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NUTRIENT-PHYTOPLANKTON-ZOOPLANKTON INTERACTION WITH VARIABLE YIELDS

Abstract. A three dimensional predator-prey-resource model is proposed and analyzed to study the dynamics of the system with resource-dependent yields of the organisms. Our analysis leads to different thresholds in terms of the model parameters acting as conditions under which the organisms associated with the system cannot thrive even in the absence of predation. Local stability of the system is obtained in the absence of one or more of the predators and in the presence of all the predators. Under appropriate circumstances global stability of the system is obtained in the absence of the predator at the highest trophic level. Moreover, it is shown that the system undergoes Hopf bifurcation if the break-even concentration crosses a certain critical value. Computer simulations have been carried out to illustrate various analytical results.

1. Introduction. In several ecological models the consumption rate of resource by an organism is assumed to be a constant multiple of resource uptake. The constant of proportionality is called the *growth yield constant.* Under the assumption of constant yield, mathematical models failed to describe non-linear phenomena like sustained oscillations, whereas experimental results exhibit oscillations [4, 10]. The growth of plankton on resource is in two steps: initially it uptakes the resource in the cell, and then uses the intracellular nutrient for the growth of cell. As a result, the ratio between cells growth rate and nutrient consumption rate is no more constant [7, 15].

We have considered a food chain model where there is a constant flow of input nutrient. Phytoplankton is growing on the nutrient at the first trophic level. Zooplankton uptakes phytoplankton by means of continuous filtering. If the yield coefficient is constant, then both these organisms are assumed to follow Holling type II functional response [16]. As observed by Jang and

Balgama [7], enrichment of some nutrients can inhibit the growth of phyto-plankton. Also, proliferation of phytoplankton reduces the dissolved oxygen content, leading to an inhibitory effect on the growth rate of zooplankton [8]. By assuming that yield as an increasing function of resource concentration, the functional response becomes unimodal and non-monotonic [12]. With this in mind, we consider a predator-prey-resource model and compare the dynamic behaviour of the system with variable yields of the organisms. The objective of our study is to explore the dynamics resulting from the consideration of yields which are functions of available resource.

In the present paper the main emphasis will be put on studying the stability of the system with variable yields. We have studied the model analytically, with the proofs all deferred to the Appendix. Numerical studies have been carried out by considering linear and quadratic yields of the organisms separately.

2. The basic model. We take the model of a simple food chain [6, 16] in which there is a constant supply of nutrient, whose concentration at time t is $S(t)$. Phytoplankton is growing on that nutrient with concentration $x(t)$ at time t. Zooplankton is introduced in the system with concentration $y(t)$ at time t, predating on phytoplankton only.

The basic equations with all the parameters are

(1)
$$\frac{dS}{dt} = (S^0 - S)D_1 - \frac{m_1 S x}{(a_1 + S)\gamma_1(S)},$$
$$\frac{dx}{dt} = x\left[\frac{m_1 S}{a_1 + S} - D_2 - \frac{m_2 y}{(a_2 + x)\gamma_2(x)}\right],$$
$$\frac{dy}{dt} = y\left(\frac{m_2 x}{a_2 + x} - D_3\right),$$

where $S(0) = S_0 \geq 0$, $x(0) = x_0 \geq 0$, $y(0) = y_0 \geq 0$.

Here S^0 is the input nutrient concentration, D_1 is the dilution (or washout) rate of nutrient, D_i $(i = 2, 3)$ are the death rates of the organisms. Also, m_i are the maximal growth rates, a_i are the half saturation constants $(i = 1, 2)$, which are the nutrient concentrations at which the functional response of the organism is half maximal. $\gamma_1(S)$ and $\gamma_2(x)$ are the resource-dependent yields of phytoplankton and zooplankton respectively; all of these are positive quantities [2]. Also, S^0 and D_1 are environmental variables while $m_i, a_i, D_2, D_3, \gamma_1(S)$ and $\gamma_2(x)$ are properties of the organisms [5].

In this paper we have taken $\gamma_1(S) = \beta_1 + \alpha_1 S^n$ and $\gamma_2(x) = \beta_2 + \alpha_2 x^n$ $(n = 0, 1, 2)$ where α_i, β_i are parameters associated with the yields so that $\gamma_i < 1$ $(i = 1, 2)$.

In the system (1), the functional response of plankton is of the form $p(u) = f(u)/\gamma(u)$, where $f(u) = mu/(a+u)$ is Holling II functional response.
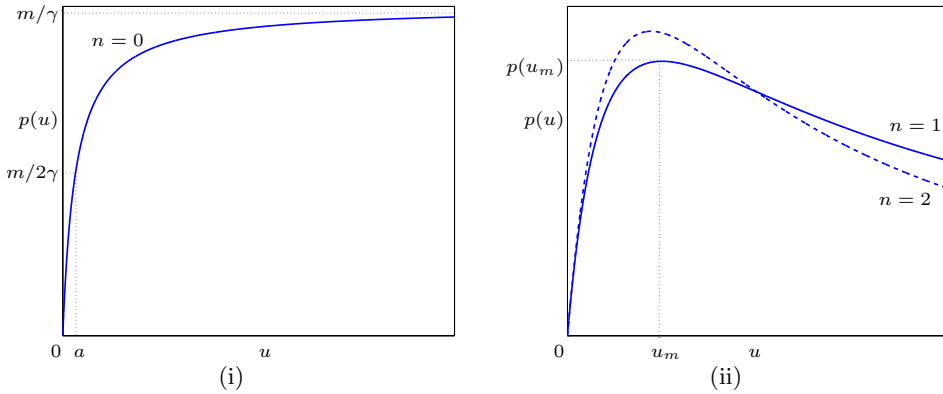
Fig. 1. (i) For $n = 0$ the functional response is Holling II. (ii) The functional responses corresponding to $n = 1$ (solid) and $n = 2$ (dotted) are unimodal and hence non-monotonic.

Taking $\gamma(u) = \beta + \alpha u$, we see that $p(u)$ is increasing for $0 \leq u \leq \sqrt{a\beta/\alpha}$ and decreasing for $u > \sqrt{a\beta/\alpha}$. In the non-monotonic case $p(u)$ reaches its maximum at $u_m = \sqrt{a\beta/\alpha}$ with $p(u_m) = m/(\sqrt{\beta} + \sqrt{a\alpha})^2$. Also, for $\gamma(u) = \beta + \alpha u^2$, the functional response is non-monotonic and unimodal (cf. Fig. 1).

3. A non-dimensionalization of the problem. Let us change the variables of the system (1) to non-dimensional ones [5] by making the substitutions $\bar{S} = S/S^0$, $\bar{x} = x/S^0$, $\bar{y} = y/S^0$, $\bar{t} = D_1 t$, $\bar{a}_1 = a_1/S^0$, $\bar{a}_2 = a_2/S^0$, $\bar{m}_1 = m_1/D_1$, $\bar{m}_2 = m_2/D_1$, $\bar{\gamma}_1(\bar{S}) = \gamma_1(S^0\bar{S})$, $\bar{\gamma}_2(\bar{x}) = \gamma_2(S^0\bar{x})$, $\bar{D}_2 = D_2/D_1$, $\bar{D}_3 = D_3/D_1$.

The $\bar{\gamma}_1(\bar{S}) = \beta_1 + \alpha_1(S^0\bar{S})^n$ and $\bar{\gamma}_2(\bar{x}) = \beta_2 + \alpha_2(S^0\bar{x})^n$ $(n = 1, 2)$.

Under these substitutions, on dropping the bars the system (1) reduces to

$$\frac{dU}{dt} = f(U)$$

where $U = [S \ x \ y]^T$ and $f(U) = [F \ G \ H]^T$ with

$$F \equiv F(S, x, y) = 1 - S - x\frac{p_1(S)}{\gamma_1(S)},$$

$$G \equiv G(S, x, y) = x(p_1(S) - D_2) - y\frac{p_2(x)}{\gamma_2(x)},$$

$$H \equiv H(S, x, y) = y(p_2(x) - D_3),$$

with

$$p_1(S) = \frac{m_1 S}{a_1 + S}, \quad p_2(x) = \frac{m_2 x}{a_2 + x},$$
$$S(0) = S_0 \geq 0, \quad x(0) = x_0 \geq 0, \quad y(0) = y_0 \geq 0.$$

The parameters have been scaled by the operating environment, determined by S^0 and D_i. The variables are non-dimensional and the parameters are scaled relative to this environment.

