E.$$

Now,

$$\dot{x}_1 = 0 \Rightarrow x_1 = 0 \quad \text{or} \quad E = \frac{\lambda_1}{q_1} - \frac{\lambda_1}{k_1 q_1} x_1 - \frac{\alpha_{12}}{q_1} x_2 - \frac{\alpha_{13}}{q_1} x_3,$$

$$\dot{x}_2 = 0 \Rightarrow x_2 = 0 \quad \text{or} \quad E = \frac{\lambda_2}{q_2} - \frac{\lambda_2}{k_2 q_2} x_2 - \frac{\alpha_{21}}{q_2} x_1 - \frac{\alpha_{23}}{q_2} x_3,$$

$$\dot{x}_3 = 0 \Rightarrow x_3 = 0 \quad \text{or} \quad x_3 = \alpha_{31} x_1 + \alpha_{32} x_2.$$

Hence the nontrivial biological equilibrium solution occurs at a point on the line

$$\left.\begin{array}{r} (\lambda_1/k_1 q_1 - \alpha_{21}/q_2)x_1 - (\lambda_2/q_2 - \alpha_{12}/q_1)x_2 \\ + (\alpha_{13}/q_1 - \alpha_{23}/q_2)x_3 + (\lambda_2/q_2 - \lambda_1/q_1) = 0, \\ \alpha_{31} x_1 + \alpha_{32} x_2 - x_3 = 0, \end{array}\right\} \tag{6.1}$$

where $0 \leq x_1 \leq k_1$, $0 \leq x_2 \leq k_2$.

The equilibrium line (6.1) meets the plane $x_1 = 0$ at $(0, \tilde{x}_2, \tilde{x}_3)$, where

$$\tilde{x}_2 = \frac{\lambda_2/q_2 - \lambda_1/q_1}{(\lambda_2/k_2 q_2 + \alpha_{23}\alpha_{32}/q_2) - (\alpha_{12}/q_1 + \alpha_{31}\alpha_{32}/q_1)}, \quad \tilde{x}_3 = \alpha_{32}\tilde{x}_2$$

provided either

(a) $\lambda_2/q_2 > \max(\lambda_1/q_1, k_2\alpha_{12}/q_1)$ and $\alpha_{23}/q_2 > \alpha_{13}/q_1$ or
(b) $\lambda_2/q_2 < \min(\lambda_1/q_1, k_2\alpha_{12}/q_1)$ and $\alpha_{23}/q_2 < \alpha_{13}/q_1$ hold.

Similarly, (6.1) meets the plane $x_2 = 0$ at $(\tilde{x}_1, 0, \tilde{x}_3)$, where

$$\tilde{x}_1 = \frac{\lambda_2/q_2 - \lambda_1/q_1}{(\alpha_{21}/q_2 + \alpha_{23}\alpha_{31}/q_2) - (\lambda_1/k_1 q_1 + \alpha_{13}\alpha_{31}/q_1)}, \quad \tilde{x}_3 = \alpha_{31}\tilde{x}_1$$

provided either

(c) $\lambda_1/q_1 > \max(\lambda_2/q_2, k_1\alpha_{21}/q_2)$ and $\alpha_{13}/q_1 > \alpha_{23}/q_2$ or
(d) $\lambda_1/q_1 < \min(\lambda_2/q_2, k_1\alpha_{21}/q_2)$ and $\alpha_{13}/q_1 < \alpha_{23}/q_2$ hold.

The bionomic equilibrium $R(x_{1\infty}, x_{2\infty}, x_{3\infty})$ will be the point of intersection (if it exists) of (6.1) and $\pi(x_1, x_2, x_3, E) = (p_1 q_1 x_1 + p_2 q_2 x_2 - C)E = 0$ in the first octant. After a little calculation, it is seen that $x_{1\infty} > 0$ provided either

