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# Stability and Optimal Harvesting in Lotka-Volterra Competition Model for Two-species with Stage Structure

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ABSTRACT. In this paper, we consider a delay differential equation model of two competing species with harvesting of the mature and immature members of each species. The time delay in the model represents the time from birth to maturity of that species, which appears in the adults recruitment terms. We study the dynamics of our model analytically and we present results on positivity and boundedness of the solution, conditions for the existence and globally asymptotically stable of equilibria, a threshold of harvesting, and the optimal harvesting of the mature populations of each species.

#### 1. Introduction

Recently, investigations of mathematical models of stage-structured population growth, where the individual members of the population have a life history that takes them through two stages, immature and mature, with the time from birth to maturity represented by either discrete or distributed time delay, have received some attention. These kinds of models are appropriate for many species in the real world, we have in mind mammalian populations and some amphibious animals. Aiello and Freedman [1] proposed and studied the following single species model which has become quite well known:

(1.1) 
$$u'_{i}(t) = \alpha u_{m}(t) - \gamma u_{i}(t) - \alpha e^{-\gamma \tau} u_{m}(t-\tau),$$
$$u'_{m}(t) = \alpha e^{-\gamma \tau} u_{m}(t-\tau) - \beta u^{2}_{m}(t),$$

where  $\alpha, \beta, \gamma$  and the delay  $\tau$  are positive constants. In this system  $u_i$  and  $u_m$  denote respectively the numbers of immature and mature members of the single-species population. The delay  $\tau$  is the time taken from birth to maturity. They considered various aspects of the above system including positivity and boundedness of solutions. They also established that all ecologically relevant solutions tend, as

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time  $t \to \infty$ , to the positive equilibrium solution

$$(u_i, u_m) \equiv \left(\frac{\alpha^2}{\beta\gamma} e^{-\gamma\tau} (1 - e^{-\gamma\tau}), \frac{\alpha}{\beta} e^{-\gamma\tau}\right).$$

Note that the equilibrium depends on the delay  $\tau$ . The model assumes that all juveniles mature at exactly the same age  $\tau$ . This is an approximation which will not always be realistic. An alternative is to use a distributed delay term allowing for a distribution of maturation times, weighted by a probability density function, for more information; see Al-Omari and Gourley [2].

Competition and unharvested systems with time delay have been studied by many others. For example, see [10] and Al-Omari and Gourley [3]. But with harvesting Song and Chen [4] have considered system (1.1) with constant harvesting of the mature population:

$$\begin{aligned} u'_i(t) &= \alpha u_m(t) - \gamma u_i(t) - \alpha \, e^{-\gamma \tau} u_m(t-\tau), \\ u'_m(t) &= \alpha \, e^{-\gamma \tau} u_m(t-\tau) - \beta u^2_m(t) - E u_m(t), \\ u_i(t) &= \phi_1(t) \ge 0, \ u_m(t) = \phi_2(t) \ge 0, \ -\tau \le t \le 0, \ u_m(0) > 0, \end{aligned}$$

where E measures the effort with which the mature population is harvested,  $\phi_2(t)$  is the given initial mature population and  $\phi_1(t)$  is the initial immature population, such that

$$u_i(0) = \int_{-\tau}^0 \alpha u_m(s) e^{-\gamma s} ds.$$

They established conditions for the global stability of the equilibria A = (0,0) and  $B = (u_i^*, u_m^*)$ , where

$$u_i^* = \frac{\alpha}{\beta\gamma}(1 - e^{-\gamma\tau})(\alpha e^{-\gamma\tau} - E)$$
 and  $u_m^* = \frac{1}{\beta}(\alpha e^{-\gamma\tau} - E).$ 

Also, see for example, ([5] and [6]).

The above models are examples of systems containing delay dependent coefficients of the form  $e^{-\gamma\tau}$ . Generally the equilibria of this kind of equation show a dependence on the time delay and, in these particular models, also as in our model below, it is because the individuals may die during the maturation phase leading to a reduced mature adult equilibrium population. The analysis of such models (even the linearised analysis) is very complicated. An interesting extension of system (1.1) is the model below studied by Al-Omari and Gourley [7] in which the delay is state-dependent, taken to be a function of the total population  $u_i + u_m$ . In [7] we proposed the following system, in which  $u = u_i + u_m$ :

$$u'_{i}(t) = R(u_{m}(t)) - \gamma u_{i}(t) - e^{-\gamma \tau(u)} R(u_{m}(t - \tau(u))),$$
  
$$u'_{m}(t) = e^{-\gamma \tau(u)} R(u_{m}(t - \tau(u))) - du_{m}(t),$$

where the function  $R(u_m(t))$  behaves linearly in  $u_m$  for small  $u_m$ , but is effectively zero for large  $u_m$ . The function  $R(u_m)$  represents the birth rate, and the two terms

 $-\gamma u_i$  and  $-du_m$  represent the deaths of immatures and matures respectively. The delayed term in both equations represents adult recruitment. The state-dependent time delay  $\tau(u)$  is taken to be an increasing differentiable function of the total population  $u = u_i + u_m$ , so that  $\tau'(u) \ge 0$ , and we shall also assume that

$$\tau_{\min} \le \tau(u) \le \tau_{\max},$$

with  $\tau(0) = \tau_{\min}$  and  $\tau(\infty) = \tau_{\max}$ . These assumptions imply that the maturation time for the species depends on the total number of them (matures plus immatures) around. The greater the number of individuals present, the longer they will take to mature. This assumption is known to be realistic in the case of Antarctic whale and seal populations [8]. Lowering the number of whales apparently causes the remaining whales to mature more quickly (presumably because there is more food for the remaining whales). Since both immature and mature whales need food, this is the motivation for having the maturation delay depending on the sum  $u_i + u_m$ of the mature and immature populations.

In this paper, we will modify system (1.1) to model two competing species with harvesting of the mature and immature members of each species. Thus we are concerned with the following system

$$(1.2) \frac{dU_{i}(t)}{dt} = \alpha_{u}U_{m}(t) - \gamma_{u}U_{i}(t) - \alpha_{u}e^{-(\gamma_{u}+E_{1})\tau_{u}}U_{m}(t-\tau_{u}) - E_{1}U_{i}(t)$$

$$\frac{dU_{m}(t)}{dt} = \alpha_{u}e^{-(\gamma_{u}+E_{1})\tau_{u}}U_{m}(t-\tau_{u}) - \beta_{u}U_{m}^{2}(t) - c_{1}U_{m}(t)V_{m}(t) - E_{2}U_{m}(t)$$

$$\frac{dV_{i}(t)}{dt} = \alpha_{v}V_{m}(t) - \gamma_{v}V_{i}(t) - \alpha_{v}e^{-(\gamma_{v}+E_{3})\tau_{v}}V_{m}(t-\tau_{v}) - E_{3}V_{i}(t)$$

$$\frac{dV_{m}(t)}{dt} = \alpha_{v}e^{-(\gamma_{v}+E_{3})\tau_{v}}V_{m}(t-\tau_{v}) - \beta_{v}V_{m}^{2}(t) - c_{2}U_{m}(t)V_{m}(t) - E_{4}V_{m}(t),$$

where  $U_i$  and  $V_i$  denote, respectively, the number of immature members and  $U_m$ and  $V_m$  are the number of mature adult members. The  $c_1$  and  $c_2$  measure the competitive effect of V on U and U on V, respectively, and  $E_1$ ,  $E_3$  denote, respectively, the harvesting effort of the two immature populations  $U_i$  and  $V_i$ ;  $E_2$ , and  $E_4$  denote, respectively, the harvesting effort of the two mature species  $U_m$  and  $V_m$ . The rate at which individuals are born is taken to be proportional to the number of matures at that time; this is the  $\alpha_u U_m$  and  $\alpha_v V_m$  terms. Death of immatures is modelled by the terms  $-\gamma_u U_i$  and  $-\gamma_v V_i$ . Death of matures populations are modelled by quadratic terms. The other terms, such as,  $\alpha_u e^{-(\gamma_u + E_1)\tau_u} U_m(t - \tau_u)$  appearing in the first and second equations of system (1.2) represents the rate at time t at which individuals leave the immature and enter the mature class, having just reached maturity. These are individuals who were born at time  $t - \tau_u$ . Therefore, the rate of entering the mature class is  $\alpha_u U_m(t-\tau_u)$  times the fraction of those born at time  $t-\tau_u$  who are still alive now and are not harvested. That this fraction is  $e^{-(\gamma_u+E_1)\tau_u}$ follows from the assumption that the death and harvesting of immatures are following a linear law given by the terms  $-\gamma_u U_i$  and  $-E_1 U_i$ . Of course,  $U_m$  and  $V_m$ 

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in (1.2) refer only to the adult members of the two species. Thus, it is assumed that competition occurs only between the adults. Since many species strongly protect their young, we feel this is not too unrealistic an assumption. Also it is assumed that competition effects are of the classical Lotka-Volterra kind, (see for example, Murray [9], Gopalsamy [10] and Kuang [11]). When two or more species interact the population dynamics of each species is affected. In a predator-prey situation the growth rate of one species is decreased and the other is increased. While in competition the growth rates of both species are decreased.

For initial data of system (1.2), we assume that

(1.3) 
$$U_i(t) = \phi_1(t) \ge 0, \ U_m = \phi_2(t) \ge 0 \ \text{for} \ -\tau_u \le t \le 0$$
$$V_i(t) = \psi_1(t) \ge 0, \ V_m = \psi_2(t) \ge 0 \ \text{for} \ -\tau_v \le t \le 0,$$

such that

$$U_i(0) = \int_{-\tau_u}^0 \alpha_u U_m(s) e^{(\gamma_u + E_1)s} ds \text{ and } V_i(0) = \int_{-\tau_v}^0 \alpha_v V_m(s) e^{(\gamma_v + E_3)s} ds,$$

which represent the number of immatures that have survived to time t = 0 (the number of those that are still alive and still immature and have not been harvested). We assume also that

(1.4) 
$$U_m(0), V_m(0), U_i(0), V_i(0) > 0.$$

#### 2. Positivity and boundedness

In this section, we address positivity and boundedness of the solution of the system (1.2). This is important since the solutions of the system represent populations, and because we anticipate that limited resources will place a natural restriction to how many individuals can survive.

**Theorem 1.** If the initial data (1.3), and the assumption (1.4) hold, then the solutions of system (1.2) are positive and bounded for all  $t \ge 0$ .