4. Boundedness of the system

THEOREM 4.1. *For all $\epsilon > 0$, there exists $t_\epsilon > 0$ such that all the solutions of* (1) *enter into the set $\{(S, x, y) \in \mathbb{R}^3 : S(t) + x(t) + y(t) \leq 1/D + \epsilon\}$ whenever $t \geq t_\epsilon$, where $D = \min\{1, D_2, D_3\}$.*

Let us define

$$\lambda_i = \frac{a_i D_{i+1}}{m_i - D_{i+1}} \quad \text{for } m_i > D_{i+1} \ (i = 1, 2).$$

Then λ_1 represents the *break-even concentration*, the concentration of nutrient for the growth of phytoplankton in the absence of zooplankton in steady state. Thus, the break-even concentration λ_1 satisfies the condition $p_1(\lambda_1) = D_2$; it represents the value of S for which the growth $p_1(S)$ of x is balanced by the death rate D_2. And λ_2 represents the break-even concentration of phytoplankton for the growth of zooplankton.

The following theorem states a condition under which the species cannot survive even in the absence of predation:

THEOREM 4.2.

(i) *If $m_1 \leq D_2$, then $\lim_{t \to \infty} x(t) = 0 = \lim_{t \to \infty} y(t)$.*
(ii) *If $m_1 > D_2$ and $\lambda_1 > 1$, then $\lim_{t \to \infty} x(t) = 0 = \lim_{t \to \infty} y(t)$.*
(iii) *If $m_2 \leq D_3$, then $\lim_{t \to \infty} y(t) = 0$.*
(iv) *If $m_2 > D_3$ and $\lambda_2 > 1/D$, then $\lim_{t \to \infty} y(t) = 0$.*

This theorem states that:

(i) If the maximal growth rate of phytoplankton is less than or equal to its death rate then phytoplankton and zooplankton will go to extinction.

(ii) If the maximal growth rate of phytoplankton is greater than its death rate and the break even concentration λ_1 is greater than unity, then none of the planktons will survive in the system.

(iii) If the maximal growth rate of zooplankton is less than or equal to its death rate then zooplankton will not survive in the system.

(iv) If the maximal growth rate of zooplankton is greater than its death rate and the break-even concentration λ_2 is greater than $1/D$, then zooplankton will become extinct.

5. Equilibria and their stability. The system (1) possesses the following equilibria:

(i) phytoplankton and zooplankton free equilibrium $E_0 = (1, 0, 0)$;
(ii) zooplankton free equilibrium $E_1 = \left(\lambda_1, \frac{1 - \lambda_1}{D_2} \gamma_1(\lambda_1), 0\right)$;

(iii) the equilibrium of coexistence $E^* = (S^*, \lambda_2, y^*)$, where S^* is a positive root of the equation $(S - 1)\gamma_1(S) + \lambda_2 p_1(S) = 0$ and $y^* = \frac{\lambda_2(p_1(S^*) - 1)\gamma_2(\lambda_2)}{D_3}$.

The organism-free equilibrium E_0 always exists. The zooplankton-free equilibrium E_1 will exist if $\lambda_1 < 1$. Also, the equilibrium of coexistence will exist if $\lambda_1 < 1$ and $\lambda_2 < 1/D$.

We analyze the local stability of system (1) by using eigenvalue analysis of the Jacobian matrix evaluated at the appropriate equilibrium. The detailed calculations are given in the Appendix.

LEMMA 5.1. *The critical point $E_0 = (1, 0, 0)$ of the system (1) is locally asymptotically stable if $\lambda_1 > 1$.*

Local stability at E_0 implies the non-existence of the equilibria E_1 and E^*.

LEMMA 5.2. *The critical point $E_1\left(\lambda_1, \frac{1-\lambda_1}{D_2}\gamma_1(\lambda_1), 0\right)$ of the system (1) is locally asymptotically stable if $\lambda_1 < 1$ and $D_2 > D_0$, where*

$$D_0 = \max\left\{\frac{m_1\lambda_1^2}{a_1}\left(\frac{\gamma_1'(\lambda_1)}{\gamma_1(\lambda_1)} - \frac{1}{1-\lambda_1}\right), \frac{(1-\lambda_1)\gamma_1(\lambda_1)}{\lambda_2}\right\}.$$

Local stability at E_1 implies that E_0 is a saddle point and E^* is non-existent. All the organisms in the system will persist if $\lim_{t\to\infty} u(t) > 0$ for each organism $u(t)$. The condition given in the following lemma rules out the possibility of extinction of any organism in the system [14].

LEMMA 5.3. *If $\lambda_1 < 1$ and $\lambda_2 \leq (1-\lambda_1)\gamma_1(\lambda_1)/D_2$ then all the three organisms will persist in the system.*

Having established the existence and uniqueness of the positive steady state E^*, we now turn our attention to its local stability.

LEMMA 5.4. *The positive equilibrium $E^*(S^*, \lambda_2, y^*)$ of the system (1) is locally asymptotically stable if $A, B, C > 0$ and $AB > C$, where*

$$A = D_2 + 1 - p_1(S^*) + y^*\left(\frac{p_2}{\gamma_2}\right)'_{x=\lambda_2} + \lambda_2\left(\frac{p_1}{\gamma_1}\right)'_{S=S^*},$$

$$B = D_2 - p_1(S^*) + y^*\left(\frac{p_2}{\gamma_2}\right)'_{x=\lambda_2} + D_2\lambda_2\left(\frac{p_1}{\gamma_1}\right)'_{S=S^*}$$
$$+ \lambda_2 p_1^2(S^*)\frac{\gamma_1'(S^*)}{\gamma_1^2(S^*)} + y^* D_3\frac{p_2'(\lambda_2)}{\gamma_2(\lambda_2)} + \lambda_2 y^*\left(\frac{p_1}{\gamma_1}\right)'_{S=S^*}\left(\frac{p_2}{\gamma_2}\right)'_{x=\lambda_2},$$

$$C = y^* D_3\frac{p_2'(\lambda_2)}{\gamma_2(\lambda_2)}\left\{1 + \lambda_2\left(\frac{p_1}{\gamma_1}\right)'_{S=S^*}\right\}.$$

LEMMA 5.5. *The system* (1) *has no periodic solution around the positive equilibrium* E^* *if* $m_1 < L$ *where*

$$L = \min\left\{ D_2 - D_3 + y^* \left(\frac{p_2}{\gamma_2}\right)'_{\lambda_2}, 1 - y^* p_2'(\lambda_2) + \lambda_2 \left(\frac{p_1}{\gamma_1}\right)'_{S^*}, \right.$$

$$\left. D_2 - \lambda_2 p_1'(S^*) + y^* \left(\frac{p_2}{\gamma_2}\right)'_{\lambda_2} \right\}.$$

COROLLARY 5.1. *If the conditions stated in Lemma* 5.3 *and* 5.5 *both hold, then the interior equilibrium is locally asymptotically stable.*

Next we study the global asymptotic stability of the system at E_1. The system (1) is studied, and a globally attractive positively invariant set is found using a suitable Lyapunov function. As a result, we find sufficient conditions for the stability of the equilibrium in the absence of zooplankton.

LEMMA 5.6. *The critical point* $E_1(\lambda_1, (1 - \lambda_1)\gamma_1(\lambda_1), 0)$ *of the system* (1) *is globally asymptotically stable if*

$$\frac{S\Phi(S)}{\gamma_2(S)(a_1 + S\lambda_1)} \le \frac{\gamma_{(\lambda_1)}}{m_1 \lambda_1 \left\{ \frac{1-\lambda_1}{D_2} \gamma_1(\lambda_1) + \epsilon_0 \right\}},$$

where $\Phi(S) = \alpha_1 S^0$ *for linear yields* $(n = 1)$, *and* $\Phi(S) = \alpha_1 (S^0)^2 (S + \lambda_1)$ *for quadratic yields* $(n = 2)$.