(e) $\left(\dfrac{\lambda_2}{k_2 q_2} + \dfrac{\alpha_{32}\alpha_{23}}{q_2} - \dfrac{\alpha_{12}}{q_1} - \dfrac{\alpha_{13}\alpha_{32}}{q_1} \right)$

$$> \max\left[\frac{p_2 q_2}{p_1 q_1} \left(\frac{\alpha_{21}}{q_1} + \frac{\alpha_{23}\alpha_{31}}{q_2} - \frac{\lambda_1}{k_1 q_1} - \frac{\alpha_{13}\alpha_{31}}{q_1} \right), \frac{p_2 q_2}{c} \left(\frac{\lambda_2}{q_2} - \frac{\lambda_1}{q_1} \right) \right]$$

or

(f) $\left(\dfrac{\lambda_2}{k_2 q_2} + \dfrac{\alpha_{32}\alpha_{23}}{q_2} - \dfrac{\alpha_{12}}{q_1} - \dfrac{\alpha_{13}\alpha_{32}}{q_1} \right)$

$$< \min\left[\frac{p_2 q_2}{p_1 q_1}\left(\frac{\alpha_{21}}{q_2} + \frac{\alpha_{23}\alpha_{31}}{q_2} - \frac{\lambda_1}{k_1 q_1} - \frac{\alpha_{13}\alpha_{31}}{q_1} \right), \frac{p_2 q_2}{c}\left(\frac{\lambda_2}{q_2} - \frac{\lambda_1}{q_1} \right) \right]$$

holds.

When either (a) or (b) holds but neither (e) nor (f) holds, the x_1-species faces extinction in the bionomic equilibrium. Proceeding in a similar manner, one can easily prove the possibility of extinction of the x_2-species.

Thus the combined harvesting of two competing fish species in the presence of a predator may drive one species to extinction while the bionomic equilibrium of the open-access fishing continues with the support of the other species. This phenomenon has been noticed by Clark [5] also in the case of combined harvesting of two eco-logically independent species. Explicit biological or bioeconomic interpretations of the conditions (a)–(f) seems to be difficult. These may simply be regarded as some conditions to be satisfied by the biological, technical and economic parameters for the existence of a bionomic equilibrium.

7. Optimal harvesting policy

The *present value J* of a continuous time-stream of revenues is given by

$$J = \int_0^\infty e^{-\delta t}[p_1 q_1 x_1 + p_2 q_2 x_2 - C]E\,dt,$$

where δ denotes the instantaneous annual rate of discount [10]. Our problem is to maximise J subject to the state equations (2.1) by invoking Pontryagin's maximal principle [9]. The *control variable $E(t)$* is subjected to the constraints $0 \le E(t) \le E_{\max}$, so that $V_t = [0, E_{\max}]$ is the *control set*.

The *Hamiltonian* for the problem is given by

$$\begin{aligned} H = e^{-\delta t}&[p_1 q_1 x_1 + p_2 q_2 x_2 - C]E \\ &+ \mu_1\big(-\lambda_1 x_1^2/k_1 - \alpha_{12}x_1 x_2 - \alpha_{13}x_1 x_3 + x_1(\lambda_1 - q_1 E) \big) \\ &+ \mu_2\big(-\lambda_2 x_2^2/k_2 - \alpha_{21}x_1 x_2 - \alpha_{23}x_2 x_3 + x_2(\lambda_2 - q_2 E) \big) \\ &+ \mu_3\big(-x_3^2 - \alpha_{31}x_1 x_3 - \alpha_{32}x_2 x_3 \big), \end{aligned} \tag{7.1}$$

where $\mu_i(t)$, $i = 1, 2, 3$, are the *adjoint variables*.

The *adjoint equations* are

$$\begin{aligned} \frac{d\mu_1}{dt} &= -\frac{\partial H}{\partial x_1} \\ &= -\big[e^{-\delta t}p_1 q_1 E - \mu_1\big(2\lambda_1 x_1/k_1 + \alpha_{12}x_2 + \alpha_{13}x_3 - (\lambda_1 - q_1 E)\big) \\ &\quad - \mu_2\alpha_{21}x_2 + \mu_3\alpha_{31}x_3 \big], \end{aligned} \tag{7.2}$$