*Proof.* We first show that  $U_m(t) > 0$  for all t > 0. Assume, for contradiction, that there exists a first time  $t_0 > 0$  such that  $U_m(t_0) = 0$ . Then  $U_m(t) > 0$  for  $t \in [0, t_0)$  and

$$\frac{dU_m(t_0)}{dt} = \alpha_u e^{-(\gamma_u + E_1)\tau_u} U_m(t_0 - \tau_u) > 0.$$

Thus,  $U'_m(t_0) > 0$ . This is a contradiction since it implies  $U_m(t)$  must be negative for t just before  $t_0$ , which contradicts the choice of  $t_0$ .

Similarly, we can prove that  $V_m(t) > 0$  for all  $t \ge 0$ .

Proving that  $U_i(t) > 0$  for t > 0 is a little more difficult. By positivity of  $U_m(t)$ , then for  $0 \le t \le \tau_u$ . We have

$$\frac{dU_i(t)}{dt} \ge -\gamma_u U_i(t) - \alpha_u e^{-(\gamma_u + E_1)\tau_u} U_m(t - \tau_u) - E_1 U_i(t).$$

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By comparison,  $U_i(t) \ge u(t)$  where u(t) is the solution of

$$\frac{du(t)}{dt} = -\gamma_u u(t) - \alpha_u e^{-(\gamma_u + E_1)\tau_u} U_m(t - \tau_u) - E_1 u(t)$$

subject to  $u(0) = U_i(0) > 0$ . But the solution of the last equation is

$$u(t) = e^{-(\gamma_u + E_1)t} \left( U_i(0) - \int_0^t \alpha_u e^{(\gamma_u + E_1)s} e^{-(\gamma_u + E_1)\tau_u} U_m(s - \tau_u) ds \right).$$

Hence, by (1.3)

$$u(\tau_{u}) = e^{-(\gamma_{u}+E_{1})\tau_{u}} \left( \int_{-\tau_{u}}^{0} \alpha_{u} U_{m}(\xi) e^{(\gamma_{u}+E_{1})\xi} d\xi - \int_{0}^{\tau_{u}} \alpha_{u} e^{(\gamma_{u}+E_{1})s} e^{-(\gamma_{u}+E_{1})\tau_{u}} U_{m}(s-\tau_{u}) ds \right),$$

which gives  $u(\tau_u) = 0$ , and therefore, u(t) > 0 for  $t \in [0, \tau_u)$ , and so  $U_i(t) > 0$  on  $[0, \tau_u)$ . Repeating this argument with  $t = \tau_u$  as the initial time yields that  $U_i(t) > 0$  on  $[\tau_u, 2\tau_u)$ . This argument can be continued to include all positive times, and so we have shown that  $U_i(t) > 0$  for all t > 0. Similarly, we can show that  $V_i(t) > 0$  for all t > 0.

Now to prove the boundedness of positive solutions of system (1.2), we choose the function

$$V(t) = U_i(t) + U_m(t) + V_i(t) + V_m(t).$$

By positivity of solutions, all terms in V are positive. Now

$$V'(t) = (\alpha_u - E_2)U_m(t) - \beta_u U_m^2(t) - (\gamma_u + E_1)U_i(t) - c_1 U_m(t)V_m(t) + (\alpha_v - E_4)V_m(t) - (\gamma_v + E_3)V_i(t) - \beta_v V_m^2(t) - c_2 U_m(t)V_m(t).$$

Since  $U_m, V_m > 0$ , then by calculating the derivative of V(t) along solutions of system (1.2), we have

$$V'(t) \le (\alpha_u - E_2)U_m(t) - (\gamma_u + E_1)U_i(t) + (\alpha_v - E_4)V_m(t) - (\gamma_v + E_3)V_i(t).$$

And for  $\varepsilon > 0$ , where  $\varepsilon < \max\{\gamma_u + E_1, \gamma_v + E_3\}$ , we have

$$V'(t) + \varepsilon V(t) \leq (\alpha_u + \varepsilon - E_2)U_m(t) - \beta_u U_m^2(t) - (\gamma_u + \varepsilon + E_1)U_i(t) + (\alpha_v + \varepsilon - E_4)V_m(t) - (\gamma_v + \varepsilon + E_3)V_i(t) - \beta_v V_m^2(t) \leq (\alpha_u + \varepsilon - E_2)U_m(t) + (\alpha_v + \varepsilon - E_4)V_m(t).$$

Hence, there exists a positive number m such that

$$V'(t) + \varepsilon V(t) < m.$$

So that

$$V(t) < \frac{m}{\varepsilon} + \left(V(0) - \frac{m}{\varepsilon}\right)e^{-\varepsilon t} < \infty.$$

Therefore, we deduce that  $U_i$ ,  $U_m$ ,  $V_i$  and  $V_m$  are bounded.

### 3. Asymtotic stability of equilibria

The equilibria of System (1.2) are determined by setting  $\dot{U}_i = \dot{U}_m = \dot{V}_i = \dot{V}_m = 0$  in system (1.2), and solving the resulting algebraic equations

$$\begin{aligned} \alpha_u U_m(t) &- \gamma_u U_i(t) - \alpha_u e^{-(\gamma_u + E_1)\tau_u} U_m(t - \tau_u) - E_1 U_i(t) &= 0, \\ \alpha_u e^{-(\gamma_u + E_1)\tau_u} U_m(t - \tau_u) - \beta_u U^2(t) - c_1 U(t) V(t) - E_2 U_m(t) &= 0, \\ \alpha_v V_m(t) - \gamma_v V_i(t) - \alpha_v e^{-(\gamma_v + E_3)\tau_v} V_m(t - \tau_v) - E_3 V_i(t) &= 0, \\ \alpha_v e^{-(\gamma_v + E_3)\tau_v} V_m(t - \tau_v) - \beta_v V_m^2(t) - c_2 U(t) V(t) - E_4 V_m(t) &= 0. \end{aligned}$$

Then system (1.2) has four equilibria:  $E_0(0, 0, 0, 0), E_u(\bar{U}_i, \bar{U}_m, 0, 0), E_v(0, 0, \bar{V}_i, \bar{V}_m)$ , and  $\hat{E}(\hat{U}_i, \hat{U}_m, \hat{V}_i, \hat{V}_m)$  where:

$$\begin{split} \bar{U}_{i} &= \frac{\alpha_{u}(\alpha_{u}e^{-(\gamma_{u}+E_{1})\tau_{u}}-E_{2})(1-e^{-(\gamma_{u}+E_{1})\tau_{u}})}{(\gamma_{u}+E_{1})\beta_{u}}, \ \bar{U}_{m} = \frac{\alpha_{u}e^{-(\gamma_{u}+E_{1})\tau_{u}}-E_{2}}{\beta_{u}}, \\ \bar{V}_{i} &= \frac{\alpha_{v}(\alpha_{v}e^{-(\gamma_{v}+E_{3})\tau_{v}}-E_{4})(1-e^{-(\gamma_{v}+E_{3})\tau_{v}})}{(\gamma_{v}+E_{3})\beta_{v}}, \ \bar{V}_{m} = \frac{\alpha_{v}e^{-(\gamma_{v}+E_{3})\tau_{v}}-E_{4}}{\beta_{v}}, \\ \hat{U}_{i} &= \frac{\alpha_{u}(1-e^{-(\gamma_{u}+E_{1})\tau_{u}})[\beta_{v}(\alpha_{u}e^{-(\gamma_{u}+E_{1})\tau_{u}}-E_{2})-c_{1}(\alpha_{v}e^{-(\gamma_{v}+E_{3})\tau_{v}}-E_{4})]}{(\gamma_{u}+E_{1})(\beta_{u}\beta_{v}-c_{1}c_{2})}, \\ \hat{U}_{m} &= \frac{\beta_{v}(\alpha_{u}e^{-(\gamma_{u}+E_{1})\tau_{u}}-E_{2})-c_{1}(\alpha_{v}e^{-(\gamma_{v}+E_{3})\tau_{v}}-E_{4})}{\beta_{u}\beta_{v}-c_{1}c_{2}}, \\ \hat{V}_{i} &= \frac{\alpha_{v}(1-e^{-(\gamma_{v}+E_{3})\tau_{v}})[\beta_{u}(\alpha_{v}e^{-(\gamma_{v}+E_{3})\tau_{v}}-E_{4})-c_{2}(\alpha_{u}e^{-(\gamma_{u}+E_{1})\tau_{u}}-E_{2})]}{(\gamma_{v}+E_{3})(\beta_{u}\beta_{v}-c_{1}c_{2})}, \\ \hat{V}_{m} &= \frac{\beta_{u}(\alpha_{v}e^{-(\gamma_{v}+E_{3})\tau_{v}}-E_{4})-c_{2}(\alpha_{u}e^{-(\gamma_{u}+E_{1})\tau_{u}}-E_{2})}{\beta_{u}\beta_{v}-c_{1}c_{2}}}. \end{split}$$

The stability of the four steady states is determined by linearizing system (1.2) about them. To do so, let  $E^* = (U_i^*, U_m^*, V_i^*, V_m^*)$  be an arbitrary equilibrium and set:  $U_i = x_i + U_i^*$ ,  $U_m = x_m + U_m^*$ ,  $V_i = y_i + V_i^*$  and  $V_m = y_m + V_m^*$  and neglecting

higher order term in  $x_i, x_m, y_i$  and  $y_m$  to obtain:

$$\begin{aligned} \frac{dx_i}{dt} &= \alpha_u x_m(t) - \gamma_u x_i(t) - \alpha_u e^{-(\gamma_u + E_1)\tau_u} x_m(t - \tau_u) - E_1 x_i(t) \\ \frac{dx_m}{dt} &= \alpha_u e^{-(\gamma_u + E_1)\tau_u} x_m(t - \tau_u) - 2\beta_u x_m(t) U_m^* - c_1 x_m(t) V_m^* - c_1 y_m(t) U_m^* \\ &- E_2 x_m(t) \\ \frac{dy_i}{dt} &= \alpha_v y_m(t) - \gamma_v y_i(t) - \alpha_v e^{-(\gamma_v + E_3)\tau_v} y_m(t - \tau_v) - E_3 y_i(t) \\ \frac{dy_m}{dt} &= \alpha_v e^{-(\gamma_v + E_3)\tau_v} y_m(t - \tau_v) - 2\beta_v y_m(t) V_m^* - c_2 x_m(t) V_m^* - c_2 y_m(t) U_m^* \\ &- E_4 y_m(t). \end{aligned}$$

