



Study of a Leslie–Gower-type tritrophic population model

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Abstract

A three-dimensional continuous time dynamical system is considered. It is a model for a tritrophic food chain, based on a modified version of the Leslie–Gower scheme. We establish and prove theorems on boundedness of the system, existence of an attracting set, existence and local or global stability of equilibria which represent the extinction of the top or intermediate predator. Using intensive numerical qualitative analysis we show that the model could exhibit chaotic dynamics for realistic parameter and state values. Transition to chaotic behavior is established via period doubling bifurcation, and some sequences of distinctive period-halving are found.

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1. Introduction

In this paper we are interested in a three-dimensional system of autonomous differential equations, modeling a tritrophic food web. Much literature exists on the general problem of food chains. It often concerns (two or) three trophic-level food chains models composed of logistic prey X and Lotka–Volterra or Holling type II specialist predator Y and top-predator Z , see for example [1–9], while the model we study here is especially based on a modified version of the Leslie–Gower scheme [10]. Given some reasonable restrictions on the model, we determine the conditions and establish results for boundedness of the system and local or global stability of equilibria which represent the extinction of the top or intermediate predator. A rapid study near the XY -plane is also performed. Studies on ‘realistic’ ecological situations exist in the literature, see [11,14,20–22,35]. By ‘realistic’ ecological situations we mean one where the regions of parameters chosen for numerical experiments contain parametric values which are not arbitrary but are quantitative measures of the system attributes. Using realistic regions of parameters, as in [14,15,20,22], numerical qualitative analysis of the asymptotic behavior of the system is performed. Some interesting numerical results on this model are given in [12,13]. The transition behavior when some parameters of the system vary is studied. Chaotic dynamics is observed via sequences of period-doubling bifurcation of limit cycles (in a relatively broad range of parameters) which however break down and reverse giving rise to a sequence of distinctive period-halving. Indeed, recent studies indicate that chaotic dynamics may play an important role in continuous time models, see [4,6,9,11,12,23,24] for example. Our intensive numerical study has a similar orientation and suggests that natural terrestrial systems may be suitable candidates for researching chaos, even though the regions of parameters, in which the dynamics is chaotic, can be small.

This paper is organized as follows. In Section 2, the model is described and rescaling transformations to obtain a simpler analytical form are given. In Section 3, the boundedness of the solutions of this system and the existence of a positively invariant attracting set are established. The equilibria, which represent the extinction of the specialist predator or top-predator, and their stability are the subject of Section 4 (the study of interior equilibria is left aside) using a study near the XY -plane. The question of existence of chaos is numerically studied in Section 5.

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2. The mathematical model

The three-species food chain model, studied analytically as well as numerically, describes a prey population X which serves as the only food for a predator Y . This specialist predator Y is, in turn, the prey of a top-predator Z . The interaction between species Y and its prey X has been modeled by the Volterra scheme (predator population dies out exponentially in the absence of its prey). But, the interaction between species Z and its prey Y has been modeled by the Leslie–Gower scheme [10,25,26] (the loss in a predator population is proportional to the reciprocal of *per capita* availability of its most favourite food), see also [14,22]. The state equations for the three components of the chain population can be written as follows:

$$\begin{aligned}\frac{dX}{dT} &= a_0X - b_0X^2 - \frac{v_0XY}{d_0 + X}, \\ \frac{dY}{dT} &= -a_1Y + \frac{v_1XY}{d_1 + X} - \frac{v_2YZ}{d_2 + Y}, \\ \frac{dZ}{dT} &= c_3Z^2 - \frac{v_3Z^2}{d_3 + Y},\end{aligned}\tag{1}$$

with $X(0) \geq 0$, $Y(0) \geq 0$ and $Z(0) \geq 0$, where X , Y and Z represent the population densities at time T ; $a_0, b_0, v_0, d_0, a_1, v_1, d_1, v_2, d_2, c_3, v_3$ and d_3 are model parameters assuming only positive values and are defined as follows: a_0 is the growth rate of prey X , b_0 measures the strength of competition among individuals of species X , v_0 is the maximum value which *per capita* reduction rate of X can attain, d_0 measures the extent to which environment provides protection to prey X , a_1 represents the rate at which Y will die out when there is no X , v_1 and d_1 have a similar meaning as v_0 and d_0 , v_2 and v_3 have a similar biological connotation as that of v_0 and v_1 , d_2 is the value of Y at which the *per capita* removal rate of Y becomes $v_2/2$, c_3 describes the growth rate of Z , assuming that the number of males and females is equal, d_3 represents the residual loss in species Z due to severe scarcity of its favorite food Y ; the second term on the right-hand side in the third equation of (1) depicts the loss in the top-predator population.

Remark (*Origin of the model*). Let us remark that the first two equations of system (1) are standard. By contrast, the third equation is absolutely not standard. The system obtained by replacing this third equation by the equation

$$\frac{dZ}{dT} = \left(\frac{k_1Y}{k_2 + Y} - k_3 \right) Z,$$

that is a system in which X is the number of logistic prey, Y the number of Holling-type II intermediate predator and Z the number of Holling-type II top-predator, has been studied by many authors, see [4,5,27] and references therein. Even if its behavior can be complicated, these authors have given a number of results including study of stability of equilibria, bifurcation phenomena or chaotic behavior. The system we study here is different due to this third equation. Indeed, an interesting formulation for the predator dynamics given by Leslie [25] and discussed by Leslie and Gower [10] and Pielou [28] is

$$\frac{dZ}{dT} = c_3Z \left(1 - \frac{Z}{S_1Y} \right),$$

where c_3 and S_1 are model parameters. In this formulation, the growth of the predator population is of logistic form (i.e., $dZ/dT = c_3Z(1 - (Z/K))$), but the conventional K , which measures the carrying capacity set by the environmental resources, is $K = S_1Y$, proportional to prey abundance. Thus, the logistic equation becomes

$$\frac{dZ}{dT} = c_3Z \left(1 - \frac{Z}{S_2 + S_1Y} \right),$$

the additional constant S_2 , appearing in the denominator, normalises the residual reduction in the predator population Z because of severe scarcity of the favourite food. We then get the following equation:

$$\frac{dZ}{dT} = c_3Z - \frac{c_3}{S_1} \left(\frac{Z^2}{\frac{S_2}{S_1} + Y} \right) = c_3Z - \frac{v_3Z^2}{d_3 + Y}.$$

Finally, we get the third equation of system (1):

$$\frac{dZ}{dT} = c_3 Z^2 - \frac{v_3 Z^2}{d_3 + Y},$$

in which the square term $c_3 Z^2$ signifies the fact that mating frequency is directly proportional to the number of males as well as to that of females, see [19,22].

This third equation says that in the absence of the intermediate predator ($Y = 0$, but the Leslie–Gower formulation of predator–prey breaks down in such a case), the top-predator Z goes extinct if

$$c_3 d_3 < v_3, \tag{2}$$

and grows unboundedly if the opposite, which is, of course, biologically not acceptable. In fact, throughout the paper, we, anyway, will assume that condition (2) holds (indeed, condition (7) of Theorem 3 implies condition (2)).

The system we study in the present paper is then different and may, for example, be considered as a representation of a rodent–snake–peacock food chain, nature abounds in systems which exemplify this model, see [22,29].

We can reduce the number of parameters in the system from 12 to 8 by the following scaling transformations, even if, for our numerical tests, we will continue to use the original system (1):

$$X = \frac{a_0}{b_0} x, \quad Y = \frac{a_0^2}{b_0 v_0} y, \quad Z = \frac{a_0^3}{b_0 v_0 v_2} z, \quad T = \frac{t}{a_0}, \tag{3}$$

and

$$a = \frac{b_0 d_0}{a_0}, \quad b = \frac{a_1}{a_0}, \quad c = \frac{v_1}{a_0}, \quad d = \frac{d_2 v_0 b_0}{a_0^2}, \quad p = \frac{c_3 a_0^2}{b_0 v_0 v_2}, \quad q = \frac{v_3}{v_2}, \quad r = \frac{d_3 v_0 b_0}{a_0^2}. \tag{4}$$

All these parameters, of course, assume only positive values. We henceforth assume, without loss of generality, that the environment provides an equal protection for species X and Y . That is, $d_0 = d_1$. Thus, system (1) becomes

$$\begin{aligned} \frac{dx}{dt} &= x(1-x) - \frac{xy}{x+a}, \\ \frac{dy}{dt} &= \frac{cxy}{x+a} - by - \frac{yz}{y+d}, \\ \frac{dz}{dt} &= pz^2 - \frac{qz^2}{y+r}, \end{aligned} \tag{5}$$

