BIFURCATION ANALYSIS OF A MODEL OF THREE-LEVEL FOOD CHAIN IN A MANGROVE ECOSYSTEM

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In this paper, we consider a three-dimensional non-linear dynamical system of predator-prey type with 12 parameters which models a food-chain in a mangrove ecosystem. Our goal is to study the dynamical properties of the model with constant rate harvesting on the top-predator. It is shown that transcritical, saddle-node and supercritical Hopf bifurcations occur when one parameter is varied. By numerical integration of the system, we plot the phase portraits for the important types of dynamics and we show the presence of a stable limit cycle. We deduce the controlling role of the harvesting rate upon the stable equlibrium or periodic state of coexistence of the species.

Keywords: Predator-prey system, Stability, Limit cycle, Bifurcation.

1. Introduction

We consider a three dimensional ordinary differential autonomous system which models a food chain in a mangrove ecosystem with detritus recycling and with constant rate harvesting of top predators. The three levels of the food chain are the detritus ($x(t)$ denotes its density at time t) which consists of algal species and leaves of the mangrove plants, then detritivores ($y(t)$)-unicellular animals, crustacean, amphiopod and others (see [4]) which depend on rich detritus-base and the predators of detritivores ($z(t)$)-fish and prawn. Some of the predators have commercial value and undergo harvesting. The system has the following form:

$$\begin{aligned} x'(t) &= x_0 - ax - \beta x y \mathrm{e}^{-\alpha x} + \gamma z \\ y'(t) &= \beta_1 x y \mathrm{e}^{-\alpha x} - d_1 y - \frac{cyz}{k+y} \\ z'(t) &= \frac{c_1 y z}{k+y} - d_2 z - hz \end{aligned} \tag{1}$$

with the initial conditions $x(0), y(0), z(0) \geq 0$.

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The main assumptions of the model are the following:

1. The detritus has a constant input rate (x_0) maintained by the decomposed mangrove leaves. [4] Also the detritus is washout from the system with a certain rate (a) and is supplied with dead organic matter converted into detritus by the action of the micro-organisms.

2. The interaction between detritus and detritivores is different from the classical models of predator-prey in that the detritivores response function is not a monotone incresing function of prey density, but rather is only monotone increasing until some critical density and then becomes monotone decreasing. (as it is described in [3] between phytoplankton and zooplankton). This phenomenon is called group defense in which predation (in our case by detritivores) decreases when the density of the prey population is sufficiently large, which is also related to the nutrient uptake inhibition phenomenon in chemical kinetics (see [1]). One of the nonmonotone functional response introduced (see [6]) is $p(x) = \beta x e^{-\alpha x}$ where $\frac{1}{\alpha} > 0$ is the density of the prey at which predation reaches its maximum.

3. The amount of detritivores consumed by the top predator is assumed to follow a Holling type-II functional response. It exhibits saturation effect when y-population is abundent and k is the half-saturation constant. The top predators ($z(t)$) are harvested with a constant rate, h.

4. The detritus-detritivores conversion rate is less then the detritus uptake rate, so $\beta_1 < \beta$.

5. For the same reason, the detritivore-predator conversion rate is $c_1 < c$.

6. The detritus recycle rate due to the death of predators, γ is less than $d_2 + h$.

First we study the boundedness of the solutions of the system (1).

Proposition 1.1. *The first octant $\mathbb{R}^3_+$ is positively invariant under the flow generated by the system (1).*

Proof. Let be (v_1, v_2, v_3) the vector field which defines the differential system (1). We study the vector-field on the boundaries of the first octant. In Oxz-plane, $v_2(x, 0, z) = 0$, therefore all trajectories which initiate in this plane, remain in it, for any $t \geq 0$, so the plane $y = 0$ is an invariant set for the system. In the same situation is the plane $z = 0$ because $v_3(x, y, 0) = 0$. But trajectories which start in Oyz-plane, $y, z > 0$ are directed towards the interior of the first octant, since $v_1(0, y, z) = x_0 + \gamma z > 0$. In consequence all solutions with $x(0), y(0), z(0) \geq 0$, remain in the first octant. □

Proposition 1.2. *With the hypothesis upon the parameters 4,5 and 6, every solution of the system (1) with positive initial values, is bounded.*