For the equilibrium  $E_0$  of (1.2), its characteristic equation is

(3.1) 
$$(\lambda + \gamma_u + E_1) \left( \lambda + E_2 - \alpha_u e^{-\tau_u (\gamma_u + E_1 + \lambda)} \right)$$
$$(\lambda + \gamma_v + E_3) \left( \lambda + E_4 - \alpha_v e^{-\tau_v (\gamma_v + E_3 + \lambda)} \right) = 0$$

has at least a positive eigenvalue, which occurs from either the roots of the second or the roots of fourth bracketed factors. If  $E_2 < \alpha_u e^{-\tau_u(\gamma_u + E_1)}$ , then the point of intersection of  $y = \lambda + E_2$  and  $y = \alpha_u e^{-\tau_u(\gamma_u + E_1 + \lambda)}$  is such a positive eigenvalue. Therefore, the equilibrium  $E_0$  is unstable. The equilibrium  $E_0$  is unstable has ecologically interpretation, if the harvesting effort of the four populations are not large enough, if the immature populations do not have a high deathrate, or the two species have a low maturation time. For the equilibrium  $E_u$  the characteristic equation is

$$(\lambda + \gamma_u + E_1) \left( \lambda + 2\beta_u \bar{U}_m + E_2 - \alpha_u e^{-\tau_u (\gamma_u + E_1 + \lambda)} \right) (\lambda + \gamma_v + E_3)$$
$$\left( \lambda + c_2 \bar{U}_m + E_4 - \alpha_v e^{-\tau_v (\gamma_v + E_3 + \lambda)} \right) = 0.$$

It has two negative eigenvalues  $\lambda = -(\gamma_u + E_1)$  and  $\lambda = -(\gamma_v + E_3)$ . The other eigenvalues are the roots  $\lambda$  of

(3.2) 
$$\lambda + 2\beta_u \bar{U}_m + E_2 - \alpha_u e^{-\tau_u (\gamma_u + E_1 + \lambda)} = 0,$$

together with the roots  $\lambda$  of the equation

(3.3) 
$$\lambda + c_2 \overline{U}_m + E_4 - \alpha_v e^{-\tau_v (\gamma_v + E_3 + \lambda)} = 0.$$

We will find the condition which determines that all roots of (3.2) satisfy  $Re\lambda < 0$ . Assume for contradiction, that there exists a root  $\lambda^*$  such that  $Re\lambda^* \ge 0$ . Then

$$\left|\lambda^* + 2\alpha_u e^{-(\gamma_u + E_1)\tau_u} - E_2\right| = \left|\alpha_u e^{-\tau_u(\gamma_u + E_1 + \lambda^*)}\right| \le \alpha_u e^{-(\gamma_u + E_1)\tau_u}$$

since  $Re\lambda^* \geq 0$ . This implies that  $\lambda^*$  is in the circle in the complex  $\lambda$  plane centered at  $\lambda = -2\alpha_u e^{-(\gamma_u + E_1)\tau_u} + E_2$  and of radius  $\alpha_u e^{-(\gamma_u + E_1)\tau_u}$ . Therefore, we will have a contradiction if

(3.4) 
$$\alpha_u e^{-(\gamma_u + E_1)\tau_u} > E_2.$$

Now, for the equation (3.3) we have

$$\left|\lambda^* + \frac{c_2\left(\alpha_u e^{-(\gamma_u + E_1)\tau_u} - E_2\right)}{\beta_u} + E_4\right| \le \alpha_v e^{-(\gamma_v + E_3)\tau_v}$$

which leads to a contradiction if

(3.5) 
$$c_2 \left( \alpha_u e^{-(\gamma_u + E_1)\tau_u} - E_2 \right) > \beta_u \left( \alpha_v e^{-(\gamma_v + E_3)\tau_v} - E_4 \right).$$

Consequently, if the two conditions (3.4) and (3.5) are both hold, then the equilibrium  $E_u$  is linearly stable. In similar way, we can show that the equilibrium  $E_v$  which has the characteristic equation

$$(\lambda + \gamma_u + E_1) \left( \lambda + 2\beta_v \bar{V}_m + E_4 - \alpha_v e^{-\tau_v (\gamma_v + E_3 + \lambda)} \right).$$
$$(\lambda + \gamma_v + E_3) \left( \lambda + c_1 \bar{V}_m + E_2 - \alpha_u e^{-\tau_u (\gamma_u + E_1 + \lambda)} \right) = 0,$$

is linearly stable if

(3.6) 
$$\alpha_v e^{-(\gamma_v + E_3)\tau_v} > E_4$$

and

(3.7) 
$$c_1\left(\alpha_v e^{-(\gamma_v + E_3)\tau_v} - E_4\right) > \beta_v\left(\alpha_u e^{-(\gamma_u + E_1)\tau_u} - E_2\right).$$

Thus if (3.4), (3.5), (3.6) and (3.7) hold then  $E_u$  and  $E_v$  are both linearly stable, and the numerators of the components  $U_i$ ,  $U_m$ ,  $V_i$  and  $V_m$  of the equilibrium  $\hat{E}$  are all negative. But, at the same time, (3.5) and (3.7) imply that

$$\beta_u < \frac{c_2(\alpha_u e^{-(\gamma_u + E_1)\tau_u} - E_2)}{\alpha_v e^{-(\gamma_v + E_3)\tau_v} - E_4}, \ \beta_v < \frac{c_1(\alpha_v e^{-(\gamma_v + E_3)\tau_v} - E_4)}{\alpha_u e^{-(\gamma_u + E_1)\tau_u} - E_2},$$

so that  $\beta_u \beta_v < c_1 c_2$ , i.e., the denominators of all components of the equilibrium  $\hat{E}$  are negative too. Thus under these circumstances  $U_i$ ,  $U_m$ ,  $V_i$ ,  $V_m > 0$  so that the equilibrium  $\hat{E}$  is feasible. Also we can see if (3.5) and (3.7) are both reversed, then the equilibria  $E_u$  and  $E_v$  are both linearly unstable and again  $\hat{E}$  is feasible under these circumstances. But if one of the equilibria  $E_u$ ,  $E_v$  is stable and the other unstable, then the coexistence equilibrium  $\hat{E}$  is not feasible. Finally, for the equilibrium  $\hat{E}$  the characteristic equation is

$$(\lambda + \gamma_u + E_1) \left( \lambda + c_1 \hat{V}_m + 2\beta_u \hat{U}_m + E_2 - \alpha_u e^{-\tau_u (\gamma_u + E_1 + \lambda)} \right) \cdot (\lambda + \gamma_v + E_3) \left( \lambda + c_2 \hat{U}_m + 2\beta_v \hat{V}_m + E_4 - \alpha_v e^{-\tau_v (\gamma_v + E_3 + \lambda)} \right) = 0.$$

It has two negative eigenvalues  $\lambda = -(\gamma_u + E_1)$  and  $\lambda = -(\gamma_v + E_3)$ . What we are looking for now is to find under what conditions the second and fourth bracketed factors have negative eigenvalues. It is not difficult to see that the conditions for all roots of these factors to satisfy  $Re\lambda < 0$  are

(3.8) 
$$c_1\left(\alpha_v e^{-(\gamma_v + E_3)\tau_v} - E_4\right) < \beta_v\left(\alpha_u e^{-(\gamma_u + E_1)\tau_u} - E_2\right),$$

and

(3.9) 
$$c_2\left(\alpha_u e^{-(\gamma_u + E_1)\tau_u} - E_2\right) < \beta_u\left(\alpha_v e^{-(\gamma_v + E_3)\tau_v} - E_4\right)$$

Therefore, the equilibrium  $\hat{E}$  is stable if equations (3.8) and (3.9) satisfy. We already know that the equilibria  $E_u$  and  $E_v$  cannot exist if  $E_2 > \alpha_u e^{-(\gamma_u + E_1)\tau_u}$  and  $E_4 > \alpha_v e^{-(\gamma_v + E_3)\tau_v}$  because  $\bar{U}$  and  $\bar{V}$  are negative under these conditions. In fact, we shall prove in the next section that under these conditions the equilibrium  $E_0$  is globally asymptotically stable. Therefore, we assume that (3.4), and (3.6) hold throughout this paper.

Before proceeding, we shall need the following theorem.

**Theorem 2.** Let u(t) be the solution of

(3.10) 
$$\frac{du}{dt} = \alpha_u e^{-(\gamma_u + E_1)\tau_u} u(t - \tau_u) - \beta_u u^2(t) - Au(t),$$

where u(t) > 0 for  $-\tau \le t \le 0$ .

(I) If 
$$0 \le A < \alpha_u e^{-(\gamma_u + E_1)\tau_u}$$
, then  $\lim_{t \to \infty} u(t) = \hat{u}$ , where

(3.11) 
$$\hat{u} = \frac{1}{\beta_u} \left[ \alpha_u e^{-(\gamma_u + E_1)\tau_u} - A \right].$$

(II) If 
$$A > \alpha_u e^{-(\gamma_u + E_1)\tau_u}$$
, then  $\lim_{t \to \infty} u(t) = 0$ .