$x(0) = x_0 \geq 0$, $y(0) = y_0 \geq 0$ and $z(0) = z_0 \geq 0$. The state space of the system is the non-negative cone

$$\mathbb{R}_+^3 = \{(x, y, z) \in \mathbb{R}^3, x \geq 0, y \geq 0, z \geq 0\}.$$

We will investigate the asymptotic behavior of orbits starting in the positive cone

$$\text{Int}(\mathbb{R}_+^3) = \{(x, y, z) \in \mathbb{R}^3, x > 0, y > 0, z > 0\}.$$

We will also note \mathbb{R}_{xy}^+ the first non-negative quadrant

$$\mathbb{R}_{xy}^+ = \{(x, y) \in \mathbb{R}_{xy}^2, x \geq 0, y \geq 0\}.$$

3. Boundedness of the solutions

Lemma 1. *The positive cone $\text{Int}(\mathbb{R}_+^3)$ is invariant for system (5).*

Proof. We first observe that the boundaries of the non-negative cone \mathbb{R}_+^3 are invariant, this is obvious from system (5). Therefore, the densities $x(t)$, $y(t)$ and $z(t)$ are positive: for $t \geq 0$, if $x(0) > 0$, $y(0) > 0$ and $z(0) > 0$ then $x(t) > 0$, $y(t) > 0$ and $z(t) > 0$. The basic existence and uniqueness theorem for differential equations ensures that positive solutions and the axis cannot intersect. \square

We will show that, under some assumptions, solutions $x(t)$, $y(t)$, $z(t)$ of system (5) are bounded, for t sufficiently large. First, to make the paper more readable, let us recall and prove the (classical) following comparison lemma.

Lemma 2. Let ϕ be an absolutely continuous function satisfying the differential inequality:

$$\frac{d\phi(t)}{dt} + k_1\phi(t) \leq k_2, \quad t \geq 0, \quad (6)$$

where $(k_1, k_2) \in \mathbb{R}^2$, $k_1 \neq 0$. Then, for all $t \geq \tilde{T} \geq 0$,

$$\phi(t) \leq \frac{k_2}{k_1} - \left(\frac{k_2}{k_1} - \phi(\tilde{T}) \right) e^{-k_1(t-\tilde{T})}.$$

Proof. Multiply both sides of (6) by $e^{k_1 t}$ to get

$$\left(\frac{d\phi(t)}{dt} + k_1\phi(t) \right) e^{k_1 t} \leq k_2 e^{k_1 t}.$$

Then

$$\left(\frac{d\phi(t)}{dt} + k_1\phi(t) - k_2 \right) e^{k_1 t} \leq 0,$$

which is equivalent to

$$\frac{d}{dt} \left(\left(\phi(t) - \frac{k_2}{k_1} \right) e^{k_1 t} \right) \leq 0.$$

Thus the function

$$\left(\phi(t) - \frac{k_2}{k_1} \right) e^{k_1 t},$$

has a non-positive derivative and so is non-increasing for $t \geq 0$. Therefore, for all $t \geq \tilde{T} \geq 0$,

$$\left(\phi(t) - \frac{k_2}{k_1} \right) e^{k_1 t} \leq \left(\phi(\tilde{T}) - \frac{k_2}{k_1} \right) e^{k_1 \tilde{T}},$$

and hence,

$$\phi(t) \leq \frac{k_2}{k_1} - \left(\frac{k_2}{k_1} - \phi(\tilde{T}) \right) e^{-k_1(t-\tilde{T})},$$

which is equivalent to

$$\phi(t) \leq \frac{k_2}{k_1} (1 - e^{-k_1(t-\tilde{T})}) + \phi(\tilde{T}) e^{-k_1(t-\tilde{T})}.$$

For $\tilde{T} = 0$, this formula becomes

$$\phi(t) \leq \frac{k_2}{k_1} (1 - e^{-k_1 t}) + \phi(0) e^{-k_1 t}. \quad \square$$

Theorem 3. Let us assume

$$c + \frac{c}{4b} + r < \frac{q}{p}, \quad (7)$$

and let \mathbb{A} be the set defined by:

$$\mathbb{A} = \left\{ (x, y, z) \in \mathbb{R}_+^3 : 0 \leq x \leq 1, 0 \leq x + \frac{y}{c} \leq 1 + \frac{1}{4b}, 0 \leq x + \frac{y}{c} + \alpha z \leq 1 + \frac{1}{4b} + \frac{M}{b} \right\},$$

where

$$\alpha = \frac{1}{b^2(c + \frac{c}{4b} + r)} \quad \text{and} \quad M = \frac{1}{4(q - (c + \frac{c}{4b} + r)p)}.$$

Then

- (i) \mathbb{A} is positively invariant,
- (2i) all non-negative solutions (i.e. solutions initiating in \mathbb{R}_+^3) of (5) are uniformly bounded forward in time, (thus they exist for all positive times), they eventually enter the attracting set \mathbb{A} .
- (3i) system (5) is dissipative.

Proof. (i) Let $(x(0), y(0), z(0)) \in \mathbb{A}$, obviously, from Lemma 1, $(x(t), y(t), z(t))$ remain non-negative; we will show that $(x(t), y(t), z(t)) \in \mathbb{A}$ for all $t \geq 0$, we then have to prove that for all $t \geq 0$,

- Step (i-a): $x(t) \leq 1$;
- Step (i-b): $x(t) + y(t)/c \leq 1 + 1/4b$;
- Step (i-c): $x(t) + y(t)/c + \alpha z(t) \leq 1 + 1/4b + M/b$.
- Step (i-a). We first prove that $x(t) \leq 1$ for all $t \geq 0$. Since $x > 0$, $y > 0$ and $z > 0$ in $\text{Int}(\mathbb{R}_+^3)$, any solution $\phi(t) = (x(t), y(t), z(t))$ of (5), which starts in $\text{Int}(\mathbb{R}_+^3)$, satisfies the differential inequation $dx/dt \leq x(1 - x)$, this is obvious by considering the first equation of (5), moreover, due to the Lemma 1, these solutions remain non-negative. Thus, $x(t)$ may be compared with solutions of

$$\frac{ds(t)}{dt} = s(t)(1 - s(t)), \quad s(0) = x(0) > 0,$$

to get $x(t) \leq 1/(1 + c_0 e^{-t})$ for $t \geq 0$ (where $c_0 = 1/x_0 - 1$). It follows that any non-negative solution $\phi(t)$ of (5) satisfies

$$x(t) \leq 1 \quad \text{for all } t \geq 0. \tag{8}$$

- Step (i-b). We prove now that

$$x(t) + \frac{1}{c}y(t) \leq 1 + \frac{1}{4b} \quad \text{for all } t \geq 0.$$

We define function $\sigma(t) = x(t) + (1/c)y(t)$, the time derivative of which is

$$\frac{d\sigma}{dt} = \frac{dx}{dt} + \frac{1}{c} \frac{dy}{dt} = x(1 - x) - \frac{b}{c}y - \frac{1}{c} \frac{yz}{y + d}.$$

Since all parameters are positive, and solutions initiating in \mathbb{R}_+^3 remain in the non-negative cone then,

$$\frac{d\sigma}{dt} \leq x(1 - x) - (b/c)y$$

holds for all x, y and z non-negative. Thus,

$$\frac{d\sigma}{dt} \leq x(1 - x) + bx - b(x + y/c),$$

so

$$\frac{d\sigma(t)}{dt} + b\sigma(t) \leq b + \frac{1}{4},$$

since, in \mathbb{A} , $0 \leq x \leq 1$ and $\max_{[0,1]}(x(1 - x)) = 1/4$. Using Lemma 2, we get, for all $t \geq \tilde{T} \geq 0$,

$$\sigma(t) \leq 1 + \frac{1}{4b} - \left(1 + \frac{1}{4b} - \sigma(\tilde{T})\right) e^{-b(t-\tilde{T})}, \tag{9}$$

then, if $\tilde{T} = 0$,

$$\sigma(t) \leq 1 + \frac{1}{4b} - \left[1 + \frac{1}{4b} - \left(x(0) + \frac{y(0)}{c}\right)\right] e^{-bt}. \tag{10}$$

Hence, since $(x(0), y(0), z(0)) \in \mathbb{A}$,

$$x(t) + \frac{1}{c}y(t) \leq 1 + \frac{1}{4b} \quad \text{for all } t \geq 0. \quad (11)$$

