Food-chain dynamics in a mangrove ecosystem with harvesting

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Abstract. In this paper we have considered a three dimensional ordinary differential system which models a food-chain in a mangrove ecosystem. The important characteristics of the model are the phenomenon of group defense between the populations of level 1 and 2 and harvesting with a constant rate on the top predator. We establish the domains in the parameters space where the equilibrium points exist and also those that insure their local stability. We find numerically a point of supercritical Hopf bifurcation as the value of the harvesting rate parameter is varied and in consequence the system admits a stable limit cycle. We deduce the important types of dynamics of the system and by numerical integration, we obtain the phase portraits for these dynamics and plots of time course for the corresponding solutions.

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1 Introduction

Mangroves are intertidal plant communities grown up in marine sediments which are mostly found along marine coasts and estuaries. Mangrove forests consist of shrub or tree-like plants. The leaves of these plants fall into the mud and sand flats below, disintegrate by grazing and microbial activity, and in the process contribute to a huge resource of detrital material. Some algal species present within the mud act as a secondary source of detritus for this ecosystem. The food resource of mangrove plants (detritus) is consumed by small unicellular animals, crustacean, amphiopod and so forth. These are considered as detritivores. These detritivores, in turn, act as an ideal food source for fish, insect intruders, and so on, namely the predators of detritivores. This has created a three-level food chain for the ecosystem. The model we have proposed is a three dimensional ordinary differential autonomous system of

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predator-prey type. After we non-dimensionalized the system in [1], we obtained the form

$$\begin{cases} x'(t) = X_0 - x - xy\mathrm{e}^{-\alpha x} + \mu z \\ y'(t) = bxy\mathrm{e}^{-\alpha x} - D_1 y - \frac{yz}{K+y} \\ z'(t) = \frac{ryz}{K+y} - Hz, \end{cases} \tag{1.1}$$

where $x(t)$ is the detritus density at time t, $y(t)$ is the detritivores population density and $z(t)$-the top predator density. The initial conditions are $x(0), y(0), z(0) \geq 0$. 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.[6] Also the detritus is supplied with dead organic matter converted into detritus by the action of the micro-organisms.

2. The interaction between detritus and detritivores differs 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 [5] 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. (see [2]). One of the nonmonotone functional response introduced by Ruand and Freedman [7] is $p(x) = bx\mathrm{e}^{-\alpha x}$, 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 which includes the death rate of fish population.

4. The detritus-detritivores conversion rate, b is less then the detritus uptake rate, so $b < 1$.

5. For the same reason, the detritivore-predator conversion rate is $r < 1$.

6. Also, the detritus recycle rate due to the death of predators, μ is less than H.

We shall perform a bifurcation study of the system and deduce the important types of its dynamical behavior. We proved in [1] that the first octant $\mathbb{R}^3_+$ is positively invariant under the flow generated by the system (1.1) and with the assumptions 4,5 and 6, we found that every solution of the system with positive initial values, is bounded, so the first octant will be the domain of variables.

2 The equilibrium points and stability analysis

Now we determine the location and the existence criteria for the equilibria of the system (1.1) in the first octant.

Proposition 2.1. *a) There is an axial equilibrium* $E_0(X_0, 0, 0)$, *for any values of the parameters;*
b) If $\alpha\mathrm{e} < \frac{b}{D_1} < \frac{\mathrm{e}^{\alpha X_0}}{X_0} =: b_0$ *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* $x\mathrm{e}^{-\alpha x} = \frac{D_1}{b}$ *and* $y_i^* = (X_0 - x_i^*)\frac{b}{D_1}$, $i = \overline{1,2}$;

c) If $\frac{b}{D_1} > b_0$*, there exists only one boundary equilibrium* $E_1(x_1^*, y_1^*, 0)$ *with* x_1^* *and* y_1^* *given in b) and* $x_1^* < \frac{1}{\alpha}$*;*
d) If $\frac{b}{D_1} < \alpha \mathrm{e}$*, there are no boundary equilibria in* $\mathbb{R}_+^3$*.*

Next we give a sufficient existence criterion for the interior equilibrium $E_3(x_3, y_3, z_3)$, where x_3 is a solution of the equation:

$$g(x) := K\frac{H - \mu br}{r - H} x\mathrm{e}^{-\alpha x} + x + \frac{\mu D_1 rK}{r - H} - X_0 = 0, \tag{2.1}$$

$y_3 = \frac{HK}{r-H}$ and $z_3 = (bx_3\mathrm{e}^{-\alpha x_3} - D_1)\frac{rK}{r-H}$. We assume that $r > H$ from now on.