*Proof.* (I) We can show that u(t) is bounded and positive by the same way we have done in section 1. The prove of this theorem is in several stages. First we deal with the cases when u(t) is eventually monotonically decreasing or increasing, i.e., monotone for all t sufficiently large. But by positivity of solutions, u(t) is not eventually monotonically decreasing because if so, then u(t) must approaches some limit  $\hat{u} \geq 0$ . This limit must be an equilibrium of (3.10) and therefore, either zero or the value stated. Zero is ruled out since a standard linearized analysis yields that the zero solution of (3.10) is linearly unstable under the stated condition on A. So now assume, for contradiction, that u(t) is eventually monotonic increasing with  $u(t) \to \infty$  as  $t \to \infty$  then in this case  $u(t - \tau) \leq u(t)$  for all t sufficiently large, and therefore,

$$\frac{du(t)}{dt} \le \alpha_u e^{-(\gamma_u + E_1)\tau_u} u(t) - \beta_u u^2(t) - Au(t).$$

But  $u(t) \to \infty$ . So, for t sufficiently large, we must have  $\dot{u}(t) < 0$  contradicting the assumption that u(t) is eventually monotonic increasing. We must now conclude that any eventually monotone solution approaches a non-zero limit, say  $\bar{u}$ . This limit must be an equilibrium of (3.10) and so, since  $\bar{u} > 0$  we must have  $\bar{u} = \hat{u}$ . We now consider the case when u(t) is not eventually monotonic. Then there exists a sequence  $t_k \to \infty$  as  $t \to \infty$  such that  $u'(t_k) = 0$  and  $u(t_k) \to l_m := \limsup_{t \to \infty} u(t)$ . We want to show that  $l_m = \hat{u}$ . Suppose for contradiction that  $l_m > \hat{u}$ . Let  $\varepsilon > 0$  be sufficiently small. Then there exists T > 0 such that if  $t \ge T > \tau$  we have

$$u(t) \le l_m + \varepsilon$$

Since  $t_k \to \infty$  as  $k \to \infty$ , there exists K such that if  $k \ge K$  then

$$t_k - \tau_u \ge T$$

Then, for  $k \geq K$ 

$$u(t_k - \tau_u) \le l_m + \varepsilon.$$

Applying equation (3.10) when  $t = t_k$  where  $k \ge K$ , we have

$$0 = u'(t_k) \le \alpha_u e^{-(\gamma_u + E_1)\tau_u} (l_m + \varepsilon) - \beta_u u^2(t_k) - Au(t_k).$$

Letting  $k \to \infty$ ,

$$0 \le \alpha_u e^{-(\gamma_u + E_1)\tau_u} (l_m + \varepsilon) - \beta_u l_m^2 - A l_m$$

This is true for all  $\varepsilon > 0$  sufficiently small. Thus we must have

$$0 \le \alpha_u e^{-(\gamma_u + E_1)\tau_u} l_m - \beta_u l_m^2 - A l_m.$$

But since  $l_m > \hat{u}$ , we have

$$\alpha_u e^{-(\gamma_u + E_1)\tau_u} < \beta_u l_m + A.$$

Therefore,

$$0 \leq \alpha_u e^{-(\gamma_u + E_1)\tau_u} l_m - \beta_u l_m^2 - A l_m$$
  
$$< (\beta_u l_m + A) l_m - \beta_u l_m^2 - A l_m = 0.$$

Contradiction. Hence  $l_m = \hat{u}$ , that is  $\lim_{t \to \infty} u(t) = \hat{u}$ .

(II) This can be achieved in three stages. We shall first prove that u(t) is not eventually monotonic increasing. Suppose on the contrary. We already know that u(t) is bounded above. Therefore there exists  $l_m \geq 0$  with

$$u(t) \to l_m \text{ as } t \to \infty.$$

We want to show that  $l_m = 0$ . Assume that  $l_m > 0$  then, letting  $t \to \infty$ , equation (3.10) gives

$$0 \le \alpha_u e^{-(\gamma_u + E_1)\tau_u} l_m - A l_m$$

which leads to

$$0 \le l_m \left( \alpha_u e^{-(\gamma_u + E_1)\tau_u} - A \right).$$

But since  $l_m > 0$  we must have

$$\alpha_u e^{-(\gamma_u + E_1)\tau_u} - A \ge 0.$$

This contradicts the hypothesis of the theorem that  $A > \alpha_u e^{-(\gamma_u + E_1)\tau_u}$ . The second stage is to consider the possibility that u(t) is eventually monotonic decreasing. Then since  $u(t) \ge 0$ , u(t) must approach a limit  $l_m$  as  $t \to \infty$ . We want to show that  $l_m = 0$ . This is trivial, since the assumption that  $l_m > 0$  leads to contradiction by following the same arguments as described above. The final step in our proof is to consider the case when u(t) is not monotonic. Then there exists a sequence of times  $t_k \to \infty$  such that  $u'(t_k) = 0$  and  $u(t_k) \to l_m := \limsup_{t \to \infty} u(t)$ . We want to show that  $l_m = 0$ . Let  $\varepsilon > 0$  be sufficiently small. Then there exists T > 0 such that if  $t \ge T$  we have

$$u(t) \le l_m + \varepsilon.$$

Since  $t_k \to \infty$  as  $k \to \infty$ , there exists K such that if  $k \ge K$  then

$$t_k - \tau_u \ge T.$$

Then, for  $k \geq K$ 

$$u(t_k - \tau_u) \le l_m + \varepsilon.$$

Applying equation (3.10) when  $t = t_k$  where  $k \ge K$ , we have

$$0 = u'(t_k) \le \alpha_u e^{-(\gamma_u + E_1)\tau_u} (l_m + \varepsilon) - \beta_u u^2(t_k) - Au(t_k).$$

Letting  $k \to \infty$ ,

$$0 \le \alpha_u e^{-(\gamma_u + E_1)\tau_u} (l_m + \varepsilon) - A l_m$$

This is true for all  $\varepsilon > 0$  sufficiently small. Thus we must have

$$e^{-(\gamma_u + E_1)\tau_u} > A.$$

This contradicts the hypothesis of the theorem unless  $l_m = 0$ , and the proof of Theorem 2 is complete.

In the proof of theorem 3 below, and in subsequent theorems, we shall use a comparison principle. For scalar equations, the essential requirement for a comparison principle to hold is that the reaction term be a nondecreasing function of the delay variable (see, for example, Martin and Smith [12]). The following lemma will be useful and follows easily from the results in [12].

**Lemma 1.** Let v(t) be a solution of

$$\frac{dv(t)}{dt} = \alpha e^{-\gamma\tau} v(t-\tau) - \beta v^2(t) - \lambda v(t), \qquad t > 0$$

and u(t) some function satisfying

(3.12) 
$$\frac{du(t)}{dt} \ge \alpha e^{-\gamma \tau} u(t-\tau) - \beta u^2(t) - \lambda u(t), \qquad t > 0.$$

Assume also that  $u(t) \ge v(t)$  for all  $t \in [-\tau, 0]$ . Then  $u(t) \ge v(t)$  for all t > 0.

**Remarks.** An analogous result holds with the inequalities reversed, and we shall need this also. In our applications of these comparison results we shall often find that a differential inequality of the form (3.12) holds only for t above some value, say  $t_1$ , and not for all t > 0. In that case the initial time is simply thought of as  $t_1$  rather than 0, and  $u(t) \ge v(t)$  is arranged to hold for  $t \le t_1$  by appropriate definition of v(t) for values of  $t \le t_1$ . In the interests of clarity, we shall not always elaborate on this latter point in detail.

### **3.1.** Global asymptotically stable of $E_0$

If  $E_2 > \alpha_u e^{-(\gamma_u + E_1)\tau_u}$  and  $E_4 > \alpha_v e^{-(\gamma_v + E_3)\tau_v}$ , then system (1.2) has a nonnegative equilibrium  $E_0(0, 0, 0, 0)$ . We shall prove that  $E_0$  is globally asymptotically stable. It is easy to show that  $E_0$  is locally asymptotically stable since all eigenvalues of the characteristic equation (3.1) have  $Re(\lambda) < 0$  under these asymptotics. The biological meaning of the conditions are obvious: if the harvesting efforts of the two species (immatures and matures) are large enough, if the two species have a long maturation time delay  $\tau_u$  and  $\tau_v$ , if they have a large immature mortality rate  $\gamma_u$  and  $\gamma_v$ , or if they have insufficient live births  $\alpha_u$  and  $\alpha_v$ .

**Theorem 3.** Let the initial data (1.3), and (1.4) hold, and assume that

 $E_2 > \alpha_u e^{-(\gamma_u + E_1)\tau_u}$  and  $E_4 > \alpha_v e^{-(\gamma_v + E_3)\tau_v}$ .

Then  $(U_i(t), U_m(t), V_i(t), V_m(t)) \to (0, 0, 0, 0)$  as  $t \to \infty$ . *Proof.* Since  $U_m(t) \ge 0$  and  $V_m(t) \ge 0$  we have

$$\frac{dU_m(t)}{dt} = \alpha_u e^{-(\gamma_u + E_1)\tau_u} U_m(t - \tau_u) - \beta_u U_m^2(t) - c_1 U_m(t) V_m(t) - E_2 U_m(t)$$
  
$$\leq \alpha_u e^{-(\gamma_u + E_1)\tau_u} U_m(t - \tau_u) - \beta_u U_m^2(t) - E_1 U_m(t).$$

Therefore, by the comparison theorem,  $0 \leq U_m(t) \leq u(t)$  where

$$\frac{du(t)}{dt} = \alpha_u e^{-(\gamma_u + E_1)\tau_u} u(t - \tau_u) - \beta_u u^2(t) - E_1 u(t),$$

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since  $E_1 > \alpha_u e^{-(\gamma_u + E_1)\tau_u}$ , then by Theorem 2(**II**), we conclude that  $u(t) \to 0$  which leads to  $U_m(t) \to 0$ . Similarly, we can prove that  $V_m(t) \to 0$ . Now we show that  $U_i \to 0$  as  $t \to 0$ . The first equation of system (1.2) is

$$\frac{dU_i(t)}{dt} = \alpha_u U_m(t) - \gamma_u U_i(t) - \alpha_u e^{-(\gamma_u + E_1)\tau_u} U_m(t - \tau_u) - E_1 U_i(t).$$

Suppose  $\lim_{t\to\infty} U_i(t)$  does not exist, then there exist two sequences  $t_n^m$  and  $t_n^M$  such that

$$\lim_{t \to \infty} U_i(t_n^m) = U_{im} \quad , \, \dot{U}_i(t_n^m) = 0$$

and

$$\lim_{t \to \infty} U_i(t_n^M) = U_{iM} \quad , \dot{U}_i(t_n^M) = 0,$$

such that  $U_{im} < U_{iM}, U_i(t_n^m) \neq 0$  and  $U_i(t_n^M) \neq 0$ . Therefore,

$$0 = \dot{U}_{i}(t_{n}^{m}) = \alpha_{u}U_{m}(t_{n}^{m}) - \gamma_{u}U_{i}(t_{n}^{m}) - \alpha_{u}e^{-(\gamma_{u}+E_{1})\tau_{u}}U_{m}(t_{n}^{m}-\tau_{u}) - E_{1}U_{i}(t_{n}^{m})$$
  
$$0 = \dot{U}_{i}(t_{n}^{M}) = \alpha_{u}U_{m}(t_{n}^{M}) - \gamma_{u}U_{i}(t_{n}^{M}) - \alpha_{u}e^{-(\gamma_{u}+E_{1})\tau_{u}}U_{m}(t_{n}^{M}-\tau_{u}) - E_{1}U_{i}(t_{n}^{M})$$

But since  $\lim_{t \to \infty} U_m(t) = 0$ , then we have

$$U_{im} = \lim_{t \to \infty} U_i(t_n^m) = \lim_{t \to \infty} U_i(t_n^M) = U_{iM},$$

a contradiction. Therefore,  $\lim_{t\to\infty} U_i(t)$  exists. But since  $U_i(t)$  is bounded, then

$$\lim_{t \to \infty} \dot{U}_i(t) = 0.$$

Thus, by the first equation of system (1.2), we have

$$\lim_{t \to \infty} U_i(t) = 0.$$

Similarly we can show that

$$\lim_{t \to \infty} V_i(t) = 0.$$

This completes the proof of Theorem 3.

