

ANALYTICAL STUDY OF A TRIPLE HOPF BIFURCATION IN A TRITROPHIC FOOD CHAIN MODEL

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ABSTRACT. We provide an analytical proof of the existence of a stable periodic orbit contained in the region of coexistence of the three species of a tritrophic chain. The method used consists in analyzing a triple Hopf bifurcation. For some values of the parameters three limit cycles born via this bifurcation. One is contained in the plane where the top-predator is absent. Another one is not contained in the domain of interest where all variables are positive. The third one is contained where the three species coexist. The techniques for proving these results have been introduced in previous articles by the second author and are based on the averaging theory of second-order. Existence of this triple Hopf bifurcation has been previously discovered numerically by Kooi, Boer and Kooijman.

1. INTRODUCTION

During these last 80 years, after the seminal works of Lotka [17] and Volterra [27], one of the main topics in mathematical ecology has been the study of (di)trophic food chains. This has been made by analyzing many different planar differential systems under the common name of prey-predator models, for instance see [1, 7]. The existence of limit cycles, attractors, and several kind of bifurcations are the characteristics of those models which have been used to explain the complex behaviors observed in such systems.

In the late seventies some interest in the mathematics of tritrophic food chain models (composed of prey, predator, and top-predator) appeared, see for example [9, 10, 8] and Predator-Prey models with parasitic infection [11]. The model we analyze in this article describes a tritrophic food chain composed of a logistic prey (x), a Holling type II predator (y), and a Holling type II top-predator (z). After a rescaling of the variables, it is given by the following system of ordinary differential equations (see [12, 22, 16, 13, 20] for more details):

$$\begin{aligned} \varepsilon^2 \dot{x} &= x \left(\rho - \frac{x}{k} - \frac{a_1 y}{b_1 + x} \right), \\ \varepsilon \dot{y} &= y \left(\frac{a_1 x}{b_1 + x} - \frac{a_2 z}{b_2 + y} - d_1 \right), \\ \dot{z} &= z \left(\frac{a_2 y}{b_2 + y} - d_2 \right). \end{aligned} \tag{1}$$

In order to preserve the biological meaning of the model, the 8 parameters of this system are assumed to be strictly positive. Similar types of systems have been

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studied in the case when time scales of the variables are different so that methods of approximations of slow-fast systems can be applied [25, 26]. We emphasize that we do need here this type of approximation. To clarify possible applications of our result, we focus in a range where the population of the superpredator z remains small (near $z = 0$). So in our view here the superpredator remains of small amplitude compared with the two other populations. Within this range, we look for the possibility of a periodic rhythms which is stable and where the three species coexist.

The bifurcation analysis can be carried out with respect to the two parameters (d_1, d_2) . The normal form analysis around one of the stationary points (called latter p_3 in this article was first carried out by Klebanoff and Hastings ([13]) and latter improved by [15]. These authors (Kuznetsov and Rinaldi) also discovered numerically the existence of a strange attractor. In the limit of slow-fast systems Muratori and Rinaldi ([22]) developed a singular perturbation approach which supports the existence of a homoclinic intersection of the stable and unstable manifolds of the limit cycle which is contained in the (x, y) -plane. Classical arguments in the theory of dynamical systems can then be used to deduce the existence of infinitely many limit cycles of increasing period (but nothing is known in general on their stability). See also ([25] and [26]).

We are interested in the limit cycles of system (1), mainly in the ones which come from a Hopf bifurcation. There are several papers dedicated to these limit cycles see for instance [19, 3, 4, 5, 6, 21, 16]. But in all these papers the existence of a triple Hopf bifurcation was not proved analytically, the results there are essentially numerical. The existence of the triple Hopf bifurcation was discovered in [14]. We prove here that there are systems (1) having 1 or 3 small amplitude limit cycles coming from a Hopf bifurcation, and we show how to study the type of stability of such limit cycles. The tool for obtaining these results is the theory of averaging of second order. In fact as we shall show from the singular point bifurcate 3 small amplitude limit cycles one of them is contained in $z > 0$, the other in $z = 0$ and the last in $z < 0$. Of course the unique small amplitude limit cycles which have biological meaning are the ones contained in $z \geq 0$.