6. Hopf bifurcation. We choose λ_2 as bifurcation parameter. The characteristic equation of the variational matrix at E^* is $\mu^3 + A\mu^2 + B\mu + C = 0$, where

$$A = -(G_x|_{E^*} + F_S|_{E^*}) = 2 - p_1(S^*) + y^* \left(\frac{p_2(x)}{\gamma_2(x)}\right)'_{x=\lambda_2} + \lambda_2 \left(\frac{p_1(S)}{\gamma_1(S)}\right)'_{S=S^*},$$

$$B = 1 + \lambda_2 \left(\frac{p_1(S)}{\gamma_1(S)}\right)'_{S^*} + y^* \left(\frac{p_2(x)}{\gamma_2(x)}\right)'_{\lambda_2} + \lambda_2 y^* \left(\frac{p_2(x)}{\gamma_2(x)}\right)'_{\lambda_2} \left(\frac{p_1(S)}{\gamma_1(S)}\right)'_{S^*}$$

$$- p_1(S^*) - p_1(S^*)\lambda_2 \left(\frac{p_1(S)}{\gamma_1(S)}\right)'_{S^*} + y^* \frac{p_2'(\lambda_2)}{\gamma_2(\lambda_2)} + \frac{\lambda_2 p_1'(S^*) p_1(S^*)}{\gamma_1(S^*)},$$

$$C = -\frac{y^* p_2'(\lambda_2)}{\gamma_2(\lambda_2)} F_S|_{E^*} = \frac{y^* p_2'(\lambda_2)}{\gamma_2(\lambda_2)} \left(1 + \lambda_2 \left(\frac{p_1(S)}{\gamma_1(S)}\right)'_{S^*}\right).$$

Necessary and sufficient conditions for Hopf bifurcation to occur at $\lambda_2 = \lambda_{\mathrm{cr}}$ are that

   (i) $A(\lambda_{\mathrm{cr}}) > 0, B(\lambda_{\mathrm{cr}}) > 0$ and $C(\lambda_{\mathrm{cr}}) > 0$,
   (ii) $C(\lambda_{\mathrm{cr}}) = A(\lambda_{\mathrm{cr}})B(\lambda_{\mathrm{cr}})$,
   (iii) $\mathrm{Re}\left[\frac{d\mu_j}{d\lambda_2}\right]_{\lambda_2=\lambda_{\mathrm{cr}}} \ne 0, j = 1, 2, 3$.

Condition (i) will be satisfied if

$$D_2 > D_H = \max\{d_1, d_2\} \quad \text{and} \quad 1 + \lambda_2(p_1/\gamma_1)'_{S^*} > 0 \quad \text{where}$$

$$d_1 = p_1(S^*) - 1 - y^* \left(\frac{p_2}{\gamma_2}\right)'_{\lambda_{\text{cr}}} - \lambda_{\text{cr}} \left(\frac{p_1}{\gamma_1}\right)'_{S^*},$$

$$d_2 = \frac{p_1(S^*)\left\{1 - \lambda_{\text{cr}}p_1(S^*)\frac{\gamma_1'(S^*)}{\gamma_1^2(S^*)}\right\} - y^*\left\{\left(\frac{p_2}{\gamma_2}\right)'_{\lambda_{\text{cr}}} - \frac{D_3 p_2'(\lambda_{\text{cr}})}{\gamma_2(\lambda_{\text{cr}})} - \lambda_{\text{cr}}\left(\frac{p_1}{\gamma_1}\right)'_{S^*}\left(\frac{p_2}{\gamma_2}\right)'_{\lambda_{\text{cr}}}\right\}}{\left\{1 + \lambda_{\text{cr}}\left(\frac{p_1}{\gamma_1}\right)'_{S^*}\right\}}.$$

For $\lambda_2 = \lambda_{\text{cr}}$, the characteristic equation becomes $(\mu + A)(\mu^2 + B) = 0$, hence $\mu = -A, \pm i\sqrt{B}$.

For $\lambda \in (\lambda_{\text{cr}} - \epsilon, \lambda_{\text{cr}} + \epsilon)$, the roots are in general of the form

$$\mu_1(\lambda) = \beta_1(\lambda) + i\beta_2(\lambda),$$
$$\mu_2(\lambda) = \beta_1(\lambda) - i\beta_2(\lambda),$$
$$\mu_3(\lambda) = -A(\lambda).$$

Therefore, $\frac{d}{d\lambda}(\mu^3 + A\mu^2 + B\mu + C) = 0$ gives

$$(K + iL)\frac{d\mu}{d\lambda} + (M + iN) = 0,$$

where

$$K(\lambda) = 3\beta_1^2(\lambda) - 3\beta_2^2(\lambda) + 2A(\lambda)\beta_1(\lambda) + B(\lambda),$$
$$L(\lambda) = 6\beta_1(\lambda)\beta_2(\lambda) + 2A(\lambda)\beta_2(\lambda),$$
$$M(\lambda) = C'(\lambda) + \{\beta_1^2(\lambda) - \beta_2^2(\lambda)\}A'(\lambda) + \beta_1 B'(\lambda),$$
$$N(\lambda) = 2\beta_1(\lambda)\beta_2(\lambda)A'(\lambda) + \beta_2(\lambda)B'(\lambda).$$

Therefore,

$$\frac{d\mu}{d\lambda} = -\frac{\{M(\lambda)K(\lambda) + N(\lambda)L(\lambda)\} + i\{N(\lambda)K(\lambda) - M(\lambda)L(\lambda)\}}{K^2(\lambda) + L^2(\lambda)}.$$

If $\{M(\lambda)K(\lambda) + N(\lambda)L(\lambda)\}_{\lambda=\lambda_{\text{cr}}} \neq 0$, then $\text{Re}\left[\frac{d\mu_j}{d\lambda}\right]_{\lambda=\lambda_{\text{cr}}} \neq 0$. Therefore, if

(a) $D_2 > D_H$,
(b) $C(\lambda_{\text{cr}}) = A(\lambda_{\text{cr}})B(\lambda_{\text{cr}})$,
(c) $\{M(\lambda)K(\lambda) + N(\lambda)L(\lambda)\}_{\lambda=\lambda_{\text{cr}}} \neq 0$,

then a Hopf bifurcation occurs at $\lambda_2 = \lambda_{\text{cr}}$ and also it is non-degenerate.

7. Numerical simulations. In this section, we investigate numerically as demonstrated in [1, 3, 11] the effect of the various parameters on the qualitative behaviour of the system using parameter values given in Table 1

Table 1. Parameter values used in the numerical analysis

Original parameters	Description of parameters	Default value	Dimension
S^0	Constant input nutrient	0.3	mass/volume
a_1	Half saturation constant for uptake of S by x	0.5	mass/volume
a_2	Half saturation constant for uptake of x by y	0.3	mass/volume
m_1	Maximal growth rate of x on S	4	1/time
m_2	Maximal growth rate of y on x	3	1/time
D_1	Dilution (washout) rate of S	0.5	1/time
D_2	Death rate of x	0.5	1/time
D_3	Death rate of y	0.5	1/time
α_1, α_2	Parameters associated with yield	0.2	—
β_1, β_2	Parameters associated with yield	0.1	—

throughout, unless otherwise stated. Also, while analyzing the system with constant yields we have considered $\alpha_1 = 0 = \alpha_2$ and other parameter values as given in Table 1.

Under the given set of parameter values (cf. Table 1) we see that the system is locally asymptotically stable at E^* for constant yields (cf. Fig. 2(i)) and for quadratic yields (cf. Fig. 2(iii)), whereas the system is oscillatory at E^* for linear yields (cf. Fig. 2(ii)).

The qualitative behaviour of the system (for $n = 0, 1, 2$) is given in Tables 2-4, obtained by sequentially altering the value of a particular parameter of the system while leaving all other parameters unchanged. We observe that the system exhibits similar qualitative behaviour for constant yields and quadratic yields, whereas the system with linear yields is more prone to oscillation.

We will now verify the feasibility of the stability criterion of Section 5.

EXAMPLE 1. For $S^0 \le 0.07$ and all other parameters as in Table 1, it is observed that phytoplankton and zooplankton cannot survive in the system with linear yields (cf. Fig. 3). It is observed that for $S^0 = 0.01$, E_0 is a stable node with eigenvalues $-1, -1, -0.8431$. Also we obtain $\lambda_1 = 7.1429 > 1$, satisfying the condition of Lemma 5.1.