#### **3.2.** Global stability of $E_u$

We shall prove a theorem on the global stability of the equilibrium point  $E_u(\bar{U}_i, \bar{U}_m, 0, 0)$  of system (1.2), in the situation when the other equilibrium  $E_v(0, 0, \bar{V}_i, \bar{V}_m)$  of system (1.2) is linearly unstable. This means that the competition between the two species  $U_m$  and  $V_m$  is strong and/or significant adult harvesting in  $V_m$  species, and the species cannot coexist. One of them, in this case the  $V_m$  population (immature and mature), dies out.

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Theorem 4. Let the initial data (1.3), and (1.4) hold, and assume that

(3.13) 
$$c_2 \left( \alpha_u e^{-(\gamma_u + E_1)\tau_u} - E_2 \right) > \beta_u \left( \alpha_v e^{-(\gamma_v + E_3)\tau_v} - E_4 \right)$$

and

(3.14) 
$$c_1 \left( \alpha_v e^{-(\gamma_v + E_3)\tau_v} - E_4 \right) < \beta_v \left( \alpha_u e^{-(\gamma_u + E_1)\tau_u} - E_2 \right).$$

Then  $(U_i(t), U_m(t), V_i(t), V_m(t)) \to (\overline{U}_i, \overline{U}_m, 0, 0)$  as  $t \to \infty$ . *Proof.* We shall first show that  $(U_m(t), V_m(t)) \to (\overline{U}_m, 0)$ . Let  $\overline{U} = \limsup_{t \to \infty} U_m(t)$ ,  $\underline{U} = \liminf_{t \to \infty} U_m(t), \ \overline{V} = \limsup_{t \to \infty} V_m(t)$  and  $\underline{V} = \liminf_{t \to \infty} V_m(t)$ . Now, since

$$\frac{dU_m(t)}{dt} = \alpha_u e^{-(\gamma_u + E_1)\tau_u} U_m(t - \tau_u) - \beta_u U_m^2(t) - c_1 U_m(t) V_m(t) - E_2 U_m(t) \leq \alpha_u e^{-(\gamma_u + E_1)\tau_u} U_m(t - \tau_u) - \beta_u U_m^2(t) - E_2 U_m(t),$$

we can conclude from this and Theorem 2(**I**) that  $\overline{U} \leq U_B$  where

$$U_B = \frac{\alpha_u e^{-(\gamma_u + E_1)\tau_u} - E_2}{\beta_u},$$

is the  $U_m$  component of the equilibrium  $\hat{E}_u$ . By positivity of  $V_m(t)$  we also know that  $\underline{V} \geq 0$ . To complete the proof it suffices to find two sequences  $\{M_m^u\}, \{N_m^v\}$ with the properties that  $\underline{U} \geq M_m^u$  for each m with  $M_m^u \to U_B$  as  $m \to \infty$  (so that  $\underline{U} \geq U_B$ ), and  $\overline{V} \leq N_m^v$  for each m with  $N_m^v \to 0$  as  $m \to \infty$ . As a first step in this process, let  $v_1(t)$  satisfy

$$\frac{dv_1(t)}{dt} = \alpha_v e^{-(\gamma_v + E_3)\tau_v} v_1(t - \tau_v) - \beta_v v_1^2(t) - E_4 v_1(t), \quad t > 0$$

with, for  $t \le 0$ ,  $v_1(t) \equiv \max\{V(t), t \in [-\tau_v, 0]\} > 0$ . Then

$$\lim_{t \to \infty} v_1(t) = \frac{\alpha_v e^{-(\gamma_v + E_3)\tau_v} - E_4}{\beta_v}.$$

Since  $U_m(t)$  and  $V_m(t)$  are non-negative,

$$\frac{dV_m(t)}{dt} = \alpha_v e^{-(\gamma_v + E_3)\tau_v} V_m(t - \tau_v) - \beta_v V_m^2(t) - c_2 U_m(t) V_m(t) - E_4 V_m(t) 
\leq \alpha_v e^{-(\gamma_v + E_3)\tau_v} V_m(t - \tau_v) - \beta_v V_m^2(t) - E_4 V_m(t).$$

By comparison,  $V_m(t) \leq v_1(t)$  and therefore

$$\overline{V} = \limsup_{t \to \infty} V_m(t) \le \lim_{t \to \infty} v_1(t) = \frac{\alpha_v e^{-(\gamma_v + E_3)\tau_v} - E_4}{\beta_v} := N_1^v.$$

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Let  $\varepsilon > 0$  be sufficiently small that

(3.15) 
$$0 < \varepsilon < \frac{\beta_v (\alpha_u e^{-(\gamma_u + E_1)\tau_u} - E_2) - c_1 (\alpha_v e^{-(\gamma_v + E_3)\tau_v} - E_4)}{\beta_v c_1}$$

There exists  $t_1 > \tau$  such that  $V_m(t) \leq N_1^v + \varepsilon$  for all  $t \geq t_1$ . For  $t > t_1$  let  $u_1(t)$  evolve according to

$$\frac{du_1(t)}{dt} = \alpha_u e^{-(\gamma_u + E_1)\tau_u} u_1(t - \tau_u) - \beta_u u_1^2(t) - c_1 u_1(t)(N_1^v + \varepsilon) - E_2 u_1(t),$$

and, for  $t \in [t_1 - \tau_u, t_1]$ , let

$$u_1(t) \equiv \min\{U(t), t \in [t_1 - \tau_u, t_1]\},\$$

which is strictly positive, since  $U_m(t) > 0$  on  $(0, \infty)$ . It is not necessary to define  $u_1(t)$  for  $t < t_1 - \tau_u$  since Lemma 1 is now being applied with initial time  $t_1$  rather than 0.

Since  $\varepsilon$  satisfies (3.15), Theorem 2(**I**) yields that

$$\lim_{t \to \infty} u_1(t) = \frac{1}{\beta_u} \left[ \alpha_u e^{-(\gamma_u + E_1)\tau_u} - E_2 - c_1(N_1^v + \varepsilon) \right]$$

Now, since  $N_1^v + \varepsilon \ge V_m(t)$  for  $t \ge t_1$ , we have, for such t,

$$\frac{dU_m(t)}{dt} = \alpha_u e^{-(\gamma_u + E_1)\tau_u} U_m(t - \tau_u) - \beta_u U_m^2(t) - c_1 U_m(t) V_m(t) - E_2 U_m(t)$$
  

$$\geq \alpha_u e^{-(\gamma_u + E_1)\tau_u} U_m(t - \tau_u) - \beta_u U_m^2(t) - c_1 U(t) (N_1^v + \varepsilon) - E_2 U_m(t).$$

By comparison,  $U_m(t) \ge u_1(t)$  and therefore

$$\underline{U} = \liminf_{t \to \infty} U_m(t) \ge \lim_{t \to \infty} u_1(t) = \frac{1}{\beta_u} \left[ \alpha_u e^{-(\gamma_u + E_1)\tau_u} - E_2 - c_1(N_1^v + \varepsilon) \right].$$

Since this is true for any  $\varepsilon > 0$  satisfying (3.15), it follows that  $\underline{U} \ge M_1^u$  where

$$M_1^u = \frac{1}{\beta_u} \left[ \alpha_u e^{-(\gamma_u + E_1)\tau_u} - E_2 - c_1 N_1^v \right].$$

Let  $\varepsilon > 0$ . There exists  $t_2 > 0$  such that  $U_m(t) \ge M_1^u - \varepsilon$  for all  $t \ge t_2$ . For  $t > t_2$  let  $v_2(t)$  be the solution of

$$\begin{aligned} \frac{dv_2(t)}{dt} &= & \alpha_v e^{-(\gamma_v + E_3)\tau_v} v_2(t - \tau_v) - \beta_v v_2^2(t) \\ &- \frac{\beta_u (\alpha_v e^{-(\gamma_v + E_3)\tau_v} - E_4)}{\alpha_u e^{-(\gamma_u + E_1)\tau_u} - E_2} (M_1^u - \varepsilon) v_2(t) - E_4 v_2(t), \end{aligned}$$

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with appropriate "initial data" on the interval  $[t_2 - \tau, t_2]$ . Now

$$\frac{dV_m(t)}{dt} = \alpha_v e^{-(\gamma_v + E_3)\tau_v} V_m(t - \tau_v) - \beta_v V_m^2(t) - c_2 U_m(t) V_m(t) - E_4 V_m(t) \\
\leq \alpha_v e^{-(\gamma_v + E_3)\tau_v} V_m(t - \tau_v) - \beta_v V_m^2(t) \\
- \frac{\beta_u (\alpha_v e^{-(\gamma_v + E_3)\tau_v} - E_4)}{\alpha_u e^{-(\gamma_u + E_1)\tau_u} - E_2} (M_1^u - \varepsilon) V_m(t) - E_4 V_m(t),$$

where we have used (3.13). By comparison,  $V_m(t) \le v_2(t)$ . But, by Theorem 2, and using the fact that

$$M_{1}^{u} < \frac{1}{\beta_{u}} \left[ \alpha_{u} e^{-(\gamma_{u} + E_{1})\tau_{u}} - E_{2} \right],$$
$$\lim_{t \to \infty} v_{2}(t) = \frac{1}{\beta_{v}} \left[ \alpha_{v} e^{-(\gamma_{v} + E_{3})\tau_{v}} - E_{4} - \frac{\beta_{u}(\alpha_{v} e^{-(\gamma_{v} + E_{3})\tau_{v}} - E_{4})}{\alpha_{u} e^{-(\gamma_{u} + E_{1})\tau_{u}} - E_{2}} (M_{1}^{u} - \varepsilon) \right]$$

Hence

$$\overline{V} = \limsup_{t \to \infty} V_m(t) \le \lim_{t \to \infty} v_2(t)$$
$$= \frac{1}{\beta_v} \left[ \alpha_v e^{-(\gamma_v + E_3)\tau_v} - E_4 - \frac{\beta_u(\alpha_v e^{-(\gamma_v + E_3)\tau_v} - E_4)}{\alpha_u e^{-(\gamma_u + E_1)\tau_u} - E_2} (M_1^u - \varepsilon) \right].$$