Proposition 2.2. *i) If* $\alpha\mathrm{e} < \frac{\mathrm{b}}{\mathrm{D_1}} < \mathrm{b}_0$ *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* $H_i := \frac{br(X_0 - x_i^*)}{KD_1 + b(X_0 - x_i^*)}$*,* $i = \overline{1, 2}$*;*
ii) If $\frac{b}{D_1} > b_0$ *(i.e. there exists only one boundary equilibrium) and* $H < H_1$*, then it is also at least one interior equilibrium,* E_3*.*

Remark The equilibria E_1 and E_3 coincide for $H = H_1$; E_2 and E_3 coincide for $H = H_2$. When the system has two boundary equilibria, $H_2 < H_1$.

Corollary 2.3. *If, in addition to the conditions in Proposition 2.2 we require* $H < r\frac{K\mu b + \mathrm{e}^2}{K + \mathrm{e}^2}$*, it follows that the equation* $g(x) = 0$ *has only one solution* $x_3 \in (x_1^*, x_2^*)$*, that is the interior 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.*

Proposition 2.4. *i) The equilibrium* E_0 *is a hyperbolic stable node if* $\frac{b}{D_1} < b_0$*.* E_0 *is a hyperbolic saddle if* $\frac{b}{D_1} > b_0$*;*
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* $\alpha\mathrm{e} < \frac{b}{D_1} < b_0$*,* $X_0 > \frac{1}{\alpha}$ *and for any* H*.*

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

$$\lambda^3 + A_1\lambda^2 + A_2\lambda + A_3 = 0, \tag{2.2}$$

where

$$\begin{aligned}
A_1 &= \tfrac{D_1 H}{r} + 1 + \tfrac{H}{r(r-H)} e^{-\alpha x_3}[Kr - x_3(b(r - H) + \alpha Kr)];\\
A_2 &= \tfrac{H}{r}(bx_3 e^{-\alpha x_3} - D_1)[r - H - 1 - \tfrac{KH}{r-H} e^{-\alpha x_3}(1 - \alpha x_3)] + \tfrac{bKH}{r-H} e^{-2\alpha x_3} x_3(1 - \alpha x_3);\\
A_3 &= (bx_3 e^{-\alpha x_3} - D_1)(r - H)\left[\tfrac{KH}{r-H} e^{-\alpha x_3}(1 - \alpha x_3)\left(\tfrac{H}{r} - \mu b\right) + \tfrac{H}{r}\right].
\end{aligned} \tag{2.3}$$

The necessary and sufficient condition for $E_3(x_3, y_3, z_3)$ to be asymptotically stable is given by the Routh-Hurwitz criterion, i.e. $A_1 A_2 > A_3$ and $A_1, A_3 > 0$.

Proposition 2.5. *If the interior equilibrium* E_3 *exists,* $x_3 < \frac{rK}{b(r-H) + \alpha Kr}$ *and* $A_1 A_2 > A_3$ *then* E_3 *is locally asymptotically stable.*

3 Bifurcation analysis

We take H as a control parameter. We proved in [1] that the values $H = H_1$ and $H = H_2$ determine static bifurcation (the second one, only in the case when the system admits two boundary equilibria), so when the parameter H passes through these values, the topological structure of the phase portrait changes, more precise the number of equilibria and their stability properties change. We are now investigating whether the system admits a stable limit cycle because it also represents a state of coexistence for the ecological system as it does the stable interior equilibrium. When we talk about periodic solutions, Hopf bifurcation points are first to be considered.

Suppose we have an autonomous system of ODE $u' = F(u,p)$, where $u \in \mathbb{R}^n$ is the vector of variables and $p \in \mathbb{R}^m$ is the vector of parameters. Then $(u_0, p_0) \in \mathbb{R}^n \times \mathbb{R}^m$ is a Hopf point, provided there exists $a > 0$ such that there is a smooth function $\varphi : [-a,a] \to \mathbb{R}^{n+m}$, $\varphi(\xi) = (u(\xi), p(\xi))$ such that
i) $\varphi(0) = (u_0, p_0)$;
ii) $F(\varphi(\xi)) = 0, \forall \xi \in [-a,a]$;
iii) The Jacobian matrix $\frac{DF}{Du}(u(\xi), p(\xi))$ has at least one pair of conjugated complex eigenvalues $\mu(\xi) \pm i\omega(\xi)$, $\forall \xi \in [-a,a]$ with $\mu(0) = 0, \mu'(0) \neq 0, \omega(0) \neq 0$;
iv) All others eigenvalues of the Jacobian matrix except $\pm i\omega(0)$, evaluated at $\xi = 0$, have nonzero real parts.