As a guide to the potential “ecological user”, we should emphasize that we can prove the existence of a Hopf bifurcation of second order provided that the logistic growth of the prey satisfies the two relations:

$$\rho = \frac{b_1(a_1 + d_1)}{(a_1 - d_1)k},$$

and

$$k = \frac{2a_1b_1^2d_1}{(a_1 - d_1)^2(a_1b_1 - 2b_2d_1)},$$

and that the rate of exponential decay of the superpredator satisfies:

$$d_2 = \frac{a_1a_2b_1^2}{a_1^2b_2k + b_2d_1^2k + a_1(b_1^2 - 2b_2d_1k)}.$$

There is also a fourth condition which defines a full open set in the parameter space:

$$a_1b_1 > 2b_2d_1.$$

These four conditions ensure the existence of a periodic orbit contained in the domain of coexistence of the three species. A last inequality is required to ensure

the stability of this periodic orbit. Although from the viewpoint of applications imposing inequalities on the parameters is not constraining too much (provided they are compatible and we check that the set of existence of a stable periodic orbit is not empty by giving one example), it is of course much less natural to impose the three first conditions above. These conditions seem necessary for the analytical proof. Practically it might be enough to check that the values of the parameters remain close to those prescribed above but this last point is beyond the dynamical systems techniques we use here.

The paper is structured as follows. In the appendix 4 we summarize the basic results on the averaging theory of second order that we shall need for studying the Hopf bifurcation. The explicit results on the Hopf bifurcation are stated in Theorem 1 at the end of section 2. In this section is also proved Theorem 1. An example showing the existence of three stable small amplitude limit cycles bifurcating from a singular point of system (1) is given in Section 3.

2. THE HOPF BIFURCATION

We separate the study of the Hopf bifurcation in different subsections.

2.1. The singular point which will exhibit the Hopf bifurcation. The differential system (1) can have the following six singular points:

$$p_1 = (0, 0, 0),$$

$$p_2 = (k\rho, 0, 0),$$

$$p_3 = \left(\frac{b_1 d_1}{a_1 - d_1}, -\frac{b_1(b_1 d_1 + (d_1 - a_1)k\rho)}{(a_1 - d_1)^2 k}, 0 \right),$$

$$p_4 = \left(0, \frac{b_2 d_2}{a_2 - d_2}, -\frac{b_2 d_1}{a_2 - d_2} \right),$$

$$p_5 = \left(\frac{A + \sqrt{B}}{2(a_2 - d_2)}, \frac{b_2 d_2}{a_2 - d_2}, \frac{b_2(a_1 - d_1)\sqrt{B} - b_2 C(a_2 - d_2)}{(a_2 - d_2)(\sqrt{B} + D)} \right),$$

$$p_6 = \left(\frac{A - \sqrt{B}}{2(a_2 - d_2)}, \frac{b_2 d_2}{a_2 - d_2}, \frac{b_2(a_1 - d_1)\sqrt{B} + b_2 C(a_2 - d_2)}{(a_2 - d_2)(\sqrt{B} - D)} \right),$$

where

$$\begin{aligned} A &= -a_2 b_1 + b_1 d_2 + a_2 k\rho - d_2 k\rho, \\ B &= 4(a_2 - d_2)(a_2(b_1 + k\rho)^2 - d_2(b_1^2 + 4a_1 b_2 k + 2b_1 k\rho + k^2 \rho^2)), \\ C &= a_1 b_1 + b_1 d_1 - a_1 k\rho + d_1 k\rho, \\ D &= a_2 b_1 - b_1 d_2 + a_2 k\rho - d_2 k\rho. \end{aligned}$$

Of course such singular points exist always that their denominators are nonzero and the expression $B \geq 0$.

The study of the stability of p_5 and p_6 looks very tedious in full generality due to the very long expressions of their eigenvalues. So the analysis of their possible Hopf bifurcations is out of scope. Since the eigenvalues of p_1 and p_2 are always real, we must put our interest in the points p_3 and p_4 . We choose here to study p_3

because it seems more meaningful to proceed in the neighborhood of $z = 0$ if we keep in mind the situation of biological interest we presented in the introduction. It could be quite possible to proceed with p_4 .

We shall study the Hopf bifurcation at the singular point p_3 . The eigenvalues at this singular point are

$$\lambda_{\pm} = \frac{1}{2a_1(a_1 - d_1)k} \left(-a_1b_1d_1 - b_1d_1^2 + a_1d_1k\rho - d_1^2k\rho \pm \sqrt{\Delta} \right),$$

$$\mu = -d_2 + \frac{a_2b_1(b_1d_1 + (-a_1 + d_1)k\rho)}{b_1^2d_1 - b_2(a_1 - d_1)^2k + b_1(-a_1 + d_1)k\rho}$$

where

$$\Delta = d_1(-4a_1(a_1 - d_1)^2k(-b_1d_1 + (a_1 - d_1)k\rho) + d_1(a_1(b_1 - k\rho) + d_1(b_1 + k\rho))^2).$$

It is well known that a necessary condition in order to have a Hopf bifurcation at p_3 is that their pair of complex eigenvalues λ_{\pm} when $\Delta < 0$ must cross the imaginary axis. So we will take

$$(2) \quad \text{Re}(\lambda_{\pm}) = \frac{-a_1b_1d_1 - b_1d_1^2 + a_1d_1k\rho - d_1^2k\rho}{2a_1(a_1 - d_1)k} = \varepsilon^2l,$$

where ε is a small parameter necessary for applying the averaging theory in order to study the Hopf bifurcation and l is an arbitrary parameter. Initially we had taken instead of ε^2l the expression $\varepsilon l_1 + \varepsilon^2l_2$. But applying the averaging theory of first order we do not obtain any information about the Hopf bifurcation and in order that the averaged function of first order F_{10} (see the appendix) becomes identically zero we must take $l_1 = 0$. This is the reason that now we are taking directly ε^2l instead of $\varepsilon l_1 + \varepsilon^2l_2$.