Since  $\varepsilon$  is arbitrary, we conclude that  $\overline{V} \leq N_2^v$  where

(3.16) 
$$N_2^v = \frac{1}{\beta_v} \left[ \alpha_v e^{-(\gamma_v + E_3)\tau_v} - E_4 - \frac{\beta_u (\alpha_v e^{-(\gamma_v + E_3)\tau_v} - E_4)}{\alpha_u e^{-(\gamma_u + E_1)\tau_u} - E_2} M_1^u \right].$$

Now, let  $\varepsilon > 0$  be sufficiently small that the expression given below for  $\lim_{t\to\infty} u_2(t)$  is positive. That this is possible follows from the second inequality (3.14) in the hypotheses of Theorem 4, together with the fact that  $N_2^v$  satisfies

$$N_2^v < \frac{1}{\beta_v} \left[ \alpha_v e^{-(\gamma_v + E_3)\tau_v} - E_4 \right].$$

There exists  $t_3 > 0$  such that  $V_m(t) \leq N_2^v + \varepsilon$  for all  $t \geq t_3$ . For  $t > t_3$  let  $u_2(t)$  be a suitable solution of

$$\frac{du_2(t)}{dt} = \alpha_u e^{-(\gamma_u + E_1)\tau_u} u_2(t - \tau_u) - \beta_u u_2^2(t) - E_2 u_2(t) - c_1(N_2^v + \varepsilon) u_2(t).$$

Then, since

$$\frac{dU_m(t)}{dt} = \alpha_u e^{-(\gamma_u + E_1)\tau_u} U_m(t - \tau_u) - \beta_u U_m^2(t) - E_2 U_m(t) - c_1 U(t) V(t) 
\geq \alpha_u e^{-(\gamma_u + E_1)\tau_u} U_m(t - \tau_u) - \beta_u U_m^2(t) - E_2 U_m(t) - c_1 (N_2^v + \varepsilon) U_m(t),$$

we have  $U_m(t) \ge u_2(t)$ . Also

$$\lim_{t \to \infty} u_2(t) = \frac{1}{\beta_u} \left[ \alpha_u e^{-(\gamma_u + E_1)\tau_u} - E_2 - c_1(N_2^v + \varepsilon) \right].$$

Hence

$$\underline{U} \ge \frac{1}{\beta_u} \left[ \alpha_u e^{-\gamma_u + E_1)\tau_u} - E_2 - c_1 (N_2^v + \varepsilon) \right].$$

By the arbitrariness of  $\varepsilon > 0, \, \underline{U} \ge M_2^u$  where

(3.17) 
$$M_2^u = \frac{1}{\beta_u} \left[ \alpha_u e^{-(\gamma_u + E_1)\tau_u} - E_2 - c_1 N_2^v \right].$$

Continuing this process, we obtain two sequences  $N_m^v$ ,  $M_m^u$ ,  $m = 1, 2, 3, \cdots$  such that, for  $m \ge 2$ ,

(3.18) 
$$N_m^v = \frac{1}{\beta_v} \left[ \alpha_v e^{-(\gamma_v + E_3)\tau_v} - E_4 - \frac{\beta_u (\alpha_v e^{-(\gamma_v + E_3)\tau_v} - E_4)}{\alpha_u e^{-(\gamma_u + E_1)\tau_u} - E_2} M_{m-1}^u \right],$$

and

(3.19) 
$$M_m^u = \frac{1}{\beta_u} \left[ \alpha_u e^{-(\gamma_u + E_1)\tau_u} - E_2 - c_1 N_m^v \right].$$

Combining these,

$$N_m^v = \frac{c_1(\alpha_v e^{-(\gamma_v + E_3)\tau_v} - E_4)}{\beta_v(\alpha_u e^{-(\gamma_u + E_1)\tau_u} - E_2)} N_{m-1}^v,$$

which confirms that all the  $N_m^v$  are positive. Furthermore, by assumption (3.14),  $N_m^v \to 0$  as  $m \to \infty$ . Hence, by (3.19),

$$\lim_{m \to \infty} M_m^u = \frac{1}{\beta_u} [\alpha_u e^{-(\gamma_u + E_1)\tau_u} - E_2] = U_B.$$

Therefore

$$\lim_{t \to \infty} U_m(t) = U_B,$$

and

$$\lim_{t \to \infty} V_m(t) = 0.$$

Now we show that  $\lim_{t\to\infty} U_i(t) = \overline{U}_i$ . Since  $U_m(t) \to \overline{U}_m$  then for any  $t \ge T > \tau$ , and solving the first equation of system (1.2) for  $U_i$ , we have

$$U_{i}(t) = U_{i}(T)e^{-(\gamma_{u}+E_{1})(t-T)} + \alpha e^{-(\gamma_{u}+E_{1})t} \int_{T}^{t} e^{(\gamma_{u}+E_{1})s} \left[ U_{m}(s) - e^{-(\gamma_{u}+E_{1})\tau_{u}} U_{m}(s-\tau_{u}) \right] ds.$$

Hence

$$\begin{aligned} \left| U_i(t) - \bar{U}_i \right| &\leq U_i(T) e^{-(\gamma_u + E_1)(t-T)} \\ &+ \left| \alpha_u e^{-(\gamma_u + E_1)t} \int_T^t e^{(\gamma_u + E_1)s} \left[ U_m(s) - e^{-(\gamma_u + E_1)\tau_u} U_m(s-\tau_u) \right] ds - \bar{U}_i \right|. \end{aligned}$$

Now, by using the fact that if  $\lim_{s\to\infty} f(s) = f_0$ , then

$$\lim_{t \to \infty} \int_T^t e^{-(\gamma_u + E_1)(t-s)} f(s) ds = f_0 \lim_{t \to \infty} \int_T^t e^{-(\gamma_u + E_1)(t-s)} ds = f_0(\gamma_u + E_1)^{-1},$$

we have

$$\begin{split} \lim_{t \to \infty} |U_i(t) - \bar{U}_i| &\leq \left| (\gamma_u + E_1)^{-1} \left( \alpha_u \bar{U}_m - \alpha_u e^{-(\gamma_u + E_1)\tau_u} \bar{U}_m \right) - \bar{U}_i \right| \\ &= \left| (\gamma_u + E_1)^{-1} \alpha_u \beta_u^{-1} \left( \alpha_u e^{-(\gamma_u + E_1)\tau_u} - E_2 \right) \left( 1 - e^{-(\gamma_u + E_1)\tau_u} \right) - \bar{U}_i \right| \\ &= 0. \end{split}$$

Therefore, we have

$$\lim_{t \to \infty} U_i(t) = \bar{U}_i.$$

Now, we show that  $\lim_{t\to\infty} V_i(t) = 0$ . The fourth equation of system (1.2) is

$$V'_{i}(t) = \alpha_{v}V_{m}(t) - \gamma_{v}V_{i}(t) - \alpha_{v}e^{-(\gamma_{v} + E_{3})\tau_{v}}V_{m}(t - \tau_{v}) - E_{3}V_{i}(t).$$

Since  $V_m(t) \to 0$  as  $t \to \infty$ , then for  $\varepsilon > 0$ , there exists T > 0 such that, for  $t \ge T$ ,

$$-\varepsilon < \alpha_v V_m(t) - \alpha_v e^{-(\gamma_v + E_3)\tau_v} V_m(t - \tau_v) < \varepsilon.$$

Then, for  $t \geq T$ ,

$$V_i'(t) < \varepsilon - (\gamma_v + E_3)V_i(t).$$

Hence

(3.20) 
$$\limsup_{t \to \infty} V_i(t) \le \frac{\varepsilon}{\gamma_v + E_3}.$$

Also, for  $t \geq T$ ,

$$V_i'(t) > -\varepsilon - (\gamma_v + E_3)V_i(t),$$

which gives

(3.21) 
$$\liminf_{t \to \infty} V_i(t) \ge -\frac{\varepsilon}{\gamma_v + E_3}.$$

Since (3.20) and (3.21) are true for all  $\varepsilon > 0$ , then

$$0 \le \liminf_{t \to \infty} V_i(t) \le \limsup_{t \to \infty} V_i(t) \le 0.$$

Consequently, we have

$$\lim_{t \to \infty} V_i(t) = 0$$

This completes the proof of Theorem 4.

The following theorem is an analogue of Theorem 4, for the situation when the equilibrium  $E_u$  is unstable and  $E_v$  is asymptotically stable. The proof is similar to that of Theorem 4.

**Theorem 5.** Let the initial data (1.3), and (1.4) hold, and assume that

(3.22) 
$$c_2 \left( \alpha_u e^{-(\gamma_u + E_1)\tau_u} - E_2 \right) < \beta_u \left( \alpha_v e^{-(\gamma_v + E_3)\tau_v} - E_4 \right),$$

and

(3.23) 
$$c_1\left(\alpha_v e^{-(\gamma_v + E_3)\tau_v} - E_4\right) > \beta_v\left(\alpha_u e^{-(\gamma_u + E_1)\tau_u} - E_2\right).$$

Then  $(U_i(t), U_m(t), V_i(t), V_m(t)) \rightarrow (0, 0, \overline{V}_i, \overline{V}_m)$  as  $t \rightarrow \infty$ .

# 3.3. Global stability of $\hat{E}$

We will prove that the coexistence equilibrium  $\hat{E}(U_i, U_m, V_i, V_m)$  is globally asymptotically stable. The hypotheses in Theorem 6 below are those which imply linear instability of both  $E_u$  and  $E_v$ . These hypotheses have various ecological interpretations including weak interspecific competitio

**Theorem 6.** Let the initial data (1.3), and (1.4) hold, and assume that

(3.24) 
$$c_2 \left( \alpha_u e^{-(\gamma_u + E_1)\tau_u} - E_2 \right) < \beta_u \left( \alpha_v e^{-(\gamma_v + E_3)\tau_v} - E_4 \right),$$

and

(3.25) 
$$c_1 \left( \alpha_v e^{-(\gamma_v + E_3)\tau_v} - E_4 \right) < \beta_v \left( \alpha_u e^{-(\gamma_u + E_1)\tau_u} - E_2 \right).$$

 $Then \ (U_i(t), U_m(t), V_i(t), V_m(t)) \to (\hat{U}_i, \hat{U}_m, \hat{V}_i, \hat{V}_m) \ as \ t \to \infty.$ 

Proof. Similar to the proof of theorem 4, we can easily have  $(U_i(t), V_i(t)) \rightarrow (\hat{U}_i, \hat{V}_i)$ . Our approach to proving Theorem 4 is similar to prove  $(U_m(t), V_m(t)) \rightarrow (\hat{U}_m, \hat{V}_m)$ , but the situation is more complicated since we shall need four sequences,  $N_m^u, N_m^v$ ,  $M_m^u$  and  $M_m^v$ ,  $m = 1, 2, 3, \cdots$ . It is helpful to remember that  $N_m$  denotes an upper bound, and  $M_m$  a lower bound, on the limsup and liminf respectively as  $t \rightarrow \infty$ , of the variable in the superscript. We shall derive recursion formulae for these bounds and use them to deduce the result.