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 can be reformulated as $A_1 A_2 = A_3$, $A_2 > 0$ (A_i given by (2.3)) together with the sufficient conditions for the existence of the interior equilibrium (see Proposition 2.2).

Denote by H_{cr} a value of the harvesting rate which verifies the necessary condition. Let $\lambda_{1,2}(H) = \mu(H) \pm i\omega(H)$ and $\lambda_3(H)$ be the solutions of the characteristic equation (2.2) defined in a neighborhood of H_{cr} with $\lambda_{1,2}(H_{cr}) = \pm i\omega_0$, $\omega_0 > 0$. The others conditions for Hopf bifurcation are the nondegeneracy condition $\lambda_3(H_{cr}) \neq 0$;
and the transversality condition $\mu'(H_{cr}) \neq 0$.
The characteristic equation (2.2) for $H = H_{cr}$ takes the form $(\lambda - \lambda_3)(\lambda^2 + \omega_0^2) = 0$ and in consequence $\lambda_3 = -A_1 = -\frac{A_3}{\omega_0^2}$. Note that $A_3 > 0$ if $x_3 < \frac{1}{\alpha}$ and in this case $\lambda_3(H_{cr}) < 0$. Applying theorems 5.2 and 5.4 from [4], we deduce that the system has a parameter-dependent 2-dimensional local invariant manifold, where the Hopf bifurcation takes place, namely the center manifold. For values of H close to H_{cr}, this manifold is attracting. Simple algebra gives that $\mu(H)$ verifies the relation:

$$8\mu^3 + 8\mu^2 A_1 + 2(A_2 + A_1^2)\mu + A_1 A_2 - A_3 = 0. \tag{3.1}$$

We obtain $\mu'(H_{cr}) = \frac{d}{dH}(A_3 - A_1 A_2) \frac{1}{2(A_2 + A_1^2)}\Big|_{H_{cr}}$ so the transversality condition is equivalent to $\frac{d}{dH}(A_3 - A_1 A_2)\Big|_{H_{cr}} \neq 0$.

Theorem 3.1. *The point (E_3, H_{cr}) is a Hopf bifurcation point, if it verifies the system* (3.2)

$$A_1 A_2 = A_3, A_2 > 0, \quad g(x_3) = 0, \quad b x_3 e^{-\alpha x_3} > D_1, \quad x_3 < \frac{1}{\alpha}, \quad \frac{d}{dH}(A_3 - A_1 A_2) \neq 0.$$

The bifurcation takes place on some 2-dimensional attracting manifold.

The direction and type of the Hopf bifurcation will be investigated with numerical methods.

4 Numerical results

H is the control parameter. We fix the parameters in order to be in the Case I) $D_1\alpha\mathrm{e} < \mathrm{b} < \mathrm{D_1b_0}$ (Proposition 2.1b)): $K = 1; \alpha = 1.2; r = 0.3; D_1 = 0.2; \mu = 0.1; X_0 = 1; b = 0.66$. 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 $x\mathrm{e}^{-\alpha \mathrm{x}} = \frac{\mathrm{D_1}}{\mathrm{b}}$, $x_1^* = 0.71276$, $x_2^* = 0.96679$, then $y_1^* = 0.94789$, $y_2^* = 0.10958$. We solve numerically the system (3.2) from the theorem of bifurcation and we detect a point of Hopf bifurcation for E_3, $H = H_{cr} = 0.112115$ and $x_3 = 0.81746422$. The static bifurcation parameters are $H = H_2 = 0.029628$ when $E_2 = E_3$ and $H = H_1 = 0.1459872$ when $E_3 = E_1$.