- *Step (i-c).* We finally prove, provided $c + c/4b + r \leq q/p$, that

$$0 \leq x + \frac{y}{c} + \alpha z \leq 1 + \frac{1}{4b} + \frac{M}{b}$$

holds, with

$$\alpha = \frac{1}{b^2(c + \frac{c}{4b} + r)}$$

and

$$M = \frac{1}{4(q - (c + \frac{c}{4b} + r)p)}.$$

The proof is similar as done above; we define the following function:

$$\eta(t) = x(t) + \frac{1}{c}y(t) + \alpha z(t),$$

the time derivative of which is

$$\frac{d\eta}{dt} = \frac{dx}{dt} + \frac{1}{c}\frac{dy}{dt} + \alpha\frac{dz}{dt} = x(1-x) - \frac{b}{c}y - \frac{1}{c}\frac{yz}{y+d} + \alpha\left(p - \frac{q}{y+r}\right)z^2.$$

Similarly to the previous Step (i-b), since every solution initiating in \mathbb{R}_+^3 remains non-negative, all parameters are positive, $0 \leq x \leq 1$ and $\max_{[0,1]}(x(1-x)) = 1/4$, we get,

$$\frac{d\eta(t)}{dt} \leq \frac{1}{4} + b - b\eta(t) + \alpha bz + \alpha\left(p - \frac{q}{y+r}\right)z^2,$$

thus, as in \mathbb{A} , $y \leq c + c/4b$, one gets

$$\frac{d\eta(t)}{dt} \leq \frac{1}{4} + b - b\eta(t) + \alpha bz + \alpha\left(p - \frac{q}{c + \frac{c}{4b} + r}\right)z^2,$$

hence

$$\frac{d\eta(t)}{dt} + b\eta(t) \leq \frac{1}{4} + b + M, \quad (12)$$

where

$$M = \max_{z \in \mathbb{R}^+} \left(\alpha bz + \alpha\left(p - \frac{q}{c + \frac{c}{4b} + r}\right)z^2 \right).$$

The maximum M exists since, from formula (7), one easily gets

$$p - \frac{q}{(c + \frac{c}{4b} + r)} < 0,$$

and simple algebraic computations show that with

$$\alpha = \frac{1}{b^2(c + \frac{c}{4b} + r)},$$

$$M = \frac{\alpha b^2(c + \frac{c}{4b} + r)}{4(q - (c + \frac{c}{4b} + r)p)} = \frac{1}{4(q - (c + \frac{c}{4b} + r)p)}.$$

Therefore, from Eq. (12), and using Lemma 2, we get for all $t \geq \tilde{T} \geq 0$,

$$\eta(t) \leq 1 + \frac{1}{4b} + \frac{M}{b} - \left(1 + \frac{1}{4b} + \frac{M}{b} - \eta(\tilde{T}) \right) e^{-b(t-\tilde{T})} \quad (13)$$

then, if $\tilde{T} = 0$,

$$\eta(t) \leq 1 + \frac{1}{4b} + \frac{M}{b} - \left(1 + \frac{1}{4b} + \frac{M}{b} - \eta(0)\right) e^{-bt}.$$

Thus, since $(x(0), y(0), z(0)) \in \mathbb{A}$,

$$x + \frac{y}{c} + \alpha z \leq 1 + \frac{1}{4b} + \frac{M}{b}.$$

Consequently, we get the result

$$x + \frac{y}{c} + \frac{z}{b^2(c + \frac{c}{4b} + r)} \leq 1 + \frac{1}{4b} + \frac{1}{b} \frac{1}{4(q - (c + \frac{c}{4b} + r)p)}$$

for all $t \geq 0$.

(2i) We must prove that, for $(x(0), y(0), z(0)) \in \mathbb{R}_+^3$,

$$(x(t), y(t), z(t)) \rightarrow \mathbb{A} \text{ as } t \rightarrow +\infty.$$

We will follow the steps:

- Step (2i-a): $\lim_{t \rightarrow +\infty} \sup x(t) \leq 1$,
- Step (2i-b):

$$\lim_{t \rightarrow +\infty} \sup \left(x(t) + \frac{y(t)}{c} \right) \leq 1 + \frac{1}{4b},$$

- Step (2i-c):

$$\lim_{t \rightarrow +\infty} \sup \left(x(t) + \frac{y(t)}{c} + \alpha z(t) \right) \leq 1 + \frac{1}{4b} + \frac{M}{b}.$$

- Step (2i-a): This result follows directly from Step (i-a) and Lemma 2, since solutions of the initial value problem $dx/dt = x(1 - x)$, $x(0) \geq 0$, satisfy $\lim_{t \rightarrow +\infty} \sup x(t) \leq 1$.
- Step (2i-b): Let $\varepsilon > 0$ be given. Then there exists a $T_1 > 0$ such that $x(t) \leq 1 + \varepsilon/2$ for all $t \geq T_1$. From Eq. (9) with $\tilde{T} = T_1$, see Step (i-b), we get, for all $t \geq T_1 \geq 0$,

$$\begin{aligned} \sigma(t) &= x(t) + \frac{y(t)}{c} \leq 1 + \frac{1}{4b} - \left[1 + \frac{1}{4b} - \left(x(T_1) + \frac{y(T_1)}{c} \right) \right] e^{-b(t-T_1)} \\ &\leq 1 + \frac{1}{4b} - \left[\left(1 + \frac{1}{4b} \right) e^{bT_1} - \left(x(T_1) + \frac{y(T_1)}{c} \right) e^{bT_1} \right] e^{-bt} \\ &\leq 1 + \frac{1}{4b} - \left[\left(1 + \frac{1}{4b} \right) - \left(x(T_1) + \frac{y(T_1)}{c} \right) e^{bT_1} \right] e^{-bt}. \end{aligned}$$

Then

$$x(t) + \frac{y(t)}{c} \leq \left(1 + \frac{1}{4b} + \frac{\varepsilon}{2} \right) - \left[\left(1 + \frac{1}{4b} + \frac{\varepsilon}{2} \right) - \left(x(T_1) + \frac{y(T_1)}{c} \right) e^{bT_1} \right] e^{-bt}$$

for all $t \geq T_1$. Let $T_2 \geq T_1$ be such that

$$\left| \left(1 + \frac{1}{4b} + \frac{\varepsilon}{2} \right) - \left(x(T_1) + \frac{y(T_1)}{c} \right) e^{bT_1} \right| e^{-bt} \leq \frac{\varepsilon}{2}$$

for all $t \geq T_2$. Then

$$x(t) + \frac{y(t)}{c} \leq 1 + \frac{1}{4b} + \varepsilon \text{ for all } t \geq T_2.$$

Hence

$$\lim_{t \rightarrow +\infty} \sup \left(x(t) + \frac{y(t)}{c} \right) \leq 1 + \frac{1}{4b}.$$

- *Step (2i-c):* The proof is similar to the previous one. Let $\varepsilon > 0$ be given. Then there exists a $T_3 > 0$ such that

$$x(t) + \frac{y(t)}{c} \leq 1 + \frac{1}{4b} + \frac{\varepsilon}{2} \quad \text{for all } t \geq T_3.$$

From Eq. (13) with $\tilde{T} = T_3$, see Step (i-c), we get, for all $t \geq T_3 \geq 0$,

$$\begin{aligned} \eta(t) &= x(t) + \frac{y(t)}{c} + \alpha z(t) \\ &\leq 1 + \frac{1}{4b} + \frac{M}{b} - \left[1 + \frac{1}{4b} + \frac{M}{b} - \eta(T_3) \right] e^{-b(t-T_3)} \\ &\leq 1 + \frac{1}{4b} + \frac{M}{b} - \left[\left(1 + \frac{1}{4b} + \frac{M}{b} \right) e^{bT_3} - \eta(T_3) e^{bT_3} \right] e^{-bt} \\ &\leq 1 + \frac{1}{4b} + \frac{M}{b} - \left[\left(1 + \frac{1}{4b} + \frac{M}{b} \right) - \eta(T_3) e^{bT_3} \right] e^{-bt}. \end{aligned}$$

Then

$$\eta(t) \leq 1 + \frac{1}{4b} + \frac{M}{b} + \frac{\varepsilon}{2} - \left(1 + \frac{1}{4b} + \frac{M}{b} + \frac{\varepsilon}{2} - \eta(T_3) e^{bT_3} \right) e^{-bt}.$$

Let $T_4 \geq T_3$ be such that

$$\left| 1 + \frac{1}{4b} + \frac{M}{b} + \frac{\varepsilon}{2} - \eta(T_3) e^{bT_3} \right| e^{-bt} \leq \frac{\varepsilon}{2} \quad \text{for all } t \geq T_4.$$

Then

$$\eta(t) \leq 1 + \frac{1}{4b} + \frac{M}{b} + \varepsilon \quad \text{for all } t \geq T_4.$$

Hence

$$\limsup_{t \rightarrow +\infty} \left(x(t) + \frac{y(t)}{c} + \alpha z(t) \right) \leq 1 + \frac{1}{4b} + \frac{M}{b}.$$

(3i) System (5) is then obviously dissipative in \mathbb{R}_+^3 . \square

Remark. In the numerical simulations, last section, chosen regions of parameters always satisfy hypotheses of this theorem. However, these numerical experiments are done for system (1), therefore, conditions of the previous theorem have also to be rescaled; for instance $0 \leq x \leq 1$ will be replaced in the numerical tests by $0 \leq X \leq a_0/b_0$.