From positivity of solutions we immediately obtain  $N_1^u$  as follows:

$$\frac{dU_m(t)}{dt} \le \alpha_u e^{-(\gamma_u + E_1)\tau_u} U_m(t - \tau_u) - \beta_u U_m^2(t) - E_2 U_m(t).$$

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Hence

$$\overline{U} = \limsup_{t \to \infty} U_m(t) \le \frac{1}{\beta_u} [\alpha_u e^{-(\gamma_u + E_1)\tau_u} - E_2] := N_1^u.$$

In a similar way, we have

$$\overline{V} \le \frac{1}{\beta_v} \left[ \alpha_v e^{-(\gamma_v + E_3)\tau_v} - E_4 \right] := N_1^v.$$

Let  $\varepsilon > 0$  be sufficiently small that

(3.26) 
$$\varepsilon < \frac{\beta_u \left(\alpha_v e^{-(\gamma_v + E_3)\tau_v} - E_4\right) - c_2 \left(\alpha_u e^{-(\gamma_u + E_1)\tau_u} - E_2\right)}{\beta_u c_2},$$

which is possible by (3.24). Let  $t_1 > 0$  be such that  $U_m(t) \leq N_1^u + \varepsilon$  for all  $t \geq t_1$ , and for  $t > t_1$  let  $m_1^v(t)$  be a solution of

$$\frac{dm_1^v(t)}{dt} = \alpha_v e^{-(\gamma_v + E_3)\tau_v} m_1^v(t-\tau) - \beta_v (m_1^v(t))^2 - c_2 (N_1^u + \varepsilon) m_1^v(t) - E_4 m_1^v(t),$$

with appropriate initial data on  $[t_1 - \tau_v, t_1]$ . Since  $\varepsilon$  satisfies (3.26), Theorem 2 applies and yields

$$\lim_{t \to \infty} m_1^v(t) = \frac{1}{\beta_v} \left[ \alpha_v e^{-(\gamma_v + E_3)\tau_v} - E_4 - c_2(N_1^u + \varepsilon) \right].$$

Since  $N_1^u + \varepsilon \ge U_m(t)$  for  $t \ge t_1$ ,

$$\frac{dV_m(t)}{dt} = \alpha_v e^{-(\gamma_v + E_3)\tau_v} V_m(t-\tau) - \beta_v V_m^2(t) - c_2 U_m(t) V_m(t) - E_4 V_m(t)$$
  

$$\geq \alpha_v e^{-(\gamma_v + E_3)\tau} V_m(t-\tau_v) - \beta_v V_m^2(t) - c_2 (N_1^u + \varepsilon) V_m(t) - E_4 V_m(t),$$

so that  $V_m(t) \ge m_1^v(t)$  and hence

$$\underline{V} = \liminf_{t \to \infty} V_m(t) \ge \lim_{t \to \infty} m_1^v(t) = \frac{1}{\beta_v} \left[ \alpha_v e^{-(\gamma_v + E_3)\tau_v} - E_4 - c_2(N_1^u + \varepsilon) \right].$$

This is true for any  $\varepsilon > 0$  satisfying (3.26) and hence

$$\underline{V} \ge \frac{1}{\beta_v} \left[ \alpha_v e^{-(\gamma_v + E_3)\tau_v} - E_4 - c_2 N_1^u \right] := M_1^v.$$

In exactly the same way, we can show that

$$\underline{U} \ge \frac{1}{\beta_u} \left[ \alpha_u e^{-(\gamma_u + E_1)\tau_u} - E_2 - c_1 N_1^v \right] := M_1^u,$$

and, in doing so, the assumption (3.25) is used.

We shall now show how to find new upper bounds  $N_2^u$ ,  $N_2^v$  in terms of the old lower bounds  $M_1^v$ ,  $M_1^u$  respectively. New lower bounds are then found from the *new*  upper bounds by following the procedure already described. It will then be clear how to proceed from the (m-1) th to the m th step in this process.n and significant adult mortality.

Let  $\varepsilon > 0$ . There exists  $t_2 > 0$  such that  $V_m(t) \ge M_1^v - \varepsilon$  for all  $t \ge t_2$ . Then, for  $t \ge t_2$ ,

$$\frac{dU_m(t)}{dt} = \alpha_u e^{-(\gamma_u + E_1)\tau_u} U_m(t - \tau_u) - \beta_u U_m^2(t) - c_1 U_m(t) V_m(t) - E_2 U_m(t) 
\leq \alpha_u e^{-(\gamma_u + E_1)\tau_u} U_m(t - \tau) - \beta_u U^2(t) - c_1 (M_1^v - \varepsilon) U_m(t) - E_2 U_m(t).$$

Thus, if for  $t > t_2$  we denote by  $n_2^u(t)$  the solution of

$$\frac{dn_2^u(t)}{dt} = \alpha_u e^{-(\gamma_u + E_1)\tau_u} n_2^u(t-\tau) - \beta_u (n_2^u(t))^2 - c_1 (M_1^v - \varepsilon) n_2^u(t) - E_2 n_2^u(t),$$

with appropriate initial data, then  $U_m(t) \leq n_2^u(t)$  and thus

$$\overline{U} \leq \lim_{t \to \infty} n_2^u(t) = \frac{1}{\beta_u} \left[ \alpha_u e^{-(\gamma_u + E_1)\tau_u} - E_2 - c_1(M_1^v - \varepsilon) \right],$$

(we have used assumption (3.25) to deduce that  $n_2^u(t)$  has this limiting behaviour). Since  $\varepsilon > 0$  is arbitrary,

$$\overline{U} \le \frac{1}{\beta_u} \left[ \alpha_u e^{-(\gamma_u + E_1)\tau_u} - E_2 - c_1 M_1^v \right] := N_2^u.$$

In the same way, and using (3.24), we deduce the following estimate for  $\overline{V}$ :

$$\overline{V} \le \frac{1}{\beta_v} \left[ \alpha_v e^{-(\gamma_v + E_3)\tau_v} - E_4 - c_2 M_1^u \right] := N_2^v.$$

One now sees that the transition from the (m-1) th to the m th step in this iterative process is given by

$$\begin{split} N_m^u &= \frac{1}{\beta_u} \left[ \alpha_u e^{-(\gamma_u + E_1)\tau_u} - E_2 - c_1 M_{m-1}^v \right], \\ N_m^v &= \frac{1}{\beta_v} \left[ \alpha_v e^{-(\gamma_v + E_3)\tau_v} - E_4 - c_2 M_{m-1}^u \right], \\ M_m^u &= \frac{1}{\beta_u} \left[ \alpha_u e^{-(\gamma_u + E_1)\tau_u} - E_2 - c_1 N_m^v \right], \\ M_m^v &= \frac{1}{\beta_v} \left[ \alpha_v e^{-(\gamma_v + E_3)\tau_v} - E_4 - c_2 N_m^u \right], \end{split}$$

and, of course,

$$M_m^u \leq \underline{U} \leq \overline{U} \leq N_m^u \quad \text{ and } \quad M_m^v \leq \underline{V} \leq \overline{V} \leq N_m^v,$$

for each  $m = 1, 2, 3, \cdots$ . We need to show that  $M_m^u$  and  $N_m^u$  both approach  $\hat{U}_m$  as  $m \to \infty$ , and that  $M_m^v$  and  $N_m^v$  both approach  $\hat{V}_m$ .

We see at once that

(3.27) 
$$N_m^u = \frac{\alpha_u \beta_v e^{-(\gamma_u + E_1)\tau_u} - c_1 \alpha_v e^{-(\gamma_v + E_3)\tau_v}}{\beta_u \beta_v} + \frac{c_1 c_2}{\beta_u \beta_v} N_{m-1}^u.$$

Note that (3.24) and (3.25) imply that

$$\frac{c_1 c_2}{\beta_u \beta_v} < 1.$$

We claim that  $N_m^u$  is a monotonically decreasing sequence that is bounded below by  $\hat{U}_m$ . The boundedness below by  $\hat{U}_m$  follows immediately from (3.27) by induction. Then, by (3.27), and using (3.25),

$$\frac{N_m^u}{N_{m-1}^u} = \frac{\alpha_u \beta_v e^{-(\gamma_u + E_1)\tau_u} - c_1 \alpha_v e^{-(\gamma_v + E_3)\tau_v}}{\beta_u \beta_v N_{m-1}^u} + \frac{c_1 c_2}{\beta_u \beta_v} \\
\leq \frac{\alpha_u \beta_v e^{-(\gamma_u + E_1)\tau_u} - c_1 \alpha_v e^{-(\gamma_v + E_3)\tau_v}}{\beta_u \beta_v \hat{U}_m} + \frac{c_1 c_2}{\beta_u \beta_v} \\
= 1,$$

so that  $N_m^u$  is monotonically decreasing. Hence  $N_m^u$  converges to a limit which, by (3.27), equals  $\hat{U}_m$ .

Of course, convergence of  $N_m^u$  implies convergence of  $M_m^v$ , and it is easily checked that  $M_m^v$  has the limit  $\hat{V}_m$ . The analysis for the remaining two sequences is similar. The proof of the theorem is complete.

#### 4. Optimal harvesting policy of system (1.2)

Harvesting the species affects the mortality rate and, if it is not excessive, the population adjusts and settles down to a new equilibrium state. So that the modelling problem is how to maximize the sustained yield by determining the population growth dynamics so as to fix the harvesting rate which keeps the population at its maximum growth rate. Therefore, in this section, we will investigate the maximum sustainable yield, the optimal harvesting policy, namely, the optimal harvesting effort, when the matures of system (1.2) are harvested. Generally, the population exploitation should be of the mature population, which is more appropriate to the economic and biological views of renewable resource management.

**Case 1.** The optimal harvesting policy when the mature population  $U_m$  and  $V_m$  are harvested respectively.

If only the mature species  $U_m$  or  $V_m$  is subject to be harvested, then we have the following theorem

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## Theorem 7.