Proof. Let $(x(t), y(t), z(t))$ be a solution of the system with positive initial conditions. We deduce that $(x+y+z)'(t) < x_0 - ax(t) + (\gamma - d_2 - h)z(t) - d_1 y(t)$, $\forall t \geq 0$. If $M = min(a, d_2 + h - \gamma, d_1)$, then $(x + y + z)' < x_0 - M(x + y + z)$. Next we denote $u(t) = (x + y + z)(t)$. By multiplying the last inequality with

e^{Mt}, we get that u verifies $(ue^{Mt})' - x_0 e^{Mt} < 0$, $\forall t \geq 0$, or, equivalently from integration, $u(t) \leq (u(0) - \frac{x_0}{M})\mathrm{e}^{-Mt} + \frac{x_0}{M}$, that is $u(t) \leq max(u(0), \frac{x_0}{M})$, $\forall t \geq 0$. Therefore, any solution of the system (1) starting in $\mathbb{R}^3_+$, is bounded. □

Let us nondimensionalize the system (1) with the following scaling: $t \to at; y \to \frac{\beta}{a}y; z \to \frac{c\beta}{a^2}z$ and the system becomes

$$\begin{aligned} x'(t) &= X_0 - x - xy\mathrm{e}^{-\alpha x} + \mu z \\ y'(t) &= bxy\mathrm{e}^{-\alpha x} - D_1 y - \frac{yz}{K+y} \\ z'(t) &= \frac{ryz}{K+y} - Hz \end{aligned} \tag{2}$$

where $X_0 = \frac{x_0}{a}; b = \frac{\beta_1}{a}; D_1 = \frac{d_1}{a}; K = \frac{k\beta}{a}; r = \frac{c_1}{a}; H = \frac{d_2+h}{a}; \mu = \frac{\gamma a}{c\beta}$ are positive constants. For simplicity, we keep the ecological implications of parameters X_0, μ, b, D_1, K, r and H the same as $x_0, \gamma, \beta_1, d_1, k, c_1$ and h, respectively. In consequence, in the following study, we assume that $\mu < H, b < 1$ and $r < 1$.

2. **Stability and bifurcation analysis**

Now we determine the location and the existence criteria for the equilibria of the system (2) in the first octant.

Proposition 2.1. *a) There is an axial equlibrium $E_0(X_0, 0, 0)$, for any values of the parameters;*
b) If $\alpha\mathrm{e} < \frac{b}{D_1} < \frac{\mathrm{e}^{\alpha X_0}}{X_0}$ and $X_0 > \frac{1}{\alpha}$, the system has two boundary equilibria $E_i(x_i^*, y_i^*, 0)$, $i = \overline{1,2}$, where $x_1^* < x_2^*$ are the two solutions of the equation

$$x\mathrm{e}^{-\alpha x} = \frac{D_1}{b} \tag{3}$$

and $y_i^* = (X_0 - x_i^*)\frac{b}{D_1}$,$i = \overline{1,2}$;
c) If $\frac{b}{D_1} > \frac{\mathrm{e}^{\alpha X_0}}{X_0}$, there exists only one boundary equilibrium $E_1(x_1^*, y_1^*, 0)$ with $x_1^* < \frac{1}{\alpha}$ and y_1^* given in b);
d) If $\frac{b}{D_1} < \alpha\mathrm{e}$, there are no boundary equilibria in $\mathbb{R}^3_+$.

Proof. b) Un equilibrium with $z = 0$ has its first component, solution of the equation $x\mathrm{e}^{-\alpha x} = \frac{D_1}{b}$. A simple classical analysis shows that the equation has solutions iff $\frac{b}{D_1} \geq \alpha\mathrm{e}$ and in the case with strict inequality there are two solutions $x_1^* < x_2^*$ which are smaller than X_0 when $X_0\mathrm{e}^{-\alpha X_0} < \frac{D_1}{b}$, $X_0 > \frac{1}{\alpha}$.
c) The condition $\frac{b}{D_1} > \frac{e^{\alpha X_0}}{X_0}$ is equivalent with $x_1^* < X_0 < x_2^*$ and in consequence, only E_1 is in the first octant. □

We take the case when $(\exists)M$ such that $x\mathrm{e}^{-\alpha x}|_{x=M} > \frac{D_1}{b}$, which, from the second equation in system (2), means that otherwise y could not survive on the prey at any density in the absence of z. In the following study, $\frac{b}{D_1} \geq \alpha\mathrm{e}$ and this is the case when the equation (3) posses at least one solution.