EXAMPLE 2. For $S^0 = 0.1$ and all other parameters as in Table 1, the system with linear yields has a stable node at $E_1 = (0.7143, 0.2857, 0)$ with eigenvalues $-1, -0.35, -0.4783$ (cf. Fig. 4). In this case we obtain $\lambda_1 = 0.7143 < 1$, satisfying the criterion for existence of E_1. Also, we obtain $D_2 > D_0 = 0.4762$, satisfying the condition of Lemma 5.2.
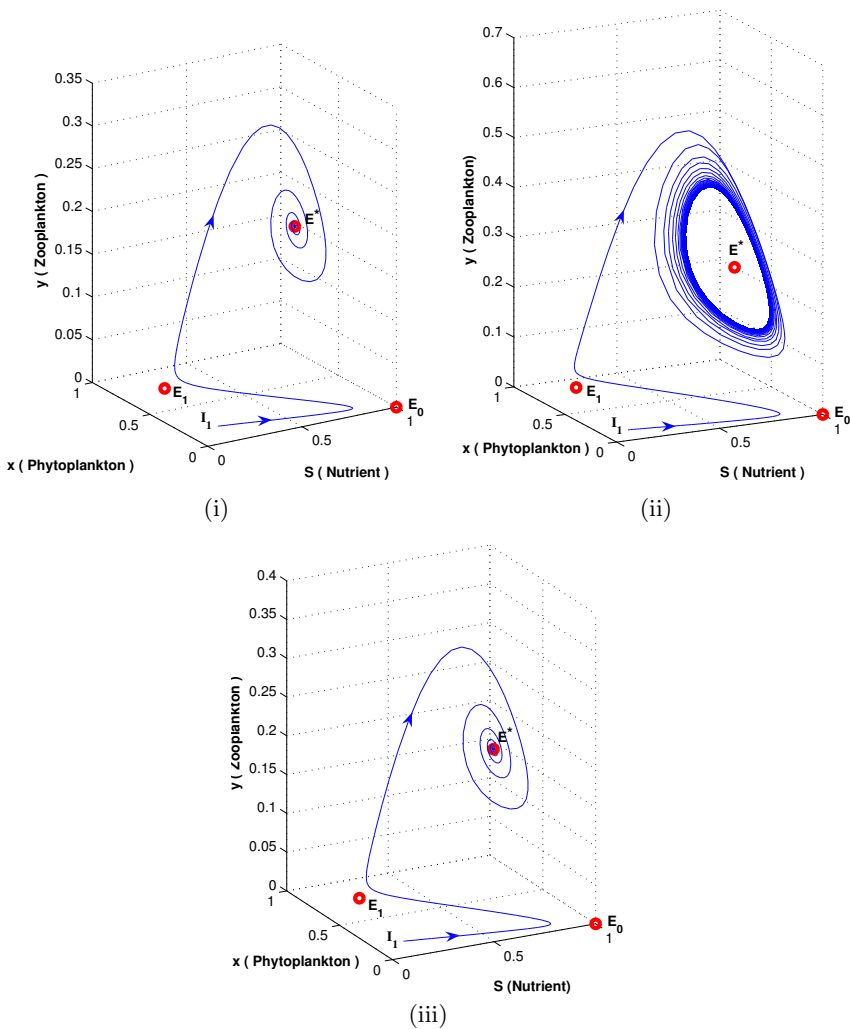
Fig. 2. Phase portraits of the system with initial value $I_1 = (0.06, 0.01, 0.02)$ for (i) constant yields of organisms with $\alpha_1 = 0 = \alpha_2$ and other parameter values as given in Table 1: the system has a stable focus at E^*; (ii) linear yields with parameter values as given in Table 1: the system is oscillatory around E^*; (iii) quadratic yields with parameter values as given in Table 1: the system has a stable focus at E^*.

EXAMPLE 3. For $\alpha_1 = 0 = \alpha_2$ and all other parameters as in Table 1, the system approaches the positive equilibrium $E^* = (0.5842, 0.2002, 0.2156)$ (cf. Fig. 2(i)) in the form of a stable focus with eigenvalues $-1, -0, -0.1733 \pm i1.1575$. In this case we obtain $\lambda_1 = 0.2381 < 1$, $\lambda_2 = 0.2$, $(1 - \lambda_1)\gamma_1(\lambda_1)/D_2 = 0.7619$, so that $\lambda_2 < (1 - \lambda_1)\gamma_1(\lambda_1)/D_2$, satisfying the condition of persistence given in Lemma 5.3. Also, we obtain $A = 1.3467$, $B = 1.7166$, $C = 1.3699$ so that $AB > C$, satisfying the condition of Lemma 5.4.
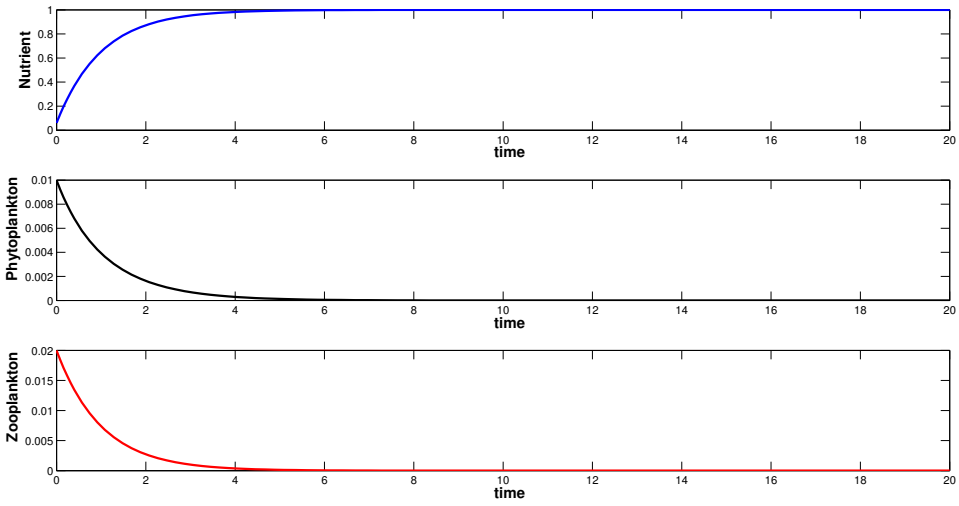
Fig. 3. Time series analysis of the system with linear yields for $S^0 = 0.01$ and other parameter values as given in Table 1. The system has a stable node at E_0.
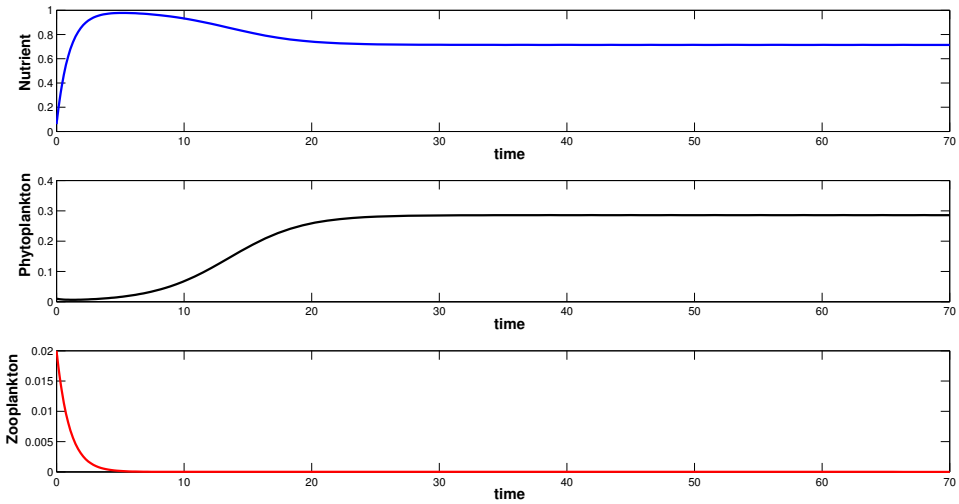

Fig. 4. Time series analysis of the system with linear yields for $S^0 = 0.1$ and other parameter values as given in Table 1. The system has a stable node at E_1.

Combined effects of input nutrient concentration, dilution rate and death rate of planktons. The system with linear yields is oscillatory around E^* under the given set of parameter values (cf. Fig. 2(ii)). The following changes in D_i restore the system to stability:

(i) If the dilution rate of nutrient is lowered (to $D_1 = 0.15$), the system becomes locally asymptotically stable at E^* (cf. Fig. 5). If we decrease the
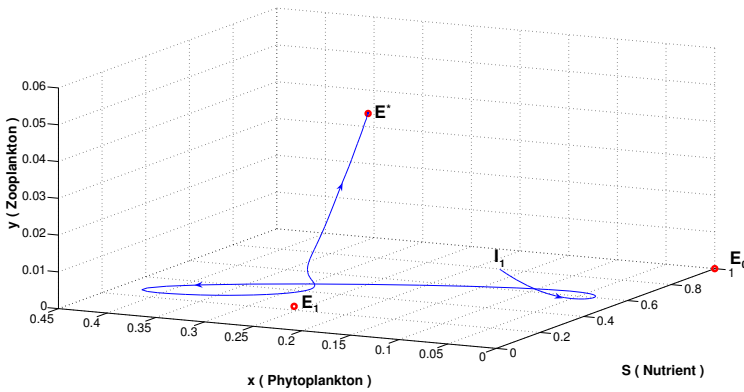
Fig. 5. Phase portrait of the system with linear yields for $S^0 = 0.3, D_1 = 0.15$ and other parameter values as given in Table 1. The system has a stable focus at E^*.

value of D_1 below 0.12, the system becomes locally asymptotically stable at E_1.