(I) If  $\beta_v \alpha_u e^{-\gamma_u \tau_u} > c_1 \alpha_v e^{-\gamma_v \tau_v}$ , then the maximum sustainable yield is

$$Y_{u} = E_{2}^{*}U_{m}^{*} = \frac{(\beta_{v}\alpha_{u}e^{-\gamma_{u}\tau_{u}} - c_{1}\alpha_{v}e^{-\gamma_{v}\tau_{v}})^{2}}{4\beta_{v}\left(\beta_{u}\beta_{v} - c_{1}c_{2}\right)},$$

where, the optimal harvesting effort

$$E_2^* = \frac{\left(\beta_v \alpha_u e^{-\gamma_u \tau_u} - c_1 \alpha_v e^{-\gamma_v \tau_v}\right)}{2\beta_v},$$

and the optimal population level

$$U_m^* = \frac{\left(\beta_v \alpha_u e^{-\gamma_u \tau_u} - c_1 \alpha_v e^{-\gamma_v \tau_v}\right)}{2\left(\beta_u \beta_v - c_1 c_2\right)}.$$

(II) If  $\beta_u \alpha_v e^{-\gamma_v \tau_v} > c_2 \alpha_u e^{-\gamma_u \tau_u}$ , then the maximum sustainable yield is

$$Y_{v} = E_{4}^{*} V_{m}^{*} = \frac{\left(\beta_{u} \alpha_{v} e^{-\gamma_{v} \tau_{v}} - c_{2} \alpha_{u} e^{-\gamma_{u} \tau_{u}}\right)^{2}}{4\beta_{u} \left(\beta_{u} \beta_{v} - c_{1} c_{2}\right)},$$

where, the optimal harvesting effort

$$E_4^* = \frac{\left(\beta_u \alpha_v e^{-\gamma_v \tau_v} - c_2 \alpha_u e^{-\gamma_u \tau_u}\right)}{2\beta_u},$$

and the optimal population level

$$V_m^* = \frac{\left(\beta_u \alpha_v e^{-\gamma_v \tau_v} - c_2 \alpha_u e^{-\gamma_u \tau_u}\right)}{2\left(\beta_u \beta_v - c_1 c_2\right)}.$$

*Proof.* (I) Let  $U_m = \hat{U}_m$ , the the harvesting of system (1.2) is

$$Y_{u} = E_{2}\hat{U}_{m} = E_{2} \left[ \frac{\beta_{v}(\alpha_{u}e^{-\gamma_{u}\tau_{u}} - E_{2}) - c_{1}\alpha_{v}e^{-\gamma_{v}\tau_{v}}}{\beta_{u}\beta_{v} - c_{1}c_{2}} \right].$$

In order to get the maximum sustainable yield, we calculate the derivative of  $Y_1(E_2)$  for  $E_2$ , we have

$$\frac{dY_u}{dE_2} = \frac{-2\beta_v E_2 + \beta_v \alpha_u e^{-\gamma_u \tau_u} - c_1 \alpha_v e^{-\gamma_v \tau_v}}{\beta_u \beta_v - c_1 c_2} = 0,$$

which gives the optimal harvesting effort

$$E_2^* = \frac{\left(\beta_v \alpha_u e^{-\gamma_u \tau_u} - c_1 \alpha_v e^{-\gamma_v \tau_v}\right)}{2\beta_v},$$

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and substituting this into  $\hat{U}_m$ , we will have the optimal population level

$$U_m^* = \frac{\left(\beta_v \alpha_u e^{-\gamma_u \tau_u} - c_1 \alpha_v e^{-\gamma_v \tau_v}\right)}{2\left(\beta_u \beta_v - c_1 c_2\right)}$$

Therefore, the maximum sustainable yield is  $Y_u = E_2^* U_m^*$ . Similarly we can prove part (**II**) of the Theorem.

**Case2.** The optimal harvesting policy when the mature populations  $U_m$  and  $V_m$  are harvested simultaneously.

**Theorem 8.** The maximum sustainable yield in system (1.2) is

$$Y_{MSY} = E_2^* U_m^* + E_4^* V_m^*,$$

where, the optimal harvesting efforts  $E_2^*$  and  $E_4^*$  are given in the proof below, provided  $E_2^*, E_4^* > 0$ .

*Proof.* The second and fourth equations of system (1.2) are

$$\frac{dU_m(t)}{dt} = \alpha_u e^{-(\gamma_u + E_1)\tau_u} U_m(t - \tau_u) - \beta_u U_m^2(t) - c_1 U_m(t) V_m(t) - E_2 U_m(t),$$

$$\frac{dV_m(t)}{dt} = \alpha_v e^{-(\gamma_v + E_3)\tau_v} V_m(t - \tau_v) - \beta_v V_m^2(t) - c_2 U_m(t) V_m(t) - E_4 V_m(t).$$

If conditions (3.24) and (3.25) are satisfied, then the only nonnegative equilibrium is  $\hat{E}(\hat{U}_i, \hat{U}_m, \hat{V}_i, \hat{V}_m)$  which is globally asymptotically stable. Therefore, to have the maximum sustainable yield, that is, to have the maximum values of equation  $Y(E_2, E_4) = E_2 \hat{U}_m + E_4 \hat{V}_m$ , we have to solve

$$\frac{\partial Y}{\partial E_2} = -2\beta_v E_2 + \beta_v \alpha_u e^{-\gamma_u \tau_u} - c_1 \alpha_v e^{-\gamma_v \tau_v} + (c_1 + c_2)E_4 = 0$$

and

$$\frac{\partial Y}{\partial E_4} = -2\beta_u E_4 + \beta_u \alpha_v e^{-\gamma_v \tau_v} - c_2 \alpha_u e^{-\gamma_u \tau_u} + (c_1 + c_2)E_2 = 0.$$

Then by solving these two equations we get the optimal harvesting effort  $E_2^*$  and  $E_4^*$ , where

$$E_{2}^{*} = \frac{\alpha_{u}e^{-\gamma_{u}\tau_{u}} \left(2\beta_{u}\beta_{v} - c_{1}c_{2} - c_{2}^{2}\right) + \alpha_{v}\beta_{u}e^{-\gamma_{v}\tau_{v}} \left(c_{2} - c_{1}\right)}{4\beta_{u}\beta_{v} - \left(c_{1} + c_{2}\right)^{2}},$$

and

$$E_{4}^{*} = \frac{\alpha_{u}\beta_{v}e^{-\gamma_{u}\tau_{u}}\left(c_{1}-c_{2}\right) + \alpha_{v}e^{-\gamma_{v}\tau_{v}}\left(2\beta_{u}\beta_{v}-c_{1}c_{2}-c_{1}^{2}\right)}{4\beta_{u}\beta_{v}-\left(c_{1}+c_{2}\right)^{2}},$$

and the optimal population levels are given by

$$U_m^* = \frac{\beta_v(\alpha_u e^{-\gamma_u \tau_u} - E_2^*) - c_1(\alpha_v e^{-\gamma_v \tau_v} - E_4^*)}{\beta_u \beta_v - c_1 c_2}$$
  
=  $\frac{2\beta_v \alpha_u e^{-\gamma_u \tau_u} - \alpha_v (c_1 + c_2) e^{-\gamma_v \tau_v}}{4\beta_u \beta_v - (c_1 + c_2)^2}$ 

and,

$$V_m^* = \frac{\beta_u(\alpha_v e^{-\gamma_v \tau_v} - E_4^*) - c_2(\alpha_u e^{-\gamma_u \tau_u} - E_2^*)}{\beta_u \beta_v - c_1 c_2}$$
  
=  $\frac{2\beta_u \alpha_v e^{-\gamma_v \tau_v} - \alpha_u (c_1 + c_2) e^{-\gamma_u \tau_u}}{4\beta_u \beta_v - (c_1 + c_2)^2}.$ 

Therefore, the maximum sustainable yield, will be

$$Y_{MSY} = E_2^* U_m^* + E_4^* V_m^*$$
  
=  $\frac{1}{\left(4\beta_u \beta_v - (c_1 + c_2)^2\right)^2} \left[\alpha_u^2 \beta_v \left(4\beta_u \beta_v - (c_1 + c_2)^2\right) e^{-2\gamma_u \tau_u} + \alpha_v^2 \beta_u \left(4\beta_u \beta_v - (c_1 + c_2)^2\right) e^{-2\gamma_v \tau_v} + (\alpha_u \alpha_v c_1 c_2 (3c_1 - c_2) - 4\alpha_u \alpha_v \beta_u \beta_v (c_1 + c_2) + \alpha_u \alpha_v (c_1^3 + c_2^3)) e^{-\gamma_u \tau_u} e^{-\gamma_v \tau_v}\right].$ 

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### 5. Discussion

In this paper, we have studied the dynamics of a two competitive stagestructured population model, where the population has two life stages, immature and mature, when the immature and mature of both species are harvested. The equilibria of our model involve the maturation delays and the harvesting effort for the immatures and the matures of each species. Therefore, the dynamics depends heavily on the maturation delays and the harvesting effort. To see the role of these, it is helpful to consider the particular case of the criteria for species  $U_m$  to win and species  $V_m$  to be driven to extinction Theorem 4, that is

$$c_2\left(\alpha_u e^{-(\gamma_u + E_1)\tau_u} - E_2\right) > \beta_u\left(\alpha_v e^{-(\gamma_v + E_3)\tau_v} - E_4\right),$$
$$c_1\left(\alpha_v e^{-(\gamma_v + E_3)\tau_v} - E_4\right) < \beta_v\left(\alpha_u e^{-(\gamma_u + E_1)\tau_u} - E_2\right).$$

and

These conditions are automatically satisfied if the  $V_m$  species has long maturation time  $\tau_v$ , a large immature mortality rate  $\gamma_v$ , insufficient live births or eggs laid per adult per unit time (this is what  $\alpha_v$  represents), or significant harvesting effort among the immature species  $V_i$ , as measured by  $E_3$ .

We obtained that  $E_2 = \alpha_u e^{-\gamma_u \tau_u}$  and  $E_4 = \alpha_v e^{-\gamma_v \tau_v}$  are thresholds of harvesting for the mature populations  $U_m$  and  $V_m$ , respectively. We showed that there exists a globally asymptotically stable equilibria for this model. That is, all populations with positive initial functions tend to a constant population level. The optimal harvest effort that maximize the sustainable yield and the corresponding optimal population level are also determined.

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