Next we give a sufficient existence criterion for the interior equilibrium $E_3(x_3, y_3, z_3)$. A simple calculation shows that x_3 is a solution of the equation:

$$g(x) := K\frac{H-\mu br}{r-H}x\mathrm{e}^{-\alpha x} + x + \frac{\mu D_1 rK}{r-H} - X_0 = 0, \tag{4}$$

$y_3 = \frac{HK}{r-H}$ and $z_3 = (bx_3\mathrm{e}^{-\alpha x_3} - D_1)\frac{rK}{r-H}$.

Remark 2.1. *We assume that $r > H$ from now on, that is the detritivore-predator conversion rate has to be greater than the harvesting rate, so that there exists un interior equilibrium which is the case with biological relevance.*

Proposition 2.2. *i) If $\frac{b}{D_1} < \frac{\mathrm{e}^{\alpha X_0}}{X_0}$ and $X_0 > \frac{1}{\alpha}$ (i.e. the system has two boundary equilibria) and $H_2 < H < H_1$, then it is at least one interior equilibrium, E_3, where*

$$H_i := \frac{br(X_0 - x_i^*)}{KD_1 + b(X_0 - x_i^*)}, i = \overline{1,2}; \tag{5}$$

ii) If $\frac{b}{D_1} > \frac{\mathrm{e}^{\alpha X_0}}{X_0}$ (i.e. there exists only one boundary equilibrium) and $H < H_1$, then it is also at least one interior equilibrium, E_3.
iii) When the system has two boundary equilibria, $H_2 < H_1$.

Proof. First of all note that $z_3 > 0$ is equivalent to $bx_3\mathrm{e}^{-\alpha x_3} > \mathrm{D}_1$ or $x_3 \in (x_1^*, x_2^*)$, where $x_1^* < x_2^*$ are the two solutions of the equation $xe^{-\alpha x} = \frac{D_1}{b}$. Then notice that in equation (4) the coefficient $H - \mu br > 0$, due to the assumptions (4,5,6) of the model. A sufficient condition for equation (4) to have a solution $x_3 \in (x_1^*, x_2^*)$ is $g(x_1^*)g(x_2^*) < 0$ or in the form $x_1^* < X_0 - \frac{KD_1H}{b(r-H)} < x_2^*$ which in case i) becomes $H_2 < H < H_1$ and in case ii), $H < H_1$. We shall see that for $H = H_1$, $E_3 = E_1$ and in case i), for $H = H_2$, $E_3 = E_2$. □

Corollary 2.1. *If, in addition to the conditions in Proposition 2.2 we require*

$$H < r\frac{K\mu b + \mathrm{e}^2}{K + \mathrm{e}^2} =: H_0, \tag{6}$$

it follows that the equation $g(x) = 0$ has only one solution $x_3 \in (x_1^*, x_2^*)$, that is the equilibrium E_3 exists and it is unique. Otherwise, $g(x) = 0$ may have maximum three positive solutions, so there are maximum three interior equilibria.

Proof. $g'(x) = 1 + K\frac{H-\mu br}{r-H}(1-\alpha x)\mathrm{e}^{-\alpha x}$ attains its minimum $m = 1 - \frac{K(H-\mu br)}{\mathrm{e}^2(\mathrm{r}-\mathrm{H})}$ at $x = \frac{2}{\alpha}$. Because $g'(0) > 0$ and $\lim\limits_{x\to\infty} g'(x) > 0$, it turns out that if $m > 0$ (the condition (6)), then g is increasing . If $m < 0$, then $g'(x) = 0$ has two solutions and in consequence, the equation $g(x) = 0$ may have three positive solutions. □