$$\frac{d\mu_2}{dt} = -\frac{\partial H}{\partial x_2}$$
$$= -\big[e^{-\delta t} p_2 q_2 E - \mu_2\big(2\lambda_2 x_2/k_2 + \alpha_{21}x_1 + \alpha_{23}x_3 - (\lambda_2 - q_2 E)\big)$$
$$- \mu_1\alpha_{12}x_1 + \mu_3\alpha_{32}x_3\big], \tag{7.3}$$

and

$$\frac{d\mu_3}{dt} = -\frac{\partial H}{\partial x_3}$$
$$= -\big[-\mu_1\alpha_{13}x_1 - \mu_2\alpha_{23}x_2 - \mu_3(2x_3 - \alpha_{31}x_1 - \alpha_{32}x_2)\big]. \tag{7.4}$$

Here we deal with an *optimal equilibrium solution*. Since we are considering an equilibrium solution, x_1, x_2 and x_3 are to be treated as constants in the subsequent steps.

Now, by eliminating μ_1 and μ_2 from (7.2)–(7.4), we get a reduced differential equation for μ_3 as

$$(a_3 D^3 + 3a_2 D^2 + 3a_1 D + a_0)\mu_3 = M_3 e^{-\delta t}, \tag{7.5}$$

where $D \equiv d/dt$, $a_3 = 1$, $3a_2 = -(x_3 + \lambda_2 x_2/k_2 + \lambda_1 x_1/k_1)$,

$$3a_1 = \frac{\lambda_1\lambda_2}{k_1 k_2}x_1 x_2 + \frac{\lambda_2}{k_2}x_2 x_3 + \frac{\lambda_1}{k_1}x_1 x_3 - \alpha_{21}\alpha_{12}x_1 x_2 + \alpha_{13}\alpha_{31}x_1 x_3 + \alpha_{32}\alpha_{23}x_2 x_3,$$

$$a_0 = -\left(\frac{\lambda_2\lambda_1}{k_2 k_1} - \alpha_{12}\alpha_{21} + \frac{\lambda_2}{k_2}\alpha_{13}\alpha_{31} + \frac{\lambda_1}{k_1}\alpha_{32}\alpha_{23} - \alpha_{32}\alpha_{21}\alpha_{13} - \alpha_{31}\alpha_{13}\alpha_{12}\right)x_1 x_2 x_3,$$

$$M_3 = p_1 q_1\big[x_2\alpha_{23}\delta + \big(-\alpha_{13}\alpha_{21} + \lambda_1\alpha_{23}/k_1\big)x_1 x_2\big]E$$
$$+ p_2 q_2\big[\alpha_{13}x_1\delta + \big(-\alpha_{23}\alpha_{12} + \lambda_2\alpha_{13}/k_2\big)x_1 x_2\big]E.$$

The complete solution of (7.5) is

$$\mu_3 = A_1 e^{m_1 t} + A_2 e^{m_2 t} + A_3 e^{m_3 t} + (M_3/N)e^{-\delta t}, \tag{7.6}$$

where A_i $(i = 1, 2, 3)$ are arbitrary constants and m_i $(i = 1, 2, 3)$ are the roots of the auxiliary equations $a_3 m^3 + 3a_2 m^2 + 3a_1 m + a_0 = 0$ and $N = \delta^3 - 3a_2\delta^2 - 3a_1\delta - a_0 \neq 0$.

It is clear from (7.6) that μ_3 is bounded if and only if $m_i < 0$, $(i = 1, 2, 3)$ or the A_i's are identically equal to zero. It being very difficult to check whether $m_i < 0$, we take $A_i = 0$ $(i = 1, 2, 3)$. Then $\mu_3 = M_3 e^{-\delta t}/N$.