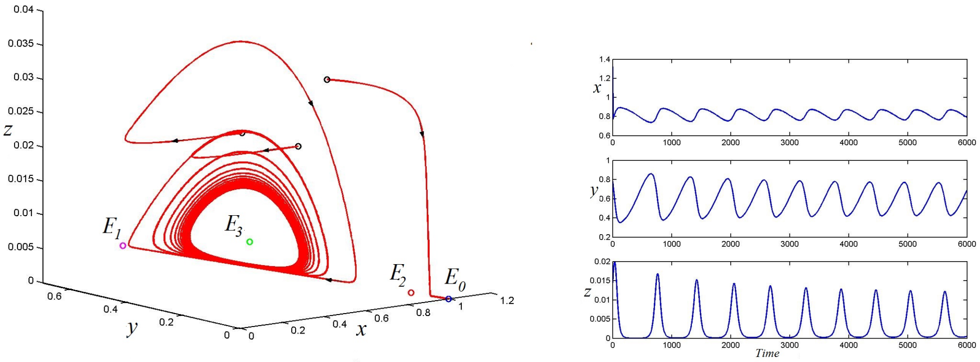

Figure 1: Left: The phase portrait when $K = 1; \alpha = 1.2; r = 0.3; D_1 = 0.2; \mu = 0.1; X_0 = 1; b = 0.66 \in (D_1\alpha\mathrm{e}, \mathrm{D_1b_0})$ and $H = 0.11 < H_{cr}$. A stable limit cycle appears. Right: Time oscillations of populations corresponding to one of the trajectories, which approach the limit cycle.

When H is in the neighborhood of H_{cr}, we find that for $H < H_{cr}$ an asymptotically stable limit cycle appears. With a program in MATLAB, we obtain the phase portrait for $H = 0.11 \in (H_2, H_{cr})$. With initial conditions close to $E_3(0.82289, 0.5789, 0.00365)$, trajectories come together close to the saddle connection between E_1 and E_2 and then tend to an asymptotically stable limit cycle, while E_3 is repelling. Other trajectories will approach E_0 for $t \to \infty$, so the stability of the limit cycle is only local.(figure 1)

For $H = 0.14 \in (H_{cr}, H_1)$, trajectories initiated in a small neighborhood of $E_3(0.73396, 0.875, 0.00145)$, come together very close to the saddle connection $E_2 \to E_1$ and tend to E_3 which is locally asymptotically stable.(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.

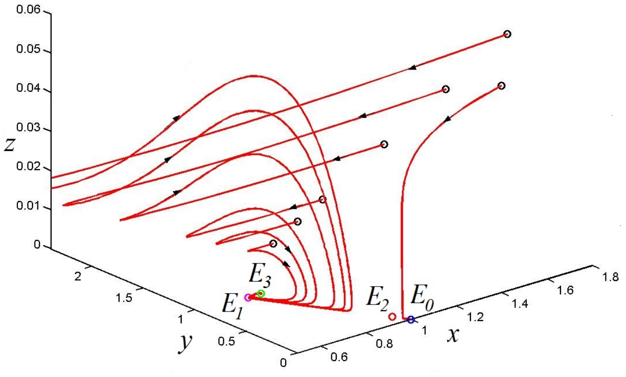

Figure 2: The phase portrait when $K = 1; \alpha = 1.2; r = 0.3; D_1 = 0.2; \mu = 0.1; X_0 = 1; b = 0.66 \in (D_1\alpha\mathrm{e}, \mathrm{D_1 b_0})$ and $H = 0.14 \in (H_{cr}, H_1)$. The interior equilibrium E_3 is a locally attractive node.

Also we fix the parameters in order to be in the
Case II) $b > D_1 b_0$ (Proposition 2.1c)):$K = 1; \alpha = 1.2; r = 0.3; D_1 = 0.2; \mu = 0.1; X_0 = 1; b = 0.9$ when there is only one boundary equilibrium, E_1. Its first coordinate is the unique solution of the equation $x\mathrm{e}^{-\alpha \mathrm{x}} = \frac{\mathrm{D_1}}{\mathrm{b}}$, $x_1^* = 0.33032 < X_0$. We detected numerically a Hopf bifurcation parameter value $H_{cr} = 0.17201$ for E_3. When $H = H_1 = 0.22525$, the branches of equilibria E_3 and E_1 intersect. With a program in MATLAB, we obtain phase portraits of the system topologically nonequivalent.

For $H = 0.16 < H_{cr}$, the trajectories with initial values which are in a neighborhood of $E_3(0.67211, 1.14285, 0.15)$, come close to the saddle connection $E_0 \rightarrow E_1$ and finally approach a stable limit cycle, while E_3 becomes unstable. Our simulations showed that the cycle is a global attractor for the interior of the first octant. (see figure 3)

For $H = 0.18 \in (H_{cr}, H_1)$, the orbits spiral to the stable focus $E_3(0.58109, 1.5, 0.151)$ as $t \rightarrow \infty$. (see figure 4)
As in the previous case, the numerical simulations for case II) indicate the supercritical type of Hopf bifurcation for the interior equilibrium.