Next we discuss the dynamics of the system (2) in the neighborhood of each equilibrium. The Jacobian matrix of the linearization of the system is

$$\frac{Dv}{D(x,y,z)} = \begin{pmatrix} -1 - ye^{-\alpha x}(1-\alpha x) & -xe^{-\alpha x} & \mu \\ bye^{-\alpha x}(1-\alpha x) & bxe^{-\alpha x} - D_1 - \frac{Kz}{(y+K)^2} & -\frac{y}{y+K} \\ 0 & \frac{rKz}{(y+K)^2} & \frac{ry}{y+K} - H \end{pmatrix} \tag{7}$$

Evaluating $\frac{Dv}{D(x,y,z)}$ at each equilibrium, we get the following results:

Proposition 2.3. *i) If $\frac{b}{D_1} < \frac{e^{\alpha X_0}}{X_0}$, the equilibrium E_0 is a hyperbolic stable node . If $\frac{b}{D_1} > \frac{e^{\alpha X_0}}{X_0}$, E_0 is a hyperbolic saddle . In any case, it is attractive in two directions in the plane $y = 0$;*
ii) The boundary equilibrium E_1 is locally asymptotically stable for $H > H_1$ and it is a hyperbolic saddle for $H < H_1$;
iii) E_2 is a hyperbolic saddle for the values of the parameters which ensure its existence, namely $\frac{b}{D_1} < \frac{e^{\alpha X_0}}{X_0}$, $X_0 > \frac{1}{\alpha}$ and for any H.

Proof. i) The eigenvalues of the Jacobian matrix evaluated at E_0 are $\lambda_1 = -1, \lambda_2 = -H, \lambda_3 = bX_0e^{-\alpha X_0} - D_1$ and the eigenvectors corresponding to $\lambda_{1,2} < 0$ are $u_1 = (1,0,0), u_2 = (\mu, 0, 1-H)$ which imply i).
ii),iii) For $E_i, i = \overline{1,2}$, the eigenvalues are $\lambda_1^i = \frac{br(X_0 - x_i^*)}{KD_1 + b(X_0 - x_i^*)} - H$ and $\lambda_{2,3}^i$ are the roots of the equation $\lambda^2 + (1+p_i)\lambda + D_1 p_i = 0$ with $p_i = \frac{(X_0 - x_i^*)(1-\alpha x_i^*)}{x_i^*}$. Hence, $p_1 > 0$ and in consequence, $Re(\lambda_{2,3}^1) < 0$, but $p_2 < 0$ so, $\lambda_2^2\lambda_3^2 < 0$ and E_2 becomes a saddle. □

The eigenvalues of the Jacobian matrix at the interior equilibrium $E_3(x_3, y_3, z_3)$ verify the characteristic equation

$$\lambda^3 + A_1\lambda^2 + A_2\lambda + A_3 = 0 \tag{8}$$

where

$$\begin{aligned} A_1 &= \frac{D_1 H}{r} + 1 + \frac{H}{r(r-H)}e^{-\alpha x_3}[Kr - x_3(b(r-H) + \alpha K r)]; \\ A_2 &= \frac{H}{r}(bx_3e^{-\alpha x_3} - D_1)[r - H - 1 - \frac{KH}{r-H}e^{-\alpha x_3}(1-\alpha x_3)] \\ &\quad + \frac{bKH}{r-H}e^{-2\alpha x_3}x_3(1-\alpha x_3); \\ A_3 &= (bx_3e^{-\alpha x_3} - D_1)(r-H)[\frac{KH}{r-H}e^{-\alpha x_3}(1-\alpha x_3)(\frac{H}{r} - \mu b) + \frac{H}{r}]. \end{aligned} \tag{9}$$

The necessary and sufficient condition for E_3 to be asymptotically stable is given by the Routh-Hurwitz criterion, i.e. $A_1A_2 > A_3$ and $A_1, A_3 > 0$;

The third component of E_3 has to be strictly positive, or equivalently $bx_3\mathrm{e}^{-\alpha x_3} - \mathrm{D}_1 > 0$. Then we notice that $A_1 > 0$ if

$$x_3 < \frac{rK}{b(r-H)+\alpha Kr}. \tag{10}$$

This implies $x_3 < \frac{1}{\alpha}$ and since $H > \mu br$, we have $A_3 > 0$.