4. Existence and stability of equilibria

The main result of this section is done by Theorem 7 in which we give conditions for global stability of the equilibria representing the extinction of the intermediate or top predator. Since we treat an ecological model, we are interested in the steady states which have non-negative coordinates. Such steady states are said to be relevant (for \mathbb{R}_+^3), or simply, exist. An equilibrium point of system (5) is found by solving the three equations $\dot{x} = \dot{y} = \dot{z} = 0$. First of all, we obtain three trivial equilibria (belonging to the boundary of $\text{Int}(\mathbb{R}_+^3)$, i.e. at which one or more of populations has zero density or is extinct):

$$E_0 = (0, 0, 0), \quad E_1 = (1, 0, 0) \quad \text{and} \quad E_2 = (\theta, (1 - \theta)(a + \theta), 0), \quad (14)$$

where

$$\theta = \frac{ab}{c - b}, \quad (15)$$

(by assuming $c \neq b$, that is $a_1 \neq v_1$: the maximum value which *per capita* reduction rate of Y can attain is different from the rate at which Y will die out when there is no X). E_2 belongs to the xy -plane and is obviously a relevant equilibrium of

system (5) (i.e. $x \geq 0, y \geq 0$) if $0 < \theta < 1$. Let us remark that $\theta \neq 0$ since all parameters of the system assume only positive values, furthermore if $\theta = 1$ then $E_1 = E_2$. The last trivial solution is the point

$$\left(0, \frac{q}{p} - r, -b\left(\frac{q}{p} - r + d\right)\right),$$

which is localized in the yz -plane but is not relevant for \mathbb{R}_+^3 , since it cannot occur in the non-negative cone \mathbb{R}_+^3 . Indeed, at least one of its coordinates is negative since, either $(q/p) - r$ is negative or, otherwise, the third coordinate $-b((q/p) - r + d)$ is negative, since all the parameters of the system assume only positives values.

Non-trivial equilibrium point is an interior one (i.e. belonging to $\text{Int}(\mathbb{R}_+^3)$), that is an equilibrium at which all species have non-zero positive densities. The possible non-trivial equilibria are

$$E_+ = (x_+, \bar{y}, z_+), \quad \text{and} \quad E_- = (x_-, \bar{y}, z_-), \tag{16}$$

where

$$\begin{aligned} x_{\pm} &= \frac{1-a}{2} \pm \left(\left(\frac{a+1}{2} \right)^2 - \bar{y} \right)^{1/2}, \\ \bar{y} &= \frac{q}{p} - r, \\ z_{\pm} &= \left(-b + \frac{cx_{\pm}}{a+x_{\pm}} \right) (\bar{y} + d). \end{aligned} \tag{17}$$

The study of these interior equilibria will be done in a forthcoming paper.

We will now investigate the behavior of the system (5) around steady states $E_{1,2}$.

4.1. Behavior near the xy -plane and Hopf bifurcation

Since top-predator Z may disappear when one of the other populations dies out, various characteristics of the system (such as persistence) depend only on its behavior near the xy -plane. Therefore, the study of the system near the xy -plane may give some relevant information. See for example [5] in which some three-species system is investigated and where the dynamic near the xy -plane is studied (z is fixed and used as a parameter).

Using only the first two equations of system (5) and removing the last term of the second member of the second equation of (5), this system becomes restricted to the xy -plane \mathbb{R}_{xy}^2 . This leads to the system

$$\begin{aligned} \frac{dx}{dt} &= x(1-x) - \frac{xy}{x+a}, \\ \frac{dy}{dt} &= \frac{cxy}{x+a} - by. \end{aligned} \tag{18}$$

Such system has been studied in [30–33] and the behavior of its solutions is well known. However, we give off (or recall) some results on system (18) which will simplify and the study of (5).

It is easy to verify that the following points are equilibria of (18): $\tilde{E}_0(0, 0)$, $\tilde{E}_1(1, 0)$ and $\tilde{E}_2(\tilde{x}_2, \tilde{y}_2)$, where

$$\tilde{x}_2 = \theta \quad \text{and} \quad \tilde{y}_2 = (1 - \theta)(a + \theta). \tag{19}$$

Obviously, these points are the restriction of E_0 , E_1 and E_2 to \mathbb{R}_{xy}^2 . Note that, in order to guarantee the existence of an interior equilibrium of (18) to the positive first quadrant $\text{Int}(\mathbb{R}_{xy}^+)$, it is necessary to assume that $0 < \theta < 1$ is satisfied ($c \neq b$ is assumed satisfied throughout all this paper).

The local stability of equilibria of (18) is determined by computing the eigenvalues of the Jacobian matrix about each equilibrium. Let \tilde{J}_0 , \tilde{J}_1 and \tilde{J}_2 be this matrix evaluated respectively at \tilde{E}_0 , \tilde{E}_1 and \tilde{E}_2 . Then,

$$\tilde{J}_0 = \begin{pmatrix} 1 & 0 \\ 0 & -b \end{pmatrix}, \quad \tilde{J}_1 = \begin{pmatrix} -1 & \frac{-1}{1+a} \\ 0 & \frac{c-b-ab}{1+a} \end{pmatrix}, \quad \tilde{J}_2 = \begin{pmatrix} \frac{-2\theta^2-(a-1)\theta}{a+\theta} & -\frac{\theta}{a+\theta} \\ \frac{ac(1-\theta)}{a+\theta} & 0 \end{pmatrix}. \tag{20}$$

From \tilde{J}_0 , since $b > 0$, \tilde{E}_0 is obviously non-stable; it is a hyperbolic saddle point which attracts in the y -direction and repels in the x -direction.

Now, for \tilde{E}_1 , the eigenvalues of \tilde{J}_1 are

$$-1 \quad \text{and} \quad \frac{(c-b-ab)}{(1+a)}.$$

If $c - b > ab$ (i.e. $0 < \theta < 1$, case of existence of \tilde{E}_2), then \tilde{E}_1 is also a hyperbolic saddle point which attracts in the x direction and repels in the y direction. If $c - b < ab$, then both eigenvalues are negative, \tilde{E}_1 is locally asymptotically stable. Furthermore, if $c < b$ (i.e., $\theta < 0$), the following result establishes the global stability of \tilde{E}_1 .

Theorem 4. *If $c < b$, then \tilde{E}_1 is globally asymptotically stable.*

Proof. First, let us remark that if hypothesis $c < b$ is satisfied. Then system (18) has only two non-negative equilibria. Indeed, under this hypothesis, \tilde{E}_2 is not in \mathbb{R}_{xy}^+ (since $c < b \Rightarrow \theta < 0$).

From the second equation of system (18), since parameters of the system are positive, $(x, y) \in \mathbb{R}_+^2$ and $c < b$, then $dy/dt \leq cxy/(x+a) - cy$, thus $dy/dt \leq -ac/(x+a)y$, and $dy/dt \leq -K_1y$, for some $K_1 > 0$, since $x(t)$ is bounded in $t \in [0, +\infty]$. As a consequence, one gets $y(t) \leq y(0)e^{-K_1t}$. Then, any solution $y(t)$ which starts on the non-negative first quadrant \mathbb{R}_{xy}^+ tends to zero as t tends to $+\infty$. Thus, the ω -limit set Ω of every solution with positive initial conditions is contained in $\{(x, 0), x \geq 0\}$. Now, the first equation of system (18) verifies,

$$\frac{dx}{dt} = x(1-x) - \frac{xy}{x+a} \leq x(1-x).$$

For $x > 1$, we have $dx/dt < 0$, so $\Omega \subset \{(x, 0), 0 \leq x \leq 1\}$. Taking into account that $\tilde{E}_0 \notin \Omega$, (\tilde{E}_0 is non-stable and repels in the x -direction) and that Ω is a non-empty closed and invariant set, we get $\Omega = \{\tilde{E}_1\}$. \square

Let us now move to \tilde{E}_2 which exists and is positive iff $0 < \theta < 1$ holds (that is if $0 < ab < c - b$, the case, $\theta = 1$ leads to $\tilde{E}_1 = \tilde{E}_2$). The eigenvalues of \tilde{J}_2 are given by

$$\tilde{\lambda}_i = \tilde{\lambda}_{\pm}(\theta) = \frac{\alpha_{11}(\tilde{x}_2, \tilde{y}_2)}{2} \pm \frac{1}{2} \sqrt{\Delta(\theta)}, \quad (21)$$

where

$$\alpha_{11}(\tilde{x}_2, \tilde{y}_2) = \frac{-2\theta^2 - (a-1)\theta}{2(a+\theta)}$$

and

$$\Delta(\theta) = \frac{1}{(a+\theta)^2} [(2\theta^2 + (a-1)\theta)^2 - 4ac\theta(1-\theta)].$$

Simple algebraic computations show that $\tilde{\lambda}_i$ have negative real parts if and only if

$$\frac{1-a}{2} < \theta < 1 \quad (22)$$

(with $\theta = ab/(c-b) > 0$). Consequently, if (22) holds, \tilde{E}_2 is locally asymptotically stable.