(ii) If the death rate of phytoplankton is increased (to $D_2 = 1.2$), the system becomes locally asymptotically stable at E_1. If we further increase the value of D_2 (to $D_2 = 1.8$), the system stabilizes at E_0 (cf. Fig. 6).
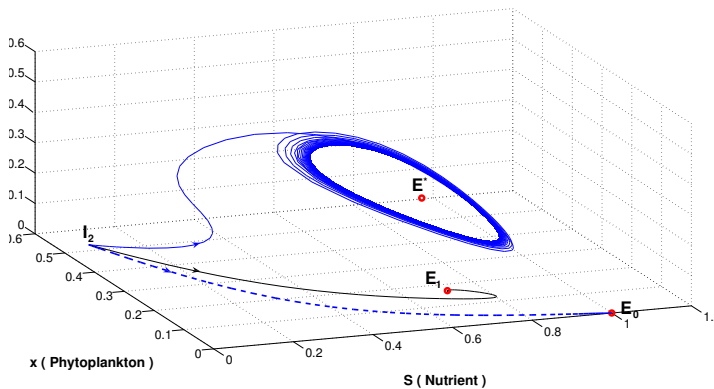

Fig. 6. Phase portrait of the system with linear yields for $S^0 = 0.3$ and other parameter values as given in Table 1 with initial value $I_2 = (0.06, 0.5, 0.02)$. The system is oscillatory around E^* (solid blue; colours refer to the pdf file). For $S^0 = 0.3, D_2 = 1.2$ and other parameter values as given in Table 1, the system has a stable focus at E_1 (solid black). For $S^0 = 0.3, D_2 = 1.8$ and other parameter values as given in Table 1, the system has a stable focus at E_0 (dotted blue).

(iii) If the death rate of zooplankton is increased (to $D_3 = 0.7$), the system becomes locally asymptotically stable at E^*. If we further increase the value of D_3 (to $D_3 = 1.8$), the system stabilizes at E_1 (cf. Fig. 7).
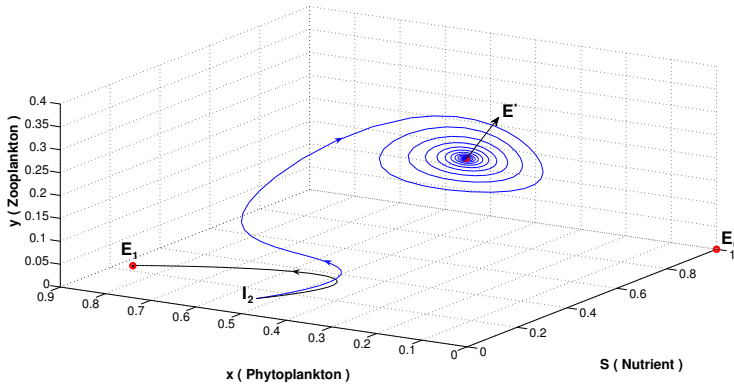
Fig. 7. Phase portrait of the system with linear yields for $S^0 = 0.3, D_3 = 0.7$ and other parameter values as given in Table 1 with initial value $I_2 = (0.06, 0.5, 0.02)$. The system is locally asymptotically stable at E^* (blue). For $S^0 = 0.3, D_3 = 1.8$ and other parameter values as given in Table 1, the system is locally asymptotically stable at E_1 (black).

Hopf bifurcation. We observe that the system becomes oscillatory when the values of the parameters a_2 and D_3 are low. Since λ_2 depends on both a_2 and D_3, λ_2 is considered as a bifurcation parameter. By decreasing the value of break-even concentration λ_2, the system exhibits oscillatory coexistence of all the species. The dynamical change due to the change in the value of λ_2 is shown by means of bifurcation diagrams. It is observed that the system undergoes a subcritical Hopf bifurcation when λ_2 is increased through some critical value. In the case of linear yields it is observed that there is a change of stability of the system when λ_2 crosses the value 0.105 (cf. Fig. 9) and in the case of constant yields the change of stability occurs when λ_2 crosses the critical value 0.21 (cf. Fig. 8).
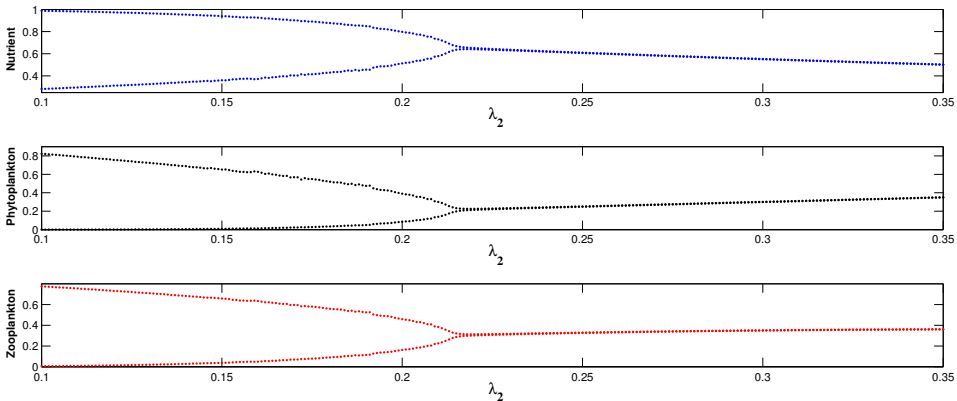

Fig. 8. The system with constant yields undergoes a subcritical Hopf bifurcation as λ_2 is increased through $\lambda_{2_{\mathrm{cr}}} = 0.21$.
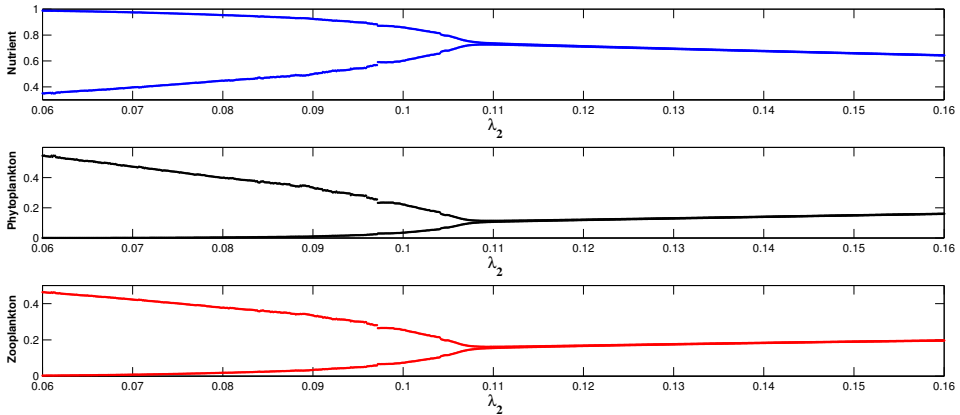
Fig. 9. The system with linear yields undergoes a subcritical Hopf bifurcation as λ_2 is increased through $\lambda_{2_{cr}} = 0.105$.

8. Discussion. We have considered a food chain with two trophic levels consisting of nutrient, phytoplankton and zooplankton. By analyzing our model we observe that if the maximal uptake rate of an organism is less than or equal to the death rate of that organism then the organism will become extinct even in the absence of predation. The threshold values for the existence and stability of various steady states of the system are worked out. Also, it is observed that if the value λ_2 of break-even concentration crosses a certain critical value, the system enters into Hopf bifurcation that induces oscillation around the positive equilibrium. We have also provided numerical simulations to substantiate our analytic results. Further, the numerical simulations demonstrate the following conclusions:

(i) With high concentration of nutrient, the system with constant or variable yields is oscillatory about the equilibrium of coexistence. This is essentially the paradox of enrichment [13].

(ii) If the concentration of nutrient is very low, all the species in the two trophic levels would go to extinction, irrespective of constant or variable yields.

(iii) With low concentration of nutrient, gradual increase of the death rates of phytoplankton and zooplankton helps stable coexistence of all the species.

(iv) With high death rate of phytoplankton it is observed that phytoplankton and zooplankton both become extinct.

(v) It is observed that low value of half saturation constant for uptake of nutrient by phytoplankton induces oscillation about the equilibrium of coexistence for the system with linear yields. On the other hand, the system with constant yields or quadratic yields exhibits no such oscillation.