By a similar process, we get $\mu_2 = M_2 e^{-\delta t}/N$ and $\mu_1 = M_1 e^{-\delta t}/N$, where

$$M_2 = p_1 q_1\big[\alpha_{12}x_1\delta + (\alpha_{12} + \alpha_{32}\alpha_{13})x_1 x_3\big]E$$
$$- p_2 q_2\big[\delta^2 + (x_3 + \lambda_1 x_1/k_1)\delta + (\lambda_1/k_1 + \alpha_{13}\alpha_{31})x_1 x_3\big]E$$

and

$$M_1 = p_2 q_2\big[\alpha_{21}x_2\delta + (\alpha_{21} + \alpha_{31}\alpha_{23})x_3 x_2\big]E$$
$$- p_1 q_1\big[\delta^2 + (x_3 + \lambda_2 x_2/k_2)\delta + (\lambda_2/k_2 + \alpha_{32}\alpha_{23})x_2 x_3\big]E.$$

We find the shadow prices $\mu_i(t)e^{\delta t}$, $i = 1, 2, 3$, of the three fish species remain bounded as $t \to \infty$ and hence satisfy the *transversality condition* at ∞ [5].

The Hamiltonian in (7.1) must be maximised for $E \in [0, E_{\max}]$. Assuming that the control constraints $0 \le E \le E_{\max}$ are not binding (that is, the optimal equilibrium does not occur either at $E = 0$ or $E = E_{\max}$), we have singular control given by [5]. Therefore

$$\frac{\partial H}{\partial E} = e^{-\delta t}(p_1 q_1 x_1 + p_2 q_2 x_2 - C) - \mu_1 q_1 x_1 - \mu_2 q_2 x_2 = 0 \qquad (7.7)$$

or $e^{-\delta t}(d\pi/dE) = \mu_1 q_1 x_1 + \mu_2 q_2 x_2$.

This indicates that the total user cost of harvest per unit effort must be equal to the discounted value of the future profit at the steady-state effort level [5].

Substituting μ_1 and μ_2 into (7.7) we get

$$x_1 q_1 (p_1 - M_1/N) + x_2 q_2 (p_2 - M_2/N) = C. \qquad (7.8)$$

The value of E at the interior equilibrium given by

$$E = \left[\lambda_1(1 - x_1/k_1) - \alpha_{12}x_2 - \alpha_{13}x_3\right]/q_1$$
$$= \left[\lambda_2(1 - x_2/k_2) - \alpha_{21}x_1 - \alpha_{23}x_3\right]/q_2$$

is to be substituted in the expressions for M_1 and M_2. We may then solve (7.8) and (6.1) to obtain the optimal equilibrium solution $x_1 = x_{1\delta}$, $x_2 = x_{2\delta}$, $x_3 = x_{3\delta}$ for a given value of δ. For different values of δ we have different optimal equilibria. When $\delta \to \infty$, (7.8) leads to the obvious result $p_1 q_1 x_{1\infty} + p_2 q_2 x_{2\infty} = C$ that implies $\pi(x_{1\infty}, x_{2\infty}, x_{2\infty}, E) = 0$.

This shows that an infinite discount rate leads to complete dissipation of economic revenue. This conclusion was also drawn by Clark [5] in the combined harvesting of two ecologically independent populations and by Chaudhuri [1] in the combined harvesting of two competing species.

Using (7.8), we have

$$\pi = (p_1 q_1 x_1 + p_2 q_2 x_2 - C)E = \frac{(M_1 q_1 x_1 + M_2 q_2 x_2)E}{N}.$$

Here we note that each of M_1 and M_2 is $0(\delta^2)$ where N is $0(\delta^3)$ so that π is $0(\delta^{-1})$. Thus π is a decreasing function of δ (≥ 0). We therefore conclude that $\delta = 0$ leads to maximisation of π.