With simple algebra, we deduce the following

Proposition 2.4. *If E_3 exists, the condition (10) holds and*

$$\left(\frac{H}{r}(bx_3e^{-\alpha x_3} - D_1) - 1 - \frac{KH}{r-H}e^{-\alpha x_3}(1-\alpha x_3)\right)\cdot$$
$$\cdot\left(\frac{bx_3e^{-\alpha x_3} - D_1}{r}\left(1 + \frac{KH}{r-H}e^{-\alpha x_3}(1-\alpha x_3)\right) - \frac{bK}{r-H}e^{-2\alpha x_3}x_3(1-\alpha x_3)\right) \tag{11}$$
$$+(bx_3e^{-\alpha x_3} - D_1)\left(b\mu Ke^{-\alpha x_3}(1-\alpha x_3) - \frac{H(r-H)}{r^2}(bx_3e^{-\alpha x_3} - D_1)\right) > 0$$

then the equilibrium E_3 is locally asymptotically stable.

The previous propositions are sintethized in the following

Theorem 2.1. *Let $X_0 > \frac{1}{\alpha}$, $H_1 < H_0$ and $D_1\alpha\mathrm{e} < b < \frac{D_1}{X_0}\mathrm{e}^{\alpha X_0}$. Then:*
i) If $H_2 > \mu$, for $H \in (\mu, H_2)$, the system (2) has at least three equilibria: E_0 as attractive node, E_1 and E_2 hyperbolic saddles;
ii) For $\max(\mu, H_2) < H < H_1$, the system has the equilibrium points E_0, E_1, E_2 as in the previous case and E_3 which is locally asymptotically stable (l.a.s.) if conditions (10) and (11) hold;
iii) For $H = H_2$, E_2 and E_3 concide;
iv) For $H = H_1$, E_1 and E_3 concide;
v) For $H_1 < H < r$, E_3 may be unphysical, E_1 becomes l.a.s., E_0 remains attractive node and E_2 hyperbolic saddle.

Theorem 2.2. *Let $H_1 < H_0$ and $b > \frac{D_1}{X_0}\mathrm{e}^{\alpha X_0}$. Then:*
i) For $\mu < H < H_1$, the system has the equilibrium points E_0, E_1 hyperbolic saddles and E_3 which is l.a.s. if conditions (10) and (11) hold;
ii) For $H = H_1$, E_1 and E_3 concide;
iii) For $H_1 < H < r$, E_3 may be unphysical, E_1 becomes l.a.s., E_0 remains hyperbolic saddle.

3. Bifurcation analysis

First we take b as the control parameter for the system (2).

Theorem 3.1. *If $H \neq \frac{\mathrm{e}r(\alpha X_0 - 1)}{\mathrm{e}(\alpha X_0-1)+K}, X_0 > \frac{1}{\alpha}$, for $b = \alpha\mathrm{e}D_1$, the boundary equilibria E_1 and E_2 appear through a saddle-node bifurcation. For $b < \alpha\mathrm{e}D_1$, these two equilibria do not exist.*

Proof. We fix $b = \alpha \mathrm{e} D_1$, then $x_1^* = x_2^* = \frac{1}{\alpha} < X_0$ and $y_1^* = y_2^*$, so $E_1 = E_2$. The eigenvalues corresponding to E_1 are $\lambda_1 = \frac{\mathrm{e}r(\alpha X_0 - 1)}{\mathrm{e}(\alpha X_0-1)+K} - H, \lambda_2 = 0, \lambda_3 = -1$, so we need $\lambda_1 \neq 0$ in order to have the codimension 1 bifurcation of saddle-node type.
Let be $\frac{DF}{Dv}(E_1, \alpha \mathrm{e} D_1)$ the Jacobian matrix of the system written in the form $v' = F(v, b)$, with b the bifurcation parameter and $v = (x, y, z)$, evaluated in E_1 for $b = \alpha \mathrm{e} D_1$. We use a theorem (Sotomayor [2]) which gives necessary and sufficient conditions for a saddle-node bifurcation. These are:
(SN1) $\frac{DF}{Dv}(E_1, \alpha \mathrm{e} D_1)$ has a single zero eigenvalue which is fulfilled, due to the hypothesis of the theorem. Let be $u = (1, -\mathrm{e}\alpha, 0)^{\mathrm{T}}$ its right eigenvector and $w = (0, r, 1)^T$ its left eigenvector.
(SN2) $w \cdot \frac{\partial F}{\partial b}(E_1, \alpha \mathrm{e} D_1) = r\alpha(\alpha X_0 - 1) \neq 0$.
(SN3) $w \cdot D_{vv}F(E_1, \alpha \mathrm{e} D_1)(u, u) = -\alpha^2 \mathrm{e D_1(\alpha X_0 - 1)r} \neq 0$.
The nonzero conditions (SN2) and (SN3) imply that $SN = \{b = \alpha \mathrm{e} D_1, H \neq \frac{\mathrm{e}r(\alpha X_0-1)}{\mathrm{e}(\alpha X_0-1)+K}, X_0 > \frac{1}{\alpha}\}$ is a saddle-node bifurcation surface in the parameters space. When the parameters pass from one side of the surface to the other side, the number of the boundary equilibria changes from zero when $b < \alpha \mathrm{e} D_1$ to two hyperbolic equilibria $E_{1,2}$ when $b > \alpha \mathrm{e} D_1$, in the neighborhood of $b = \alpha \mathrm{e} D_1$. These equilibria are connected by an orbit that is asymptotic to E_1 for $t \to \infty$ and to E_2 for $t \to -\infty$. □