Table 2. Qualitative behaviour of the system with constant yields for different parameter values

Parameter	Range	Organisms with constant yields		
		Description of stability		
		E_0	E_1	E^*
S^0	$S^0 \leq 0.07$	**Stable node**	Not feasible	Not feasible
	$0.07 < S^0 < 0.13$	Saddle point	**Stable node**	Not feasible
	$0.13 \leq S^0 < 0.5$	Saddle point	Saddle focus	**Stable focus**
	$S^0 \geq 0.5$	Saddle point	Saddle focus	**Oscillatory**
a_1	$a_1 < 1.68$	Saddle point	Saddle point	**Stable node**
	$1.68 \leq a_1 < 2.1$	Saddle point	**Stable node**	Not feasible
	$a_1 \geq 2.1$	**Stable node**	Not feasible	Not feasible
a_2	$a_2 \leq 0.16$	Saddle point	Saddle focus	**Oscillatory**
	$0.16 < a_2 < 1.14$	Saddle point	Saddle focus	**Stable focus**
	$a_2 \geq 1.14$	Saddle point	**Stable node**	Not feasible
m_1	$0.5 < m_1 \leq 1.33$	**Stable node**	Not feasible	Not feasible
	$1.33 < m_1 \leq 1.54$	Saddle point	**Stable node**	Not feasible
	$m_1 > 1.54$	Saddle point	Saddle point	**Stable focus**
m_2	$0.5 < m_2 \leq 1.15$	Saddle point	**Stable focus**	Not feasible
	$m_2 > 1.15$	Saddle point	Saddle point	**Stable focus**
D_1	$D_1 \leq 0.13$	Saddle point	**Stable node**	Not feasible
	$D_1 > 0.13$	Saddle point	Saddle focus	**Stable focus**
D_2	$D_2 < 0.104$	Saddle point	Saddle focus	**Stable focus**
	$0.104 \leq D_2 < 1.5$	Saddle point	**Stable focus**	Not feasible
	$D_2 \geq 1.5$	**Stable node**	Not feasible	Not feasible
D_3	$D_3 < 0.01$	Saddle point	Saddle point	**Oscillatory**
	$0.01 \leq D_3 < 1.3$	Saddle point	Saddle focus	**Stable focus**
	$D_3 \geq 1.3$	Saddle point	**Stable focus**	Not feasible

(vi) Increase of half saturation constant for uptake of phytoplankton by zooplankton initially transforms the oscillatory coexistence of all the species to their stable coexistence. Further increase of the value of this parameter leads to the extinction of zooplankton.

Throughout the article an attempt (analytical and numerical) is made to search for a suitable way to control the growth of nutrient, phytoplankton, zooplankton and maintain stable coexistence of all the species. It is observed

Table 3. Qualitative behaviour of the system with linear yields for different parameter values

Parameter	Organisms with linear yields			
	Range	Description of stability		
		E_0	E_1	E^*
S^0	$S^0 \leq 0.07$	**Stable node**	Not feasible	Not feasible
	$0.07 < S^0 \leq 0.12$	Saddle point	**Stable node**	Not feasible
	$0.12 < S^0 \leq 0.258$	Saddle point	Saddle point	**Stable focus**
	$S^0 \geq 0.258$	Saddle point	Saddle focus	**Oscillatory**
a_1	$(0, 1.08] \cup [0.65, 1.82]$	Saddle point	Saddle point	**Oscillatory**
	$0.12 < a_1 < 0.65$	Saddle point	Saddle point	**Stable node**
	$1.82 < a_1 < 2.1$	Saddle point	**Stable node**	Not feasible
	$a_1 \geq 2.1$	**Stable node**	Not feasible	Not feasible
a_2	$a_2 \leq 0.32$	Saddle point	Saddle focus	**Oscillatory**
	$0.32 < a_2 < 1.3$	Saddle point	Saddle focus	**Stable focus**
	$a_2 \geq 1.3$	Saddle point	**Stable node**	Not feasible
m_1	$0.5 < m_1 \leq 1.33$	**Stable node**	Not feasible	Not feasible
	$1.33 < m_1 \leq 1.46$	Saddle point	**Stable node**	Not feasible
	$m_1 > 1.46$	Saddle point	Saddle point	**Stable focus**
m_2	$0.5 < m_2 \leq 1.07$	Saddle point	**Stable focus**	Not feasible
	$m_2 > 1.07$	Saddle point	Saddle point	**Stable focus**
D_1	$D_1 \leq 0.12$	Saddle point	**Stable node**	Not feasible
	$0.12 < D_1 \leq 0.44$	Saddle point	Saddle focus	**Stable focus**
	$D_1 > 0.44$	Saddle point	Saddle point	**Oscillatory**
D_2	$D_2 < 0.54$	Saddle point	Saddle point	**Oscillatory**
	$0.54 \leq D_2 < 1.15$	Saddle point	Saddle focus	**Stable focus**
	$1.15 \leq D_2 < 1.5$	Saddle point	**Stable node**	Not feasible
	$D_2 \geq 1.5$	**Stable node**	Not feasible	Not feasible
D_3	$D_3 < 0.58$	Saddle point	Saddle point	**Oscillatory**
	$0.58 \leq D_3 < 1.4$	Saddle point	Saddle focus	**Stable focus**
	$D_3 \geq 1.4$	Saddle point	**Stable focus**	Not feasible

that organisms with linear yields are more sensitive to parameter changes than those of constant yields and quadratic yields. A numerical attempt is made to analyze the situation of extinction of some of the species in the system by changing the values of the parameters.

Table 4. Qualitative behaviour of the system with quadratic yields for different parameter values

Parameter	Range	Organisms with quadratic yields		
		Description of stability		
		E_0	E_1	E^*
S^0	$S^0 \leq 0.07$	**Stable node**	Not feasible	Not feasible
	$0.07 < S^0 < 0.13$	Saddle point	**Stable node**	Not feasible
	$0.13 \leq S^0 \leq 0.42$	Saddle point	Saddle focus	**Stable node**
	$S^0 > 0.42$	Saddle point	Saddle focus	**Oscillatory**
a_1	$a_1 < 1.72$	Saddle point	Saddle point	**Stable focus**
	$1.72 \leq a_1 < 2.1$	Saddle point	**Stable node**	Not feasible
	$a_1 \geq 2.1$	**Stable node**	Not feasible	Not feasible
a_2	$a_2 \leq 0.18$	Saddle point	Saddle point	**Oscillatory**
	$0.18 < a_2 < 1.15$	Saddle point	Saddle point	**Stable focus**
	$a_2 \geq 1.15$	Saddle point	**Stable node**	Not feasible
m_1	$0.5 < m_1 \leq 1.33$	**Stable node**	Not feasible	Not feasible
	$1.33 < m_1 \leq 1.51$	Saddle point	**Stable node**	Not feasible
	$m_1 > 1.51$	Saddle point	Saddle point	**Stable focus**
m_2	$0.5 < m_2 \leq 1.15$	Saddle point	**Stable node**	Not feasible
	$m_2 > 1.15$	Saddle point	Saddle point	**Stable focus**
D_1	$D_1 < 0.72$	Saddle point	**Stable node**	Not feasible
	$D_1 \geq 0.72$	Saddle point	Saddle focus	**Stable focus**
D_2	$D_2 < 0.1$	Saddle point	Saddle point	**Oscillatory**
	$0.1 \leq D_2 < 1.06$	Saddle point	Saddle focus	**Stable focus**
	$1.06 \leq D_2 < 1.5$	Saddle point	**Stable node**	Not feasible
	$D_2 \geq 1.5$	**Stable node**	Not feasible	Not feasible
D_3	$D_3 < 0.015$	Saddle point	Saddle point	**Oscillatory**
	$0.015 \leq D_3 < 1.31$	Saddle point	Saddle focus	**Stable focus**
	$D_3 \geq 1.31$	Saddle point	**Stable focus**	Not feasible

Appendix

Proof of boundedness of the system (Theorem 4.1). Let $\Sigma(t) = S(t) + x(t) + y(t)$. Then

$$\frac{d}{dt}(\Sigma(t)) = 1 - S - xp_1(S)\left\{\frac{1}{\gamma_1(S)} - 1\right\} - xD_2 - yp_2(x)\left\{\frac{1}{\gamma_2(x)} - 1\right\} - yD_3$$
$$\leq 1 - S - xD_2 - yD_3 = 1 - \Sigma(t)D,$$

where $D = \min\{1, D_2, D_3\}$. Let $u(t)$ be the solution of $\frac{du}{dt} + uD = 1$ satisfying $u(0) = \Sigma(0)$. Then

$$u(t) = \frac{1}{D} + \left(\Sigma(0) - \frac{1}{D}\right)e^{-tD} \to \frac{1}{D} \quad \text{as } t \to \infty.$$

By comparison, it follows that

$$\lim_{t \to \infty} \sup[S(t) + x(t) + y(t)] \le \frac{1}{D},$$

proving the theorem.