Theorem 5. *If \tilde{E}_2 exists in \mathbb{R}_{xy}^+ and if it is locally asymptotically stable (i.e. if $(1-a)/2 < \theta < 1$), then it is globally stable.*

Proof. We follow the same way as in [31] where the stability criterion of Rosenzweig and MacArthur [34] is used to establish the global stability of equilibria. Therefore, let φ the function defined as

$$\varphi(\tilde{x}_2) = \tilde{x}_2 s(\tilde{x}_2) \left(\frac{d}{dx} \ln \left(\frac{xs(x)}{u(x)} \right) \right)_{|x=\tilde{x}_2},$$

where $s(x) = 1 - x$, $u(x) = x/(a+x)$. Then,

$$\begin{aligned} \varphi(\tilde{x}_2) < 0 &\Rightarrow \text{asymptotic stability of } \tilde{E}_2, \\ \varphi(\tilde{x}_2) > 0 &\Rightarrow \text{unstability.} \end{aligned} \quad (23)$$

Here,

$$\varphi(\tilde{x}_2) = \tilde{x}_2(1-\tilde{x}_2) \left(\frac{d}{dx} \ln(1-x)(a+x) \right)_{|x=\tilde{x}_2} = \frac{-2\theta^2 - (a-1)\theta}{a+\theta}.$$

Due to (23), asymptotic stability of \tilde{E}_2 occurs if $\varphi(\tilde{x}_2) < 0$, that is if $(1 - a)/2 < \theta < 1$. This is exactly formula (22). To end the proof we use the following result, given in [32], where the author also uses Rosenzweig and MacArthur criterion.

Theorem (Hsu [32]). Assume \tilde{E}_2 , interior equilibrium of (18), is locally stable (i.e. $\varphi(\tilde{x}_2) < 0$) and let

$$\frac{d^2}{dx^2} \left(\ln \left(\frac{xs(x)}{u(x)} \right) \right) < 0 \quad \text{for } 0 < x < 1.$$

Then \tilde{E}_2 is globally stable.

Here, for system (18), $xs(x)/u(x) = (1 - x)(a + x)$, then

$$\frac{d^2}{dx^2} \left(\ln \left(\frac{xs(x)}{u(x)} \right) \right) = -2 < 0.$$

Therefore, under condition (22), \tilde{E}_2 is globally stable. \square

System (1) has non-trivial dynamics in the absence of the top-predator (i.e. case of system (18)). Indeed, the loss of stability of \tilde{E}_2 happens by a supercritical Hopf bifurcation. To study the last, every parameter will be considered fixed but a_0 which will play the role of the bifurcation parameter. Let us recall (by using notations (4)) that

$$\theta = \frac{ab}{c - b} = \frac{1}{a_0} \frac{b_0 d_0 a_1}{v_1 - a_1} = \theta(a_0).$$

Then one can also consider θ as a bifurcation parameter. In fact, one should note that a decrease in θ corresponds to an increase in a_0 which corresponds to an increase in the carrying capacity of prey species X ; and vice-versa, an increase in θ corresponds to a decrease in a_0 , then to a decrease in the carrying capacity of prey species X . Therefore, this change in θ can act to destabilize the system allowing for more complicated dynamics. In the following, we prove that a limit cycle emerges from E_2 in the xy -plane.

Theorem 6. *Suppose that conditions $(0 < \theta < 1)$ and $(a < 1)$ hold. Then, equilibrium point \tilde{E}_2 undergoes a Hopf bifurcation at $\theta = \theta_0 = (1 - a)/2$.*

Proof. The eigenvalues of J_2 are given by (21). One easily show that $\text{Re}(\tilde{\lambda}_{\pm}(\theta)) > 0$ (resp. $<$) according as $\theta < \theta_0$ (resp. $>$). At $\theta = \theta_0$, since $0 < a < 1$, the eigenvalues become

$$\tilde{\lambda}_{\pm}(\theta_0) = \pm \frac{i}{(a + 1)} (ac(1 - a^2))^{1/2},$$

which are purely imaginary and conjugate. Furthermore, the eigenvalues cross the imaginary axis with non-zero speed, that is,

$$\left(\frac{d}{d\theta} \text{Re}(\tilde{\lambda}_{\pm}(\theta)) \right)_{\theta=\theta_0} \neq 0.$$

Indeed, simple computations lead to

$$\frac{d}{d\theta} \text{Re}(\tilde{\lambda}_{\pm}(\theta)) = -1 + \frac{a^2 + a}{2(a + \theta)^2},$$

hence

$$\left(\frac{d}{d\theta} \text{Re}(\tilde{\lambda}_{\pm}(\theta)) \right)_{\theta=\theta_0} = -1 + \frac{2a}{a + 1},$$

which is non-zero since $a < 1$. Consequently, at $\theta = \theta_0$, the equilibria \tilde{E}_2 undergoes a Hopf bifurcation. \square

Moreover, one can also see that \tilde{E}_2 emerges from \tilde{E}_1 via a transcritical bifurcation (if $\theta > 1$, \tilde{E}_2 does not exist, if $\theta = \theta_0$ $\tilde{E}_2 = \tilde{E}_1$ and last if $\theta < 1$ both exist).

4.2. Stability of E_0, E_1 and E_2

Note that the existence of \tilde{E}_i will imply the existence of E_i ($i = 0, 1, 2$). The Jacobian matrix evaluated at an equilibrium $E(x^*, y^*, z^*)$ of system (5) is

$$J = \begin{pmatrix} \alpha_{11}(x^*, y^*, z^*) & \alpha_{12}(x^*, y^*, z^*) & 0 \\ \alpha_{21}(x^*, y^*, z^*) & \alpha_{22}(x^*, y^*, z^*) & \alpha_{23}(x^*, y^*, z^*) \\ 0 & \alpha_{32}(x^*, y^*, z^*) & 0 \end{pmatrix}, \tag{24}$$

where

$$\begin{aligned} \alpha_{11}(x^*, y^*, z^*) &= 1 - 2x^* - \frac{ay^*}{(a+x^*)^2}, & \alpha_{12}(x^*, y^*, z^*) &= -\frac{x^*}{a+x^*}, \\ \alpha_{21}(x^*, y^*, z^*) &= \frac{acy^*}{(a+x^*)^2}, & \alpha_{22}(x^*, y^*, z^*) &= -b + \frac{cx^*}{a+x^*} - \frac{dz^*}{(d+y^*)^2}, \\ \alpha_{23}(x^*, y^*, z^*) &= -\frac{y^*}{d+y^*}, & \alpha_{32}(x^*, y^*, z^*) &= \frac{qz^{*2}}{(y^*+r)^2}. \end{aligned}$$

Then, the Jacobian matrix evaluated at $E_0(0, 0, 0)$ and $E_1(1, 0, 0)$ are respectively:

$$J_0 = \left(\begin{array}{cc|cc} & & 0 & \\ \tilde{J}_0 & & 0 & \\ \hline & & 0 & \\ 0 & 0 & 0 & \end{array} \right) \quad \text{and} \quad J_1 = \left(\begin{array}{cc|cc} & & 0 & \\ \tilde{J}_1 & & 0 & \\ \hline & & 0 & \\ 0 & 0 & 0 & \end{array} \right)$$

where \tilde{J}_0 and \tilde{J}_1 are given by (20).

The eigenvalues of J_0 are 1, $-b$ and 0, hence E_0 is non-hyperbolic. Furthermore, as one eigenvalue is a positive real, and another one is a negative real, E_0 is always non-stable. Thus, for each orbit starting in $\text{Int}(\mathbb{R}_+^3)$, the number of prey X and specialist predator Y will not tend to zero.