8. Numerical examples

Let $\lambda_1 = 2.09$, $\lambda_2 = 2.07$, $k_1 = 200$, $k_2 = 300$, $q_1 = 0.04$, $q_2 = 0.01$, $\alpha_{12} = 0.001$, $\alpha_{21} = 0.001$, $\alpha_{13} = 0.01$, $\alpha_{31} = 0.30$, $\alpha_{23} = 0.02$, $\alpha_{32} = 0.3$, $p_1 = 6$, $p_2 = 8$, $E = 10$, $C = 50$ and $\delta = 0.05$.
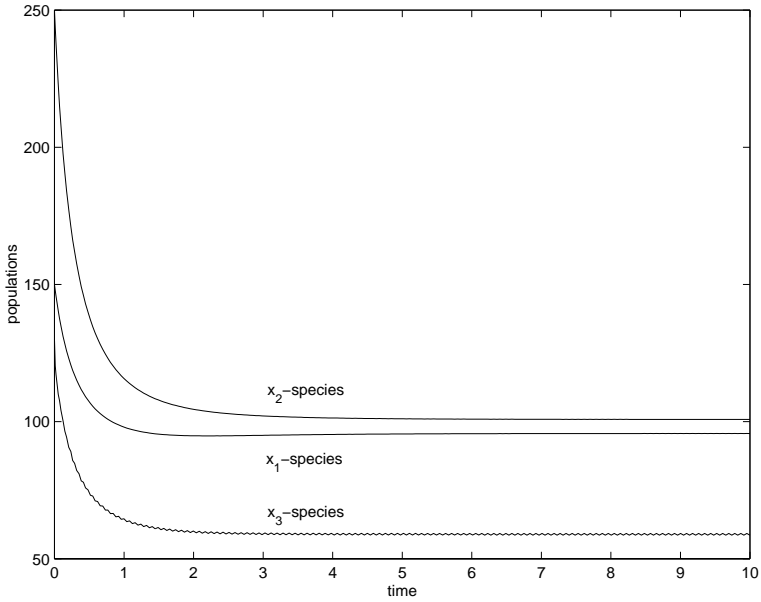
FIGURE 1. Variation of the populations against time, beginning with $x_1 = 150$, $x_2 = 250$ and $x_3 = 130$. Parameter values are the same as in Example 1.
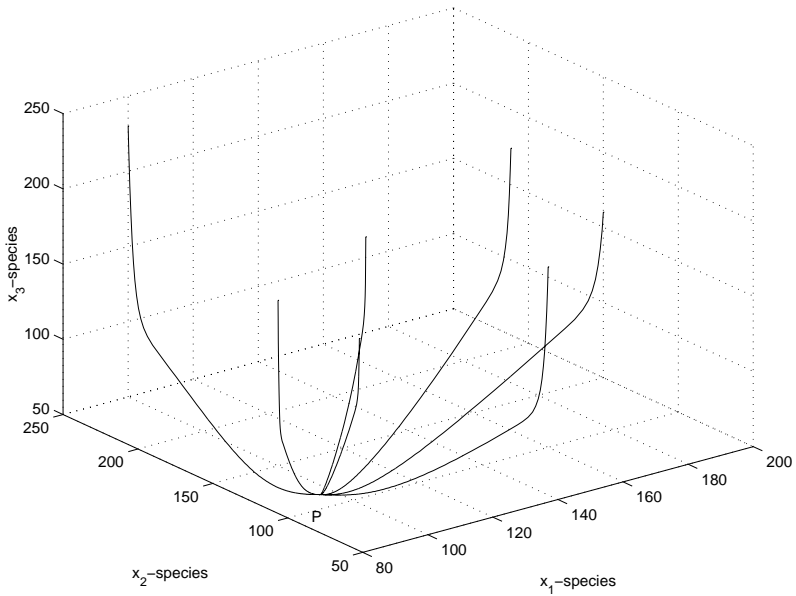

FIGURE 2. Phase-space trajectories corresponding to the optimal harvesting effort $E = 11.43$ units, with reference to different initial levels. The trajectories clearly indicate that the optimal equilibrium $P(91, 102, 58)$ is asymptotically stable.

EXAMPLE 1. For the above parameter values, it is found that

(i) $P_0(0, 0, 0)$ is unstable,
(ii) $P_1(0, 153, 46)$ is unstable,
(iii) $P_2(162, 0, 48)$ is unstable,

but (iv) the only interior steady state $P_3(96, 101, 59)$ is stable.

EXAMPLE 2. For the same parameter values as those used in Example 1 we find that the bionomic equilibrium $R(184, 74, 77)$ and the optimal equilibrium $(91, 102, 58)$ both exist. We also find that the optimal harvesting effort, E, which leads the system to the optimal equilibrium $(91, 102, 58)$, is 11.43 units.