Now we take H as a control parameter for the system.

Theorem 3.2. *If $X_0 > \frac{1}{\alpha}$, $b > \alpha \mathrm{e} D_1$ and*

$$\mu > \frac{K}{b} \frac{b(X_0 - x_1^*) - \mathrm{e}^2 D_1}{b(X_0 - x_1^*) + K D_1}, \tag{12}$$

then
a) *the equilibria E_1 and E_3 coincide for $H = \frac{br(X_0 - x_1^*)}{KD_1 + b(X_0 - x_1^*)} =: H_1$ at a point of transcritical bifurcation;*
b) *E_2 and E_3 coincide for $H = \frac{br(X_0 - x_2^*)}{KD_1 + b(X_0 - x_2^*)} =: H_2$ also at a point of transcritical bifurcation, if, in addition $b < \frac{D_1}{X_0} \mathrm{e}^{\alpha X_0}$.*

Proof. a) i) We fix $H = H_1$. The condition (12) is equivalent to $H_1 < r\frac{K\mu b + \mathrm{e}^2}{K + \mathrm{e}^2}$ which (see Proposition 2.2 and corrolary) implies that the solution x_3 of the equation (4), $g(x) = 0$, exists and it is unique. Then $H = H_1 \iff x_1^* = X_0 - \frac{KD_1 H}{b(r-H)}$. But $x_1^* < \frac{1}{\alpha}$ and verifies $x\mathrm{e}^{-\alpha x} = \frac{D_1}{b}$, in consequence $K\frac{H_1 - \mu br}{r - H_1} x_1^* \mathrm{e}^{-\alpha x_1^*} + x_1^* = X_0 - \frac{\mu D_1 r K}{r - H_1}$ and $x_1^* = x_3$. Also $y_3 = \frac{KH_1}{r - H_1} = y_1^*, z_3 = 0$ which imply $E_1 = E_3$. From the proof of Proposition 2.3, we have:
ii) For $H = H_1$, the eigenvalues for E_1 are $\lambda_1 = 0$, $Re(\lambda_{2,3}) < 0$, so only one eigenvalue is zero.
iii) On the other hand, the equilibrium E_1, from unstable (when $H < H_1$) becomes stable for $H > H_1$.
iv) We evaluate the matrix $\left(\frac{DF}{Dv} | \frac{\partial F}{\partial H}\right)$ at the bifurcation point (E_1, H_1) and we

find that $\frac{\partial F}{\partial H} = (0,0,0)^T$. It implies $rank\left(\frac{DF}{Dv}|\frac{\partial F}{\partial H}\right) = 2$.
From i)-iv) (see [5]), we deduce that in $\mathbb{R}^3_+ \times \{H > 0\}$ the branches of equilibria E_1 and E_3 intersect through a transcritical bifurcation at $H = H_1$ and change their stable manifold when we pass the critical parameter value.
b) There are similar arguments. The condition $b < \frac{D_1}{X_0}e^{\alpha X_0}$ ensures the existence of the equilibrium E_2. Then $H = H_2 \iff x_3 = x_2^* > \frac{1}{\alpha}$. Also only one eigenvalue (see proof of Proposition 2.3) corresponding to E_2 is zero for $H = H_1$. □