The eigenvalues of J_1 are

$$-1, \quad -\frac{ab+b-c}{a+1} \quad \text{and} \quad 0.$$

Hence, E_1 is also non-hyperbolic. Since all parameters of the system assume only positive values, if $ab < c - b$ (i.e. $0 < \theta < 1$), then E_1 is non-stable. Otherwise, if $ab > c - b$, two of the eigenvalues are negative real, so E_1 has a stable manifold of at least two dimensions. To know the actual dimensions of the stable and unstable manifolds of E_1 we need to compute the center manifold corresponding to the eigenvalue zero. This will be studied in a forthcoming paper [36].

The dynamic in the xy -plane, near E_2 , is locally driven by the corresponding linearized system on E_2 for which the Jacobian matrix evaluated at this equilibrium is

$$J_2 = \left(\begin{array}{cc|cc} & & 0 & \\ \tilde{J}_2 & & \frac{(1-\theta)(a+\theta)}{e+(1-\theta)(a+\theta)} & \\ \hline & & 0 & \\ 0 & 0 & 0 & \end{array} \right)$$

where \tilde{J}_2 is given by (20). The eigenvalues of J_2 are those of \tilde{J}_2 which are done by (21) and $\lambda_3 = 0$, so one can use the study on \tilde{E}_2 to have some information near the xy -plane.

The next theorem establishes the global stability of E_1 and E_2 for some reasonable conditions on the parameters.

Theorem 7. *Let us assume satisfied the following statements:*

$$p \leq q, \quad (25)$$

$$c + \frac{c}{4b} + r < 1. \quad (26)$$

- (a) *If \tilde{E}_1 is globally asymptotically stable with respect to \mathbb{R}_{xy}^+ (i.e. $c < b$ holds, see Theorem 4), then E_1 is globally asymptotically stable.*
 (b) *If \tilde{E}_2 is globally stable with respect to \mathbb{R}_{xy}^+ (i.e. $(1-a)/2 < \theta < 1$ hold, Theorem 5), then E_2 is globally stable.*

Proof. Using the third equation of system (5) and as $p \leq q$, we get

$$\frac{dz}{dt} \leq - \left(\frac{1}{y+r} - 1 \right) pz^2.$$

Now, $1/(y+r) - 1 > 0$. Indeed, if conditions (25) and (26) hold, then condition (7) of Theorem 3 holds, and then solutions of the system eventually enter the attracting set \mathbb{A} . In \mathbb{A} , we clearly have $0 \leq y \leq c + c/4b$, thus

$$0 < \frac{1}{c + (c/4b) + r} \leq \frac{1}{y+r}.$$

Eq. (26) is equivalent to

$$1 < \frac{1}{c + \frac{c}{4b} + r},$$

thus one gets $1/(y+r) - 1 > 0$. Therefore

$$\frac{dz}{dt} \leq - \left(\frac{1}{c + \frac{c}{4b} + r} - 1 \right) pz^2 = -Kz^2,$$

where

$$K = \frac{1}{c + \frac{c}{4b} + r} - 1 > 0.$$

This differential inequality leads to

$$z(t) \leq \frac{1}{Kt + 1/z_0}.$$

As a consequence, if (25) and (26) hold, any solution $z(t)$ which starts on the non-negative cone \mathbb{R}_+^3 tends to zero as t tends to $+\infty$. Thus, the ω -limit set Ω of every solution $(x(t), y(t), z(t))$ with positive initial conditions is contained in \mathbb{R}_{xy}^+ . Consequently,

- (a) since \tilde{E}_1 is globally asymptotically stable and E_1 restricted to \mathbb{R}_{xy}^+ is \tilde{E}_1 , then E_1 is globally asymptotically stable with respect to \mathbb{R}_+^3 , (the intermediate Y and the top predator Z go extinct);
 (b) since \tilde{E}_2 is globally stable with respect to \mathbb{R}_{xy}^+ and E_2 restricted to \mathbb{R}_{xy}^+ is \tilde{E}_2 , then one gets the conclusion that E_2 is globally stable with respect to \mathbb{R}_+^3 , (the top-predator Z goes extinct). \square

Thus, following a similar analysis of bifurcations given in [4], and using the study which we have done on the behavior on the xy -plane (Section 4.1), one can show that system (5) has no trivial dynamics even if the quantity of top-predator is small. This is numerically illustrated by Figs. 7–9 (see the last part of Section 5, numerical observations). Likewise, other chains of events occur leading up to and following a Hopf bifurcation which ultimately results in the chaotic behavior numerically presented in the last section.

5. Numerical results

Many studies on various, two or three, food chains strongly support the conjecture that the irregular dynamics observed in many natural food chains might be those of a strange attractor and chaos, see [4–6,8,11,21,23,24]. In this

paper, the chaotic behavior of system (1) is shown only by numerical analysis, in a different regions of the parameter space. A deep bifurcation analysis is left for a forthcoming paper.

Selection of biologically ‘realistic’ parameter values for the numerical experiments of ecological models is a difficult problem. It must be guided by biological principles. The ranges for the variation of parameters we have used in this paper for the numerical study of the dynamical behavior were chosen on the basis of values reported in [20,22], since these ranges contain parametric values which are not arbitrary but are quantitative measures of the system attributes. Nevertheless, we have enlarged these ranges and sometimes found other parameter regions in which chaotic behavior exists. These regions do not allow the existence of interior equilibria E_{\pm} given by (16) and (17), the dynamics displayed in the last section, even chaotic, does not depend on these points.

We have done the numerical calculations very accurately in double precision for different initial conditions and for different variations of parameters, and verified our results. In order to obtain reliable numerical results, the step size has been chosen to be equal to 10^{-4} or less, and the first 10^7 steps are discarded to avoid the transient regime. For all the figures, the chosen bifurcation parameters are a_0 or c_3 and the following parameters are fixed throughout:

$$b_0 = 0.06, \quad v_0 = 1.0, \quad d_0 = d_1 = d_2 = 10.0, \quad a_1 = 1.0, \quad v_1 = 2.0, \quad v_2 = 0.405, \quad v_3 = 1.0, \quad d_3 = 20.0. \quad (27)$$

The following initial condition is also used when we do not give another.

$$X_0(1.2, 1.2, 1.2). \quad (28)$$

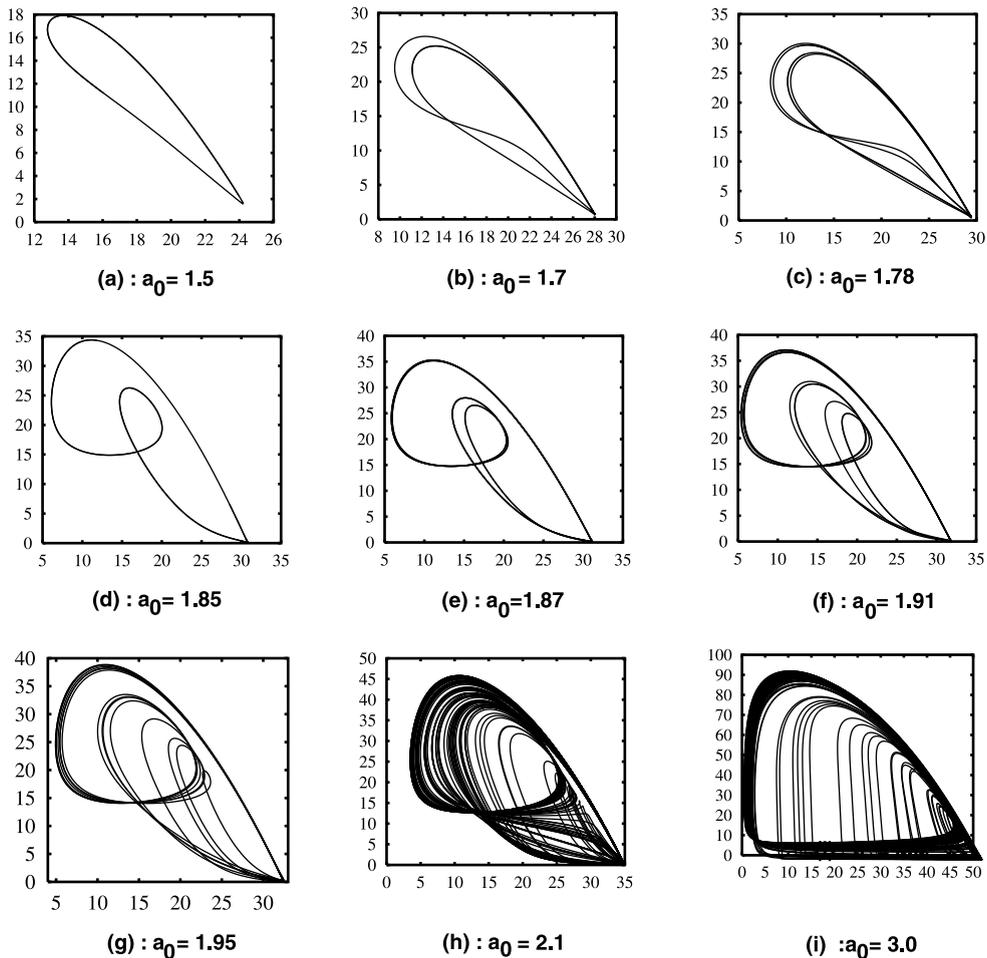


Fig. 1. Phase portraits in the XY -plane, for system (1), showing the transition to chaos, via period-doubling from a limit cycle to strange attractors, with $c_3 = 0.038$, the set of parameters given by (27) and the initial condition given by (28). Parameter a_0 is done in each figure. Figures (a)–(c) correspond to the first (type I) periodic window, and figures (d)–(i) to the second (type II).