9. Concluding remarks

In this paper, we have attempted to study the effects of harvesting in a two-species competitive system in the presence of a predator species. We have first studied the existence and stability (local as well as global) of the possible steady states.

We then examined the possibilities of the existence of a bionomic (biological as well as economic) equilibrium of the exploited system.

Next, the optimal harvest policy was discussed. The present value of a continuous time-stream of revenues is maximised by invoking Pontryagin's maximum principle. The case of an optimal equilibrium solution is studied. It is found that the shadow prices remain constant over time in optimal equilibrium when they satisfy the transversality condition. Also the total user cost of harvest per unit effort equals the discounted value of the future profit at the steady state effort level. It is proved that zero discounting leads to maximisation of economic revenue and that an infinite discount rate leads to complete dissipation of economic rent.

Last, some numerical examples are taken to obtain steady states, bionomic equilibrium, optimal equilibrium *etc*. To get the numerical results, we used Lingo and Matlab.

We have established the existence of an equilibrium solution that satisfies the necessary conditions of the maximum principle. As pointed out by Clark [5], it is extremely difficult to find an optimal approach path consisting of a combination of bang-bang controls and non-equilibrium singular controls. It is also difficult to carry out dynamic optimisation [2] taking the effort level E to be a dynamic (that is, time-dependent) variable. Due to these difficulties we have considered the optimal equilibrium solution only. The model can also be improved by assuming that the fishing effort E increases or decreases in proportion to the flow of net economic revenue from the fishery. For such a dynamic reaction model ([3, 5]), one has to introduce a fourth differential equation in (2.1) for dE/dt. It is quite likely that such

a complicated system may prove to be too formidable to solve.

Appendix A.

The variational matrix of the system of equations (2.1) is

$$V(x_1, x_2, x_3) = \begin{bmatrix} V_{11} & -\alpha_{12}x_1 & -\alpha_{13}x_3 \\ -\alpha_{21}x_2 & V_{22} & -\alpha_{23}x_2 \\ \alpha_{31}x_3 & \alpha_{32}x_3 & (\alpha_{31}x_1 + \alpha_{32}x_2 - 2x_3) \end{bmatrix}, \qquad (A.1)$$

where

$$V_{11} = \left(\lambda_1 - \frac{2\lambda_1}{k_1}x_1 - \alpha_{12}x_2 - \alpha_{13}x_3 - q_1 E \right),$$

$$V_{22} = \left(\lambda_2 - \frac{2\lambda_2}{k_2}x_2 - \alpha_{21}x_1 - \alpha_{23}x_3 - q_2 E \right).$$

Therefore

$$V(0, 0, 0) = \begin{bmatrix} \lambda_1 - q_1 E & 0 & 0 \\ 0 & \lambda_2 - q_2 E & 0 \\ 0 & 0 & 0 \end{bmatrix}.$$

The eigenvalues of this variational matrix are 0, $\lambda_1 - q_1 E$ and $\lambda_2 - q_2 E$.

Appendix B.

From (A.1), we have

$$V(0, \bar{x}_2, \bar{x}_3) = \begin{bmatrix} \lambda_1 - \alpha_{12}\bar{x}_2 - \alpha_{13}\bar{x}_3 - q_1 E & 0 & 0 \\ -\alpha_{21}\bar{x}_2 & -\lambda_2\bar{x}_2/k_2 & -\alpha_{23}\bar{x}_2 \\ \alpha_{31}\bar{x}_3 & \alpha_{32}\bar{x}_3 & -\bar{x}_3 \end{bmatrix}.$$

The characteristic equation is

$$\left[(\lambda_1 - \alpha_{12}\bar{x}_2 - \alpha_{13}\bar{x}_3 - q_1 E) - \mu \right]$$
$$\times \left[\mu^2 + \mu \left(\frac{\lambda_2}{k_2}\bar{x}_2 + \bar{x}_3 \right) + \left(\frac{\lambda_2}{k_2}\bar{x}_2\bar{x}_3 + \alpha_{23}\alpha_{32}\bar{x}_2\bar{x}_3 \right) \right] = 0.$$

Appendix C.