Proof of Theorem 4.2. (i) Since $S(t) \le 1$ as $t \to \infty$, it follows that for any $\epsilon > 0$ there exists $t_\epsilon > 0$ such that $S(t) \le 1 + \epsilon$ for all $t \ge t_\epsilon$.

If $m_1 \le D_2$, then

$$\frac{dx}{dt} \le -xD_2\left(\frac{a_1}{a_1 + S}\right) < 0.$$

Thus we get

$$\int_{x(t_\epsilon)}^{x(t)} \frac{d\xi}{\xi} \le -D_2\left(\frac{a_1}{1 + a_1 + \epsilon}\right)(t - t_\epsilon),$$

which gives

$$x(t) \le x(t_\epsilon)e^{-\frac{a_1 D_2(t - t_\epsilon)}{1 + a_1 + \epsilon}}.$$

Therefore, $\lim_{t \to \infty} x(t) = 0$ and consequently $\lim_{t \to \infty} y(t) = 0$.

(ii) For all $t \ge t_\epsilon$, if $\lambda_1 > 1 + \epsilon$ and $m_1 > D_2$ then

$$\frac{dx}{dt} \le x\frac{(m_1 - D_2)(S - \lambda_1)}{a_1} \le x\frac{(m_1 - D_2)(1 + \epsilon - \lambda_1)}{a_1} < 0.$$

Now, we obtain

$$\int_{x(t_\epsilon)}^{x(t)} \frac{d\xi}{\xi} \le \frac{(m_1 - D_2)(1 + \epsilon - \lambda_1)}{a_1}(t - t_\epsilon),$$

which gives

$$x(t) \le x(t_\epsilon)e^{\frac{-(m_1 - D_2)(\lambda_1 - 1 - \epsilon)(t - t_\epsilon)}{a_1}}.$$

This implies that if $\lambda_1 > 1$ and $m_1 > D_2$, then $x(t) \to 0$ as $t \to \infty$ and consequently $y(t) \to 0$ as $t \to \infty$.

(iii) Since $x(t) \le 1/D$ as $t \to \infty$, it follows that for every $\epsilon_1 > 0$ there exists $t_{\epsilon_1} > 0$ such that $x(t) \le 1/D + \epsilon_1$, for all $t \ge t_{\epsilon_1}$.

If $m_2 \le D_3$, then

$$\frac{dy}{dt} \le -yD_3\left(\frac{a_2}{a_2 + x}\right) < 0.$$

Thus we get

$$\int_{y(t_{\epsilon_1})}^{y(t)} \frac{d\xi}{\xi} \le -D_3\left(\frac{a_2}{1/D + a_2 + \epsilon_1}\right)(t - t_{\epsilon_1}),$$

which gives
$$y(t) \le y(t_{\epsilon_1})e^{-\frac{a_2 D_3(t-t_{\epsilon_1})}{a_2+1/D+\epsilon_1}}.$$

Therefore, $\lim_{t\to\infty} y(t) = 0$.

(iv) For all $t \ge t_{\epsilon_1}$, if $\lambda_2 > 1/D + \epsilon_1$ and $m_2 > D_3$, then
$$\frac{dy}{dt} \le y\frac{(m_2 - D_3)(x - \lambda_2)}{a_2} \le y\frac{(m_2 - D_3)(1/D + \epsilon_1 - \lambda_2)}{a_2} < 0.$$

Now, we obtain
$$\int_{y(t_{\epsilon_1})}^{y(t)} \frac{d\xi}{\xi} \le \frac{(m_2 - D_3)(1/D + \epsilon_1 - \lambda_2)}{a_2}(t - t_{\epsilon_1}),$$

which gives
$$y(t) \le y(t_{\epsilon_1})e^{\frac{-(m_2-D_3)(\lambda_2-1/D-\epsilon_1)(t-t_{\epsilon_1})}{a_2}}.$$

This implies that if $\lambda_2 > 1/D$ and $m_2 > D_3$, then $y(t) \to 0$ as $t \to \infty$.

Proof of Lemma 5.1. At E_0 the variational matrix is
$$V(E_0) = \begin{bmatrix} -1 & -p_1(1)/\gamma_1(1) & 0 \\ 0 & p_1(1) - D_2 & 0 \\ 0 & 0 & -D_3 \end{bmatrix}.$$

Its eigenvalues are -1, $-D_3$, $p_1(1) - 1$. Therefore, the system is stable at E_0 if $p_1(1) < D_2$, i.e. if $\lambda_1 > 1$.

Proof of Lemma 5.2. At E_1 the variational matrix is
$$V(E_1) = \begin{bmatrix} F_S|_{E_1} & \frac{-D_2}{\gamma_1(\lambda_1)} & 0 \\ (1-\lambda_1)\gamma_1(\lambda_1)\frac{a_1 D_2}{m_1\lambda_1^2} & 0 & \frac{-p_2|_{E_1}}{\gamma_2|_{E_1}} \\ 0 & 0 & p_2|_{E_1} - D_3 \end{bmatrix}$$

where
$$F_S|_{E_1} = -1 - \frac{(1-\lambda_1)}{D_2}\left(\frac{\gamma_1(\lambda_1)\frac{a_1 D_2^2}{m_1\lambda_1^2} - D_2\gamma_1'(\lambda_1)}{\gamma_1(\lambda_1)}\right),$$
$$p_2|_{E_1} = \frac{m_2(1-\lambda_1)\gamma_1(\lambda_1)}{a_2 D_2 + (1-\lambda_1)\gamma_1(\lambda_1)},$$
$$\gamma_2|_{E_1} = \gamma_2\left(\frac{(1-\lambda_1)}{D_2}\gamma_1(\lambda_1)\right).$$

The characteristic equation is
$$(p_2|_{E_1} - D_3 - \mu)\left(\mu^2 - \mu F_S|_{E_1} + (1-\lambda_1)\frac{a_1 D_2^2}{m_1\lambda_1^2}\right) = 0.$$

The two roots of the quadratic equation

$$\mu^2 - \mu F_S|_{E_1} + (1 - \lambda_1)\frac{a_1 D_2^2}{m_1 \lambda_1^2} = 0$$

will be negative real if $F_S|_{E_1} < 0$ and $\lambda_1 < 1$.

Now,

$$p_2|_{E_1} < D_3 \Rightarrow \frac{a_2 + \frac{(1-\lambda_1)}{D_2}\gamma_1(\lambda_1)}{m_2 \frac{(1-\lambda_1)}{D_2}\gamma_1(\lambda_1)} > \frac{1}{D_3} \Rightarrow \lambda_2 > \frac{(1-\lambda_1)\gamma_1(\lambda_1)}{D_2},$$

$$F_S|_{E_1} < 0 \Rightarrow D_2 > \frac{m_1 \lambda_1^2}{a_1}\left(\frac{\gamma_1'(\lambda_1)}{\gamma_1(\lambda_1)} - \frac{1}{1-\lambda_1}\right).$$

Therefore, the system is stable at E_1 if $D_2 > D_0$, where

$$D_0 = \max\left\{\frac{m_1 \lambda_1^2}{a_1}\left(\frac{\gamma_1'(\lambda_1)}{\gamma_1(\lambda_1)} - \frac{1}{1-\lambda_1}\right), \frac{(1-\lambda_1)\gamma_1(\lambda_1)}{\lambda_2}\right\}.$$

Proof of Lemma 5.3. In order to prove the persistence of the system we shall show that all the boundary equilibria of the system are repellers.

We observe that if $\lambda_1 < 1$, then the system is unstable at E_0. If $\lambda_2 \leq (1 - \lambda_1)\gamma_1(\lambda_1)/D_2$ then the system is unstable at E_1. Thus, if $\lambda_1 < 1$ and $\lambda_2 \leq (1 - \lambda_1)\gamma_1(\lambda_1)/D_2$ then all the boundary equilibria are repellers. Also, the system is bounded. Therefore, the system is persistent under the aforesaid conditions.