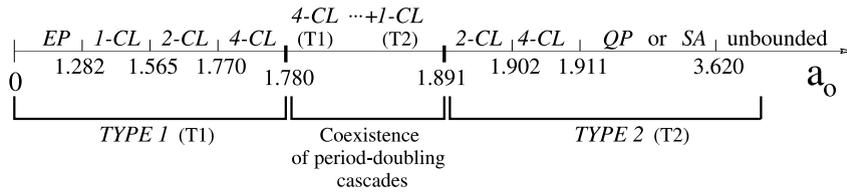


Fig. 2. Symbolic diagram specifying the attractors of system (1) for $c_3 = 0.038$, the set of parameters given by (27) with $0 \leq a_0 < \infty$, and the initial condition given by (28). A stable equilibrium point is denoted by ‘EP’, a stable limit cycle of period k by ‘k-LC’, a quasi-periodic trajectory by ‘QP’, a strange attractor by ‘SA’. For $a_0 \in [1.780, 1.891]$, two coexisting period doubling cascades are observed, they are denoted by type I (T1) and type II (T2).

Period-doubling bifurcation. Various chains of period-doubling or period-halving, wavetime forms and power spectra are done to give numerical evidence of chaotic behavior. Fig. 1 shows a sequence of period-doubling of limit cycles. This is also presented by the symbolic diagram of Fig. 2, while Fig. 3 presents a tri-dimensional view of the strange attractor displayed in Fig. 1(h), the power spectra and the timewave-form of the corresponding X -component.

The remarkable fact is that both stable attractors given by Figs. 1(c) and (d) coexist for the same parameters given by (27), $c_3 = 0.038$ and for $a_0 \in [1.780, 1.891]$, but for different initial conditions, see Figs. 2, and 4. Indeed, when more than one critical points are identified, it may appear that two bifurcations involving low periodic orbits induce simultaneously a periodic window. In such a case, two co-existing stable limit cycles may be observed, we qualify these limit cycles by solutions of type I, Figs. 1(a)–(c), or type II, Figs. 1(d)–(i). This means that it is possible for the behavior of the three species to change completely if the initial amount of one of these species changes, even if the parametric values remain unchanged, a natural fact. This may be occur when for example an epidemics arises. When two attractors co-exist the epidemic may induce a transition from one attraction basin to the other, therefore, the dynamical behavior after the disease may be different from the one observed before.

For the same parameters given by (27), if we fix $c_3 = 0.03$, the strange attractor given in the previous figures change slightly, we obtain another strange attractor (Fig. 5(a)), revealed via a period-doubling cascade the diagram of which is given by Fig. 5(b).

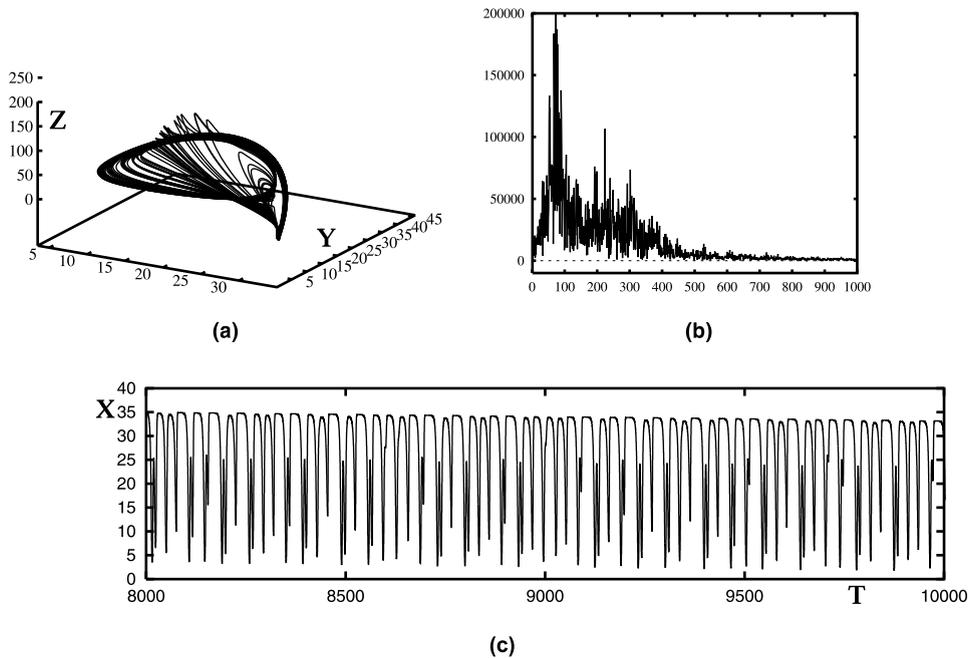


Fig. 3. (a) Tri-dimensional view of the phase portrait of the system (1) with $c_3 = 0.038$, the set of parameters given by (27), $a_0 = 2.1$ and the initial condition given by (28). (b) The corresponding power spectra for the X -component (on $2^{17} = 131072$ pts). (c) The corresponding time-waveform for the X -component.

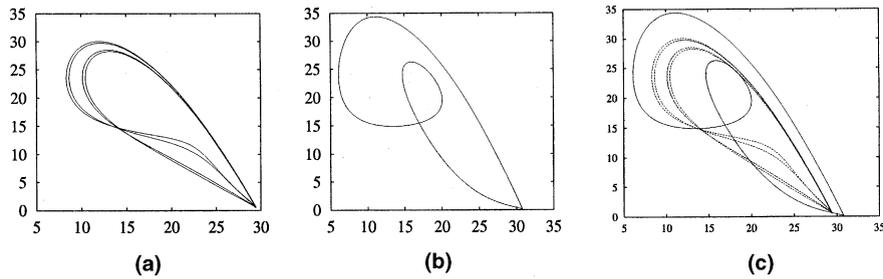
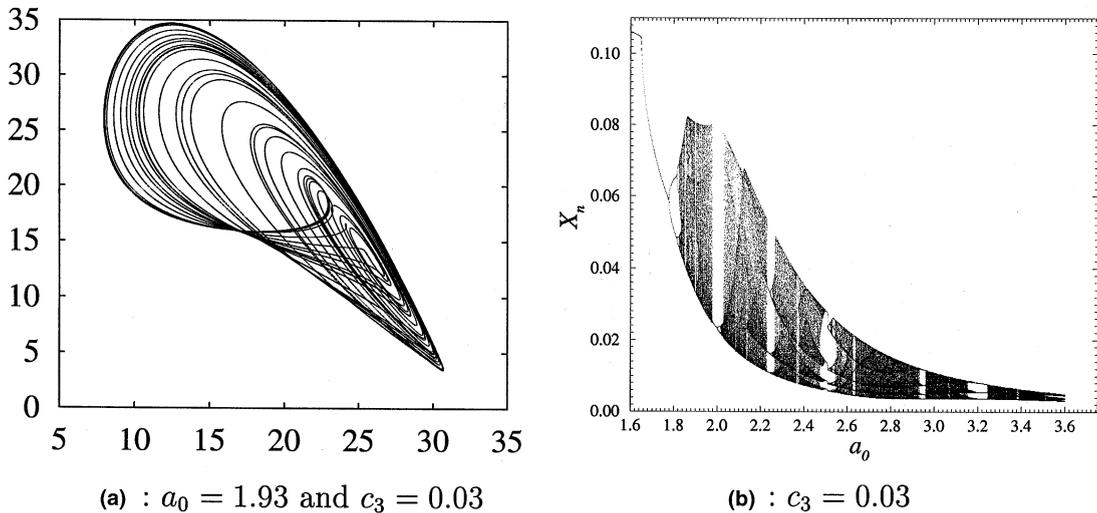


Fig. 4. Projection on the XY -plane of coexistent stable limit cycles of the system (1), for the parameters (27), $c_3 = 0.038$, and $a_0 = 1.7925$. The initial conditions are: (a) a stable limit cycle of type I for initial condition $(1.2, 1.2, 1.2)$; (b) a stable limit cycle of type II for initial condition $(0.1, 0.1, 0.1)$; (c) both cycles plotted together.