These values of the parameters $H = H_1$, $H = H_2$, $b = \alpha e D_1$ delimitate strata on parameters space induced by topological equivalence of the phase portraits.
We are now investigating dynamic bifurcations. The equilibrium E_3 is the only one which may experience Hopf bifurcation because only the interior equilibrium can have a pair of purely imaginary eigenvalues. This necessary condition for E_3 to undergo a Hopf bifurcation is equivalent to

$$A_1A_2 = A_3, A_2 > 0 \tag{13}$$

(with A_i given by (9)) together with the sufficient conditions for the existence of the interior equilibrium (see Proposition 2.2). Also we need that the third eigenvalue of E_3 to be non-zero, i.e. $A_3 \neq 0$, which is satisfied if $x_3 < \frac{1}{\alpha}$ with $g(x_3) = 0$. In this case, we have $A_3 > 0$ and so the characteristic equation (8) admits the roots $\lambda_{1,2} = \pm i\omega$, $\omega > 0$ and $\lambda_3 = -A_1 < 0$.

4. **Numerical results**

We take H as a control parameter. We fix the parameters in order to be in the case $D_1\alpha e < b < D_1\frac{e^{\alpha X_0}}{X_0}$ (see Theorem 2.1): $K = 1; \alpha = 1.2; r = 0.3; b = 0.66; D_1 = 0.2; \mu = 0.1; X_0 = 1$. This case corresponds with the existence of two boundary equilibria $E_i(x_i^*, y_i^*, 0)$, $i = \overline{1,2}$. With a program in MAPLE, we find the solutions of the equation $xe^{-\alpha x} = \frac{D_1}{b}$, $x_1^* = \frac{LambertW(0,-\frac{\alpha D_1}{b})}{\alpha} = 0.71276$,$x_2^* = \frac{LambertW(-1,-\frac{\alpha D_1}{b})}{\alpha} = 0.96679$, then $y_1^* = 0.94789$, $y_2^* = 0.10958$. The static bifurcation parameters are $H_2 = 0.029628 < H_1 = 0.1459872$.

We solve numerically the system

$$\begin{aligned} A_1A_2 &= A_3 \\ g(x_3) &= 0 \\ A_2 > 0,\ x_3 < \frac{1}{\alpha},\ bx_3e^{-\alpha x_3} - D_1 &> 0 \end{aligned} \tag{14}$$

which are the necessary conditions for Hopf bifurcation of E_3 and we find the bifurcation parameter value $H = H_{cr} = 0.112115$ and $x_3 = 0.81746422$.

$H_{cr} \in (H_2, H_1)$, $H_1 < H_0$ and we are in the hypothesis of Proposition 2.2 and its corollary. There is only one interior equilibrium for any $H \in (H_2, H_1)$.

Then, we investigate the appearance of a limit cycle when H is in the neighborhood of the critical parameter value. We find that for $H < H_{cr}$ an asymptotically stable limit cycle appears.

For example, when $H = 0.11 \in (H_2, H_{cr})$, the solution of equation $g(x_3) = 0, bx_3 e^{-\alpha x_3} > D_1$ is $x_3 = 0.822894$. Then $y_3 = 0.5789; z_3 = 0.00365$. With initial conditions close to E_3, we integrate numerically the system. With a program in MATLAB we obtain the phase portrait. The trajectories come together close to the saddle connection between E_1 and E_2, towards E_1 and then tend to a stable limit cycle, while E_3 is repelling. (see Figure 1)