From (A.1), we have

$$V(\bar{\bar{x}}_1, 0, \bar{\bar{x}}_3) = \begin{bmatrix} -\lambda_1 \bar{\bar{x}}_1/k_1 & -\alpha_{12}\bar{\bar{x}}_1 & -\alpha_{13}\bar{\bar{x}}_1 \\ 0 & \lambda_2 - \alpha_{21}\bar{\bar{x}}_1 - \alpha_{23}\bar{\bar{x}}_3 - q_2 E & 0 \\ \alpha_{31}\bar{\bar{x}}_3 & \alpha_{32}\bar{\bar{x}}_3 & -\bar{\bar{x}}_3 \end{bmatrix}.$$

The characteristic equation is

$$\left[\lambda_2 - \alpha_{21}\bar{\bar{x}}_1 - \alpha_{23}\bar{\bar{x}}_3 - q_2 E - \mu \right]$$
$$\times \left[\mu^2 + \mu \left(\frac{\lambda_1}{k_1}\bar{\bar{x}}_1 + \bar{\bar{x}}_3 \right) + \left(\frac{\lambda_1}{k_1}\bar{\bar{x}}_1\bar{\bar{x}}_3 + \alpha_{31}\alpha_{13}\bar{\bar{x}}_1\bar{\bar{x}}_3 \right) \right] = 0.$$

Appendix D.

From (A.1), we have

$$V(x_1^*, x_2^*, x_3^*) = \begin{bmatrix} -\lambda_1 x_1^*/k_1 & -\alpha_{12}x_1^* & -\alpha_{13}x_1^* \\ -\alpha_{21}x_2^* & -\lambda_2 x_2^*/k_2 & -\alpha_{23}x_2^* \\ \alpha_{31}x_3^* & \alpha_{32}x_3^* & -x_3^* \end{bmatrix}.$$

The characteristic equation is

$$\mu^3 + \mu^2 \left(\frac{\lambda_2}{k_2} x_2^* + \frac{\lambda_1}{k_1} x_1^* + x_3^* \right)$$
$$+ \mu \left(\frac{\lambda_2}{k_2} x_2^* x_3^* + \alpha_{32}\alpha_{23}x_2^* x_3^* + \frac{\lambda_1\lambda_2}{k_1 k_2} x_1^* x_2^* + \frac{\lambda_1}{k_1} x_1^* x_3^* + \alpha_{31}\alpha_{13}x_1^* x_3^* - \alpha_{12}\alpha_{21}x_1^* x_2^* \right)$$
$$+ \left(\frac{\lambda_1\lambda_2}{k_1 k_2} + \frac{\lambda_1}{k_1} \alpha_{23}\alpha_{32} - \alpha_{12}\alpha_{21} - \alpha_{12}\alpha_{31}\alpha_{23} - \alpha_{13}\alpha_{21}\alpha_{32} + \frac{\lambda_2}{k_2} \alpha_{13}\alpha_{31} \right) x_1^* x_2^* x_3^* = 0$$

or $b_3\mu^3 + b_2\mu^2 + b_1\mu + b_0 = 0$, where $b_3 = 1$, $b_2 = \lambda_2 x_2^*/k_2 + \lambda_1 x_1^*/k_1 + x_3^*$,

$$b_1 = (\lambda_2/k_2)x_2^* x_3^* + \alpha_{32}\alpha_{23}x_2^* x_3^* + (\lambda_1\lambda_2/k_1 k_2)x_1^* x_2^* + (\lambda_1/k_1)x_1^* x_3^*$$
$$+ \alpha_{31}\alpha_{13}x_1^* x_3^* - \alpha_{12}\alpha_{21}x_1^* x_2^*,$$
$$b_0 = \big((\lambda_1\lambda_2/k_1 k_2) + (\lambda_1/k_1)\alpha_{23}\alpha_{32} - \alpha_{12}\alpha_{21} - \alpha_{12}\alpha_{31}\alpha_{23} - \alpha_{13}\alpha_{21}\alpha_{32}$$
$$+ (\lambda_2/k_2)\alpha_{13}\alpha_{31} \big) x_1^* x_2^* x_3^*.$$

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