(a) : $a_0 = 1.93$ and $c_3 = 0.03$

(b) : $c_3 = 0.03$

Fig. 5. (a) Phase portrait in the XY -plane of a strange attractor exhibited by system (1) with the set of parameters given by (27), the initial condition given by (28) and with $a_0 = 1.93$, $c_3 = 0.03$. (b) The (a_0, X) bifurcation diagram for the same parameters.

Period-halving bifurcation. The period-doubling phenomenon leading to chaos is a well-known feature of a range of nonlinear differential equations, often used in modeling biological populations. Nevertheless, this phenomenon can suddenly break down and reverse, giving rise to period-halving bifurcations leading to stable limit cycles. By using the parameters given by (27) and with $c_3 = 0.03$, a_0 varying, Fig. 6 shows such a chain of period-halving.

Numerical observations on the behavior near the XY -plane close to E_2 . For small a_0 there is no limit cycle in the XY -plane and E_2 has a two-dimensional stable manifold (the XY -plane) and one-dimensional manifold transverse to the XY -plane. At this stage, even in the presence of the top-predator, the population sizes readily moves towards E_2 , see Fig. 7. As a_0 increases, (when θ becomes less than $(1 - a)/2$), and if the initial quantity Z_0 of the top-predator is small, a Hopf bifurcation occurs in the XY -plane (see Theorem 6), that is the interaction between species X and Y become oscillatory and a planar limit cycle appears, Fig. 8. If this initial quantity Z_0 is not small, even if the parameter a_0 remains fixed and does not increase, the limit cycles period doubles through a sequence of period-doubling bifurcations. Next, a connection with a broken homoclinic solution (which emanates on E_1) occurs and finally lead to the attractors shown in Fig. 9. However, there is numerical evidence of other routes to chaos, which is for example a saddle-node bifurcations of limit cycles. Via a change of various parameters, other interesting dynamics are possible for this system.

6. Conclusion

We have studied a three-dimensional continuous time dynamical system, modeling a tritrophic food chain, based especially on a modified Leslie–Gower scheme. The boundedness of the trajectories, existence of an attracting set, as

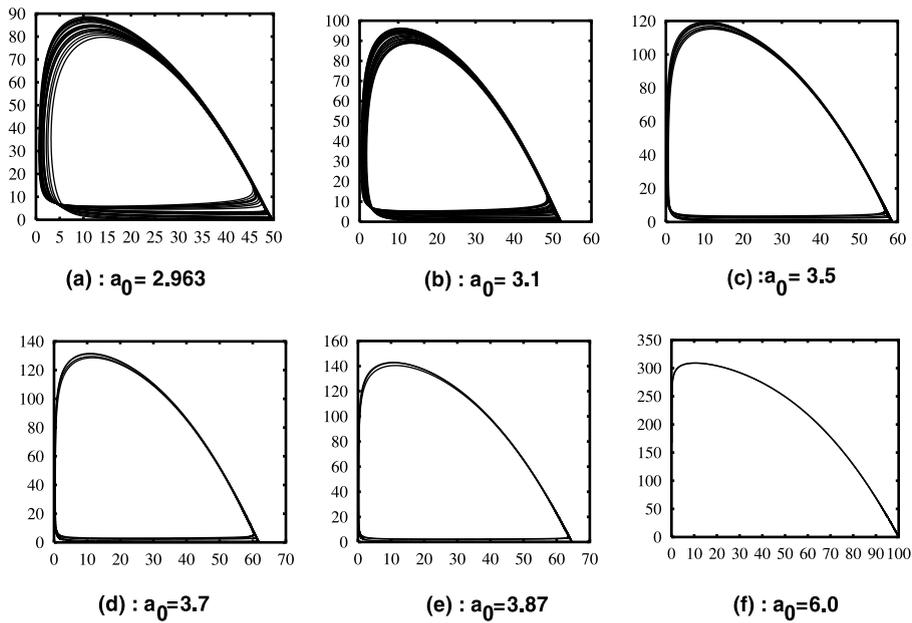


Fig. 6. Phase portraits in the XY -plane for system (1) showing the transition from chaos to a stable period-1 limit cycle via period-halving with the parameters given by (27), $c_3 = 0.03$ and the initial condition given by (28); the parameter a_0 is done in each figure.

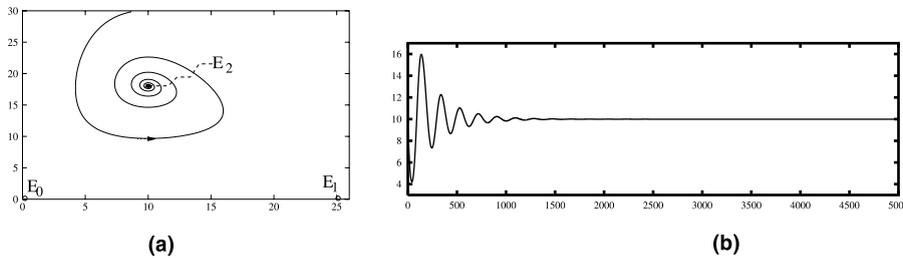


Fig. 7. (a) Projection on the XY -plane of the solution exhibited by system (1) for the parameters given by (27), $a_0 = 1.5$ and $c_3 = 0.038$. The chosen initial condition is $X_0 = 10.1$, $Y_0 = 30.1$ and $Z_0 = 0.1$: the equilibrium E_2 is globally stable. (b) The time-waveform of the x -component for the same parameters.

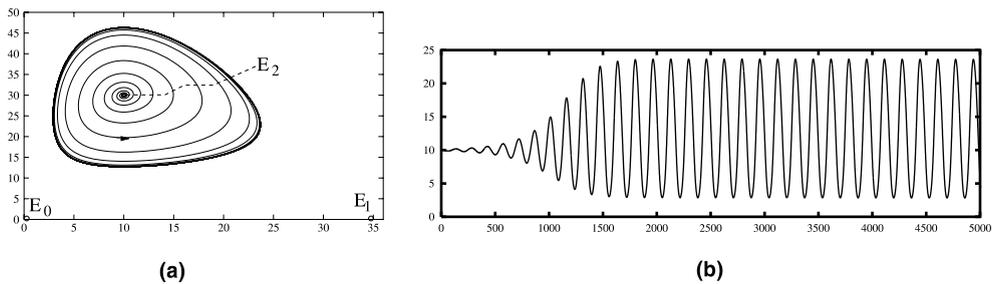


Fig. 8. (a) Projection on the XY -plane of the solution exhibited by system (1) for the same parameters as the previous figure, but $a_0 = 2.1$ and for small Z_0 . The chosen initial condition is $X_0 = 10.1$, $Y_0 = 30.1$ and $Z_0 = 0.001$: the equilibrium E_2 of the previous figure has lost its stability and a stable limit cycle appears. (b) The corresponding time-waveform of the x -component.

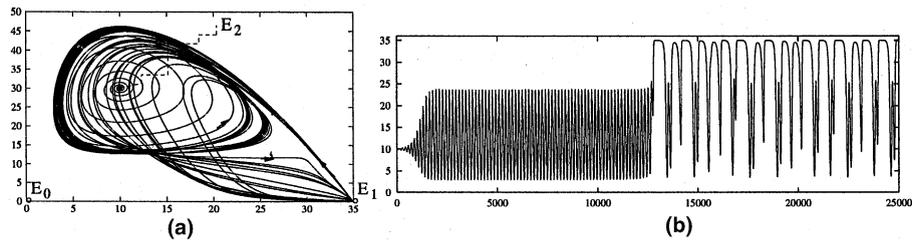


Fig. 9. (a) Projection on the XY -plane of the typical solution exhibited by system (1) for the same parameters as the previous figure, but for not enough small Z_0 . The chosen initial condition is $X_0 = 10.1$, $Y_0 = 30.1$ and $Z_0 = 0.1$: the limit cycle of previous figure is suddenly destabilized and chaotic dynamic takes place. (b) The corresponding time-waveform of the x -component.

well as the existence of the equilibria which represent the extinction of top-predator or intermediate-predator, their local or global stability, have been analyzed. We have also explored numerically the chaotic behavior of the system by plotting various phase portraits, timewave forms or power spectra. Even if the selection of biologically realistic parameter values for the numerical simulation of ecological models is difficult and our parameter range is narrow, very rich and complex dynamics are appeared, presenting various sequences of period doubling leading to chaos or sequences of period-halving leading to limit cycles.

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