In order to apply the averaging theory we must write our differential system (1) into the normal form of the averaging, i.e. into the form (12). Then we need to take

$$(3) \quad \mu = \varepsilon^2m,$$

where m is an arbitrary parameter. As in the equation (2) at the beginning we took $\varepsilon m_1 + \varepsilon^2m_2$, but for the same reason than before we must take $m_1 = 0$. In short we are taking directly ε^2m instead of $\varepsilon m_1 + \varepsilon^2m_2$.

Solving equalities (2) and (3) with respect to d_2 and ρ we obtain that

$$(4) \quad d_2 = \frac{a_1a_2b_1^2d_1 + E\varepsilon^2 + 2a_1b_1(d_1 - a_1)klm\varepsilon^4}{d_1(b_2ka_1^2 + (b_1^2 - 2b_2d_1k)a_1 + b_2d_1^2k + 2a_1b_1(a_1 - d_1)kl\varepsilon^2)},$$

$$\rho = \frac{2a_1(a_1 - d_1)kl\varepsilon^2 + b_1d_1(a_1 + d_1)}{(a_1 - d_1)d_1k},$$

with $E = -b_2kmd_1^3 + a_1(-mb_1^2 - 2a_2klb_1 + 2b_2d_1km)d_1 + a_1^2k(2a_2b_1l - b_2d_1m)$. Now the eigenvalues of the singular point p_3 become

$$\varepsilon^2l \pm \frac{\sqrt{k(\varepsilon^2kl(l\varepsilon^2 - 2a_1 + 2d_1) - b_1d_1)}}{k}, \quad \varepsilon^2m.$$

2.2. The system in the normal form for applying the averaging theory.

One of the most difficult steps for applying the averaging theory to a given differential system, as our system (1) in order to study its limit cycles, is to write it in the normal form (12) of the averaging theory. Moreover in our case we want to study the small amplitude limit cycles coming from a Hopf bifurcation. For doing all this we shall follow the next steps:

(i) First we translate the singular point p_3 at the origin of coordinates doing the change of variables $(X, Y, Z) = (x, y, z) - p_3$.

(ii) We write the linear part at the origin of the differential system $(\dot{X}, \dot{Y}, \dot{Z})$ in its real Jordan normal form. For this we do the change of variables

$$\begin{pmatrix} X \\ Y \\ Z \end{pmatrix} = \begin{pmatrix} -\frac{d_1 k}{F} & 0 & 1 \\ -\frac{\varepsilon^2 k l}{F} & 1 & \frac{\varepsilon^2(2l-m)}{d_1} \\ 0 & 0 & G \end{pmatrix} \begin{pmatrix} U \\ V \\ W \end{pmatrix},$$

where

$$\begin{aligned} F &= \sqrt{b_1 d_1 - k(\varepsilon^2 k l (l\varepsilon^2 - 2a_1 + 2d_1))}, \\ G &= HI / [a_1 a_2 b_1 d_1 k (2(a_1 - d_1) k l e^2 + b_1 d_1)], \\ H &= b_2 k d_1^3 + a_1 (b_1^2 - 2e^2 k l b_1 - 2b_2 d_1 k) d_1 + a_1^2 k (2b_1 l e^2 + b_2 d_1), \\ I &= k (m(m - 2l) e^2 + 2a_1 l - 2d_1 l) e^2 + b_1 d_1. \end{aligned}$$

(iii) We write the new differential system $(\dot{U}, \dot{V}, \dot{W})$ in the cylindrical coordinates (R, θ, W) defined through $U = R \cos \theta$, $V = R \sin \theta$ and $W = W$.

(iv) In order to study the small amplitude limit cycles around the origin of coordinates we do the rescaling $(R, \theta, W) = (\varepsilon r, \theta, \varepsilon w)$.