Proof of Lemma 5.4. At E^* the variational matrix is

$$V(E^*) = \begin{bmatrix} -1 - \lambda_2\left(\frac{p_1(S)}{\gamma_1(S)}\right)'_{S^*} & \frac{-p_1(S^*)}{\gamma_1(S^*)} & 0 \\ \lambda_2 p_1'(S^*) & p_1(S^*) - D_2 - y^*\left(\frac{p_2(x)}{\gamma_2(x)}\right)'_{\lambda_2} & \frac{-D_3}{\gamma_2(\lambda_2)} \\ 0 & y^* p_2'(\lambda_2) & 0 \end{bmatrix}$$

The characteristic equation is $\mu^3 + A\mu^2 + B\mu + C = 0$, where

$$A = -(G_x|_{E^*} + F_S|_{E^*}) = 1 + D_2 - p_1(S^*) + y^*\left(\frac{p_2}{\gamma_2}\right)'_{x=\lambda_2} + \lambda_2\left(\frac{p_1}{\gamma_1}\right)'_{S=S^*},$$

$$B = D_2 - p_1(S^*) + y^*\left(\frac{p_2}{\gamma_2}\right)'_{x=\lambda_2} + D_2\lambda_2\left(\frac{p_1}{\gamma_1}\right)'_{S=S^*} + \lambda_2 p_1^2(S^*)\frac{\gamma_1'(S^*)}{\gamma_1^2(S^*)}$$

$$+ y^* D_3\frac{p_2'(\lambda_2)}{\gamma_2(\lambda_2)} + \lambda_2 y^*\left(\frac{p_1}{\gamma_1}\right)'_{S=S^*}\left(\frac{p_2}{\gamma_2}\right)'_{x=\lambda_2},$$

$$C = y^* D_3\frac{p_2'(\lambda_2)}{\gamma_2(\lambda_2)}\left\{1 + \lambda_2\left(\frac{p_1}{\gamma_1}\right)'_{S=S^*}\right\}.$$

Therefore, if $A, B, C > 0$ and $AB > C$, then the positive equilibrium of the system (1) is locally asymptotically stable.

Proof of Lemma 5.5. The second additive compound matrix of the Jacobian of the system (1) is

$$J^{(2)} = \begin{bmatrix} F_S + G_x & G_y & -F_y \\ H_x & F_S + H_y & F_x \\ -H_S & G_S & G_x + H_y \end{bmatrix}.$$

The logarithmic norm μ_∞ of $J^{(2)}$ determined by the norm $|X|_\infty = \sup_i |X_i|$ is

$$\mu_\infty(J^{(2)}) = \sup\{F_S + G_x + |F_y| + |G_y|, F_S + H_y + |F_x| + |H_x|,$$
$$G_x + H_y + |G_S| + |H_S|\}.$$

Now,

$$(F_S + G_x + |F_y| + |G_y|)_{E^*} < m_1 + D_3 - D_2 - y^* \left(\frac{p_2}{\gamma_2}\right)'_{\lambda_2},$$

$$(F_S + H_y + |F_x| + |H_x|)_{E^*} < m_1 - 1 + y^* p_2'(\lambda_2) - \lambda_2 \left(\frac{p_1}{\gamma_1}\right)'_{S^*},$$

$$(G_x + H_y + |G_S| + |H_S|)_{E^*} = m_1 - D_2 + \lambda_2 p_1'(S^*) - y^* \left(\frac{p_2}{\gamma_2}\right)'_{\lambda_2}.$$

Therefore, $\mu_\infty(J^{(2)}) < 0$ if $m_1 < L$, where

$$L = \min\left\{ D_2 - D_3 + y^* \left(\frac{p_2}{\gamma_2}\right)'_{\lambda_2}, 1 - y^* p_2'(\lambda_2) + \lambda_2 \left(\frac{p_1}{\gamma_1}\right)'_{S^*}, \right.$$
$$\left. D_2 - \lambda_2 p_1'(S^*) + y^* \left(\frac{p_2}{\gamma_2}\right)'_{\lambda_2}\right\}.$$

A direct application of Li and Muldowney's method [9] shows that under the above circumstances there is no periodic solution for the system.

Proof of Lemma 5.6. Let us define a Lyapunov function:

$$V(S, x, y) = \int_{\lambda_1}^{S} \frac{\eta - \lambda_1}{\eta} \, d\eta + c_1 \int_{x^*}^{x} \frac{\eta - x^*}{\eta} \, d\eta,$$

where

$$c_1 = \frac{m_1}{(m_1 - D_2)\gamma_1(\lambda_1)} \quad \text{and} \quad x^* = \frac{(1 - \lambda_1)\gamma_1(\lambda_1)}{D_2}.$$

Then $\frac{dV}{dt} = V_1 + V_2$, where

$$V_1 = \frac{S - \lambda_1}{S}(1 - S) - c_1 x^* \left(\frac{m_1 S}{a_1 + S} - D_2 \right),$$

$$V_2 = -\frac{S - \lambda_1}{S} \frac{m_1 Sx}{(a_1 + S)\gamma_1(S)} + c_1 x \left(\frac{m_1 S}{a_1 + S} - D_2 \right).$$

Now,

$$V_1 = \frac{S - \lambda_1}{S}(1 - S) - c_1 x^* (\frac{m_1 S}{a_1 + S} - D_2)$$

$$= \frac{S - \lambda_1}{S}(1 - S) - c_1 x^* \frac{(m_1 - D_2)(S - \lambda_1)}{a_1 + S}$$

$$= (S - \lambda_1) \left(\frac{1 - S}{S} - \frac{m_1(1 - \lambda_1)}{D_2(a_1 + S)} \right) = (S - \lambda_1) \left(\frac{1 - S}{S} - \frac{a_1 + \lambda_1}{\lambda_1} \frac{1 - \lambda_1}{a_1 + S} \right)$$

$$= -(S - \lambda_1)^2 \frac{a_1 + S\lambda_1}{\lambda_1 S(a_1 + S)} \le 0$$

and

$$V_2 = -\frac{S - \lambda_1}{S} \frac{m_1 Sx}{(a_1 + S)\gamma_1(S)} + c_1 x \left(\frac{m_1 S}{a_1 + S} - D_2 \right)$$

$$= -\frac{S - \lambda_1}{S} \frac{m_1 Sx}{(a_1 + S)\gamma_1(S)} + \frac{m_1(S - \lambda_1)x}{(a_1 + S)\gamma_1(\lambda_1)}$$

$$= \frac{m_1 x(S - \lambda_1)(\gamma_1(S) - \gamma_1(\lambda_1))}{(a_1 + S)\gamma_1(\lambda_1)\gamma_1(S)}.$$

Hence,

$$V_1 + V_2 = -(S - \lambda_1)^2 \frac{a_1 + S\lambda_1}{\lambda_1 S(a_1 + S)} + \frac{m_1 x(S - \lambda_1)^2 \Phi(S)}{(a_1 + S)\gamma_1(\lambda_1)\gamma_2(S)},$$

where $\Phi(S) = \alpha_1 S^0$ for linear yields and $\Phi(S) = \alpha_1(S^0)^2(S + \lambda_1)$ for quadratic yields. Thus,

$$V_1 + V_2 = \frac{(S - \lambda_1)^2}{a_1 + S} \left[\frac{m_1 x \Phi(S)}{\gamma_1(\lambda_1)\gamma_2(S)} - \frac{a_1 + S\lambda_1}{\lambda_1 S} \right] \le 0 \quad \text{if}$$

$$\frac{S\Phi(S)}{(a_1 + S\lambda_1)\gamma_2(S)} \le \frac{\gamma_1(\lambda_1)}{\lambda_1 m_1 x}.$$

Therefore

$$V_1 + V_2 \le 0 \quad \text{if} \quad \frac{S\Phi(S)}{(a_1 + S\lambda_1)\gamma_2(S)} \le \frac{\gamma_1(\lambda_1)}{\lambda_1 m_1 \left\{ \frac{1 - \lambda_1}{D_2}\gamma_1(\lambda_1) + \epsilon_0 \right\}}.$$

By La Salle's lemma it follows that for $S = \lambda_1$ and $y = 0$, all the trajectories approach the set $\Delta = \{(S, x, y) : dV/dt = 0\}$.

Suppose at $y = 0$, $\{S : S = \lambda_1\}$ is invariant; then it must have

$$0 = \frac{dS}{dt} = 1 - \lambda_1 - \frac{m_1 \lambda_1 x}{(a_1 + \lambda_1)\gamma_1(\lambda_1)}.$$

This means that $x = \frac{1-\lambda_1}{D_2}\gamma_1(\lambda_1)$. Hence $\{E_1\}$ is the only invariant set in Δ. This completes the proof.

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