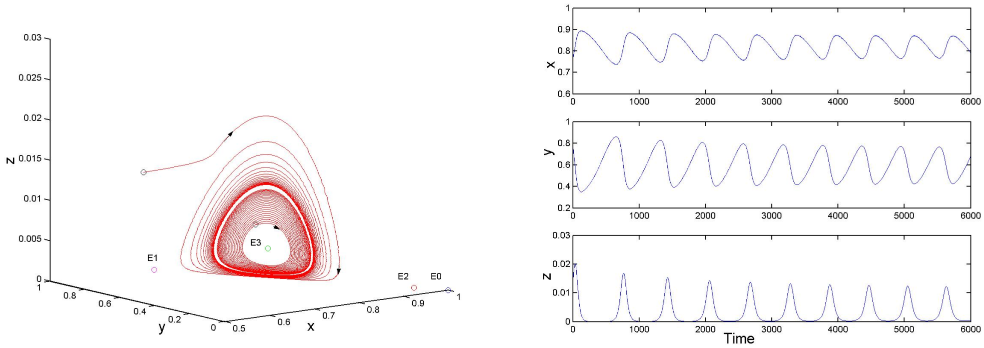

FIGURE 1. Left: A stable limit cycle when $K = 1; \alpha = 1.2; r = 0.3; b = 0.66; D_1 = 0.2; \mu = 0.1; X_0 = 1; H = 0.11 < H_{cr}$. Right: Time oscillations of populations corresponding to one of the trajectories, with initial values $(0.6228; 0.7789; 0.0136)$.

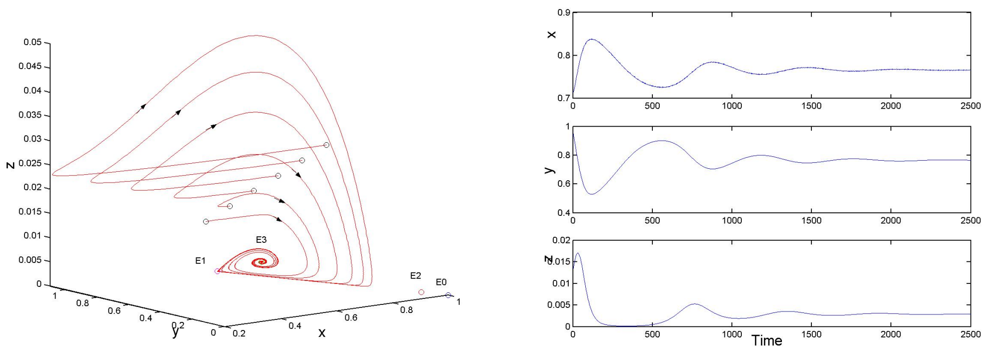

FIGURE 2. Left: Trajectories tending to the attractive focus E_3. The modified parameter is $H = 0.13 > H_{cr}$. Right: Time evolution of the three populations corresponding to one of the trajectories, with initial values $(0.7666; 0.9647; 0.0129)$.

For $H = 0.13 \in (H_{cr}, H_1)$, trajectories initiated in a small neighborhood of E_3, come together very close to the saddle connection $E_2 \to E_1$ and tend for $t \to \infty$ to E_3 as a focus. (see Figure 2)

In consequence, (E_3, H_{cr}) is a point of supercritical Hopf bifurcation because, when H varies and passes the critical value, from a stable equilibrium E_3 for $H > H_{cr}$, it appears a stable limit cycle for $H < H_{cr}$, while E_3 loses its stability.

5. **Conclusions**

The harvesting rate (H) of top predator can control the stable equilibrium point or periodic state of coexistence of the three species.

First of all, the model illustrates the phenomenon of biological overharvesting when $H > H_1$ and in this case the top-predator goes to extinction.

If the detritus-detritivores conversion rate b is not high, $D_1 \alpha \mathrm{e} < b < \frac{D_1 \mathrm{e}^{\alpha X_0}}{X_0}$, the scenario of extinction of both detritivores and top-predator is possible, for any value of the harvesting rate, depending on initial population levels.

When we decrease H, for $H \in (H_{cr}, H_1)$, all the populations coexist in a form of a stable equilibrium, under certain initial conditions. When H passes through a critical value, H_{cr}, the system undergoes a Hopf bifurcation, namely for $H \in (max(\mu, H_2), H_{cr})$, different populations of the system will start to oscillate with a finite period around the equilibrium point of coexistence.

Since $H = \frac{d_2+h}{a}$, it turns out that also for increasing large values of washout rate (a) of detritus, the system changes from a stable state to an unstable state and the populations will survive through periodic fluctuations.

Mathematically, we would like to point out here that our analysis of the model is a first look at the local bifurcations, but it is not complete. For example a study of codimension 2 bifurcations will reveal richer dynamics.

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