5 Conclusions

Our analysis of the model and the study of the local bifurcations under the variation of parameter H, lead us to establish the important types of dynamics.

The model illustrates the phenomenon of biological overharvesting when $H > H_1$ and in this case the fish-population goes to extinction.

When the detritus-detritivores conversion rate b is average (i.e. $D_1\alpha\mathrm{e} < b < D_1 b_0$), the scenario of extinction of both detritivores and top-predator is possible, for any

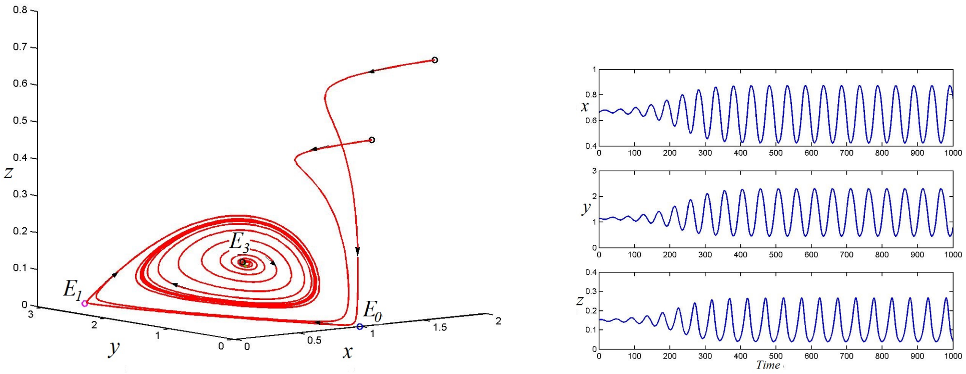

Figure 3: Left: A stable limit cycle for $K = 1; \alpha = 1.2; r = 0.3; D_1 = 0.2; \mu = 0.1; X_0 = 1; b = 0.9 > D_1 b_0$ and $H = 0.16 < H_{cr}$. Right: The time evolution of one of the solutions, which approach the limit cycle for $t \to \infty$.

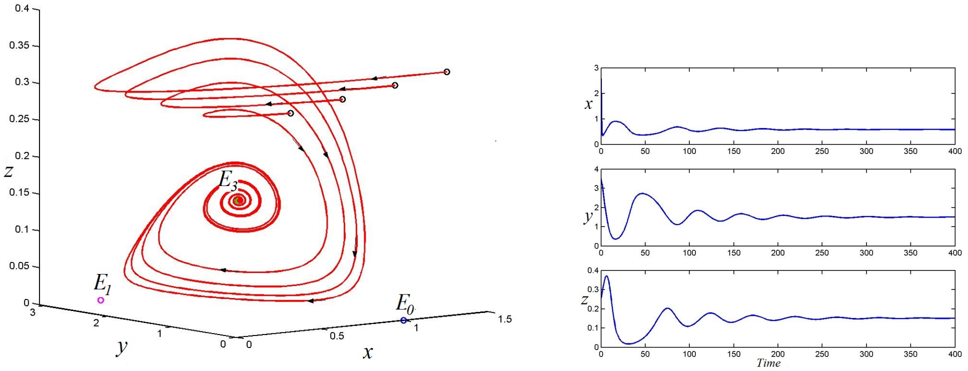

Figure 4: Left: The phase portrait for $K = 1; \alpha = 1.2; r = 0.3; D_1 = 0.2; \mu = 0.1$; $X_0 = 1; b = 0.9 > D_1 b_0$ and $H = 0.18 \in (H_{cr}, H_1)$. Right: The atenuated oscillations of the three populations which corresponds to one of the trajectories tending to the focus E_3.

value of the harvesting rate H, under certain initial population levels.

For $H \in (H_{cr}, H_1)$, the system evolves to the stable state of coexistence, E_3, but for average b this depends of the initial values of the populations.

When H decreases, we detected a Hopf bifurcation point for the interior equilibrium, namely for $H \in (max(\mu, H_2), H_{cr})$ and average b or for $H \in (\mu, H_{cr})$ and $b > D_1 b_0$, an asymptotically stable limit cycle appears, so the populations of the system will start to oscillate with a finite period around the equilibrium point of coexistence.

If the detritus recycle rate due to the death of predators, μ is not too high, namely $\mu < H_2$ and average b, then for low harvesting rate, i.e. $H \in (\mu, H_2)$, the populations of detritivores and fish go to extinction.

In consequence, the exploitation rate of top predator can control the stable equilibrium point or periodic state of coexistence of the three species.

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