(v) Finally the system $(\dot{r}, \dot{\theta}, \dot{w})$ is written as $(r', w') = (dr/d\theta, dw/d\theta)$ and we obtain the tritrophic food chain model in the normal form of averaging:

$$\begin{aligned} r' &= \varepsilon F_{11}(\theta, r, w) + \varepsilon^2 F_{21}(\theta, r, w) + O(\varepsilon^3), \\ w' &= \varepsilon F_{12}(\theta, r, w) + \varepsilon^2 F_{22}(\theta, r, w) + O(\varepsilon^3), \end{aligned}$$

where

$$\begin{aligned} F_{11} &= R_1/T_0, \\ F_{21} &= (R_2 T_0 - R_1 T_1)/T_0^2, \\ F_{21} &= W_1/T_0, \\ F_{22} &= (W_2 T_0 - W_1 T_1)/T_0^2, \end{aligned}$$

and

$$\begin{aligned}
R_1 = & \frac{d_1^2 r^2}{a_1 \sqrt{b_1 d_1 k}} \cos^3 \theta - \frac{(a_1 - d_1) r^2}{b_1} \cos^2 \theta \sin \theta - \frac{2 d_1 w r}{a_1 k} \cos^2 \theta + \\
& \frac{\sqrt{b_1 d_1 k} w^2}{a_1 k^2} \cos \theta + \frac{(a_1 - d_1)}{a_1 \sqrt{b_1 d_1 k} (b_2 k a_1^2 + b_1^2 a_1 - 2 b_2 d_1 k a_1 + b_2 d_1^2 k)^2} (b_2^2 k^2 a_1^5 + \\
& a_2 b_1 b_2 k^2 a_1^4 - 3 b_2^2 d_1 k^2 a_1^4 + 2 b_1^2 b_2 k a_1^4 + b_1^4 a_1^3 + 2 b_2^2 d_1^2 k^2 a_1^3 - 3 a_2 b_1 b_2 d_1 k^2 a_1^3 - \\
& 2 b_1^2 b_2 d_1 k a_1^3 + 2 b_2^2 d_1^3 k^2 a_1^2 + 3 a_2 b_1 b_2 d_1^2 k^2 a_1^2 + b_1^4 d_1 a_1^2 - 2 b_1^2 b_2 d_1^2 k a_1^2 - \\
& 3 b_2^2 d_1^4 k^2 a_1 - a_2 b_1 b_2 d_1^3 k^2 a_1 + 2 b_1^2 b_2 d_1^3 k a_1 + b_2^2 d_1^5 k^2) r w \cos \theta \sin \theta + \\
& \frac{(a_1 - d_1) d_1 (d_1 - a_1) k r^2}{a_1 b_1 \sqrt{b_1 d_1 k}} \cos \theta \sin^2 \theta + \\
& \frac{b_1 (a_1 - d_1)^2 r w}{b_2 k a_1^2 + b_1^2 a_1 - 2 b_2 d_1 k a_1 + b_2 d_1^2 k} \sin^2 \theta - \frac{(a_1 - d_1) w^2}{a_1 k} \sin \theta, \\
R_2 = & \frac{b_2 k^2 r^2 w (a_1 - d_1)^6}{a_1 b_1 (b_2 k a_1^2 + b_1^2 a_1 - 2 b_2 d_1 k a_1 + b_2 d_1^2 k)^2} \sin^3 \theta - \frac{d_1 r^3 (a_1 - d_1)^2}{a_1^2 b_1^2} \cos^4 \theta + \\
& \frac{w^3 (a_1 - d_1)^2}{a_1^2 b_1 k} \sin \theta - \frac{r (w^2 a_1^3 - 3 d_1 w^2 a_1^2 - b_1^2 l a_1^2 + 3 d_1^2 w^2 a_1 - d_1^3 w^2)}{a_1^2 b_1^2} \sin^2 \theta + \\
& \frac{(a_1 - d_1) d_1 (d_1 - a_1) k r^3}{a_1 b_1^2 \sqrt{b_1 d_1 k}} \cos^3 \theta \sin \theta + \frac{3 (a_1 - d_1)^2 \sqrt{b_1 d_1 k} w r^2}{a_1^2 b_1^2 k} \cos^3 \theta - \\
& \frac{(a_1 - d_1)^3 d_1 k r^3}{a_1^2 b_1^3} \cos^2 \theta \sin^2 \theta + \frac{(a_1 - d_1)^2 (2 a_1 + d_1) w r^2}{a_1^2 b_1^2} \cos^2 \theta \sin \theta + \\
& \frac{(-3 w^2 a_1^2 + b_1 k l a_1^2 + 6 d_1 w^2 a_1 - 3 d_1^2 w^2) r}{a_1^2 b_1 k} \cos^2 \theta + \frac{J}{K} \cos \theta \sin^2 \theta + \\
& \frac{\sqrt{b_1 d_1 k} w^3 (a_1 - d_1)^2}{a_1^2 b_1 d_1 k^2} \cos \theta - \frac{(a_1 + 2 d_1) r w^2 (a_1 - d_1)^2}{a_1^2 b_1 \sqrt{b_1 d_1 k}} \cos \theta \sin \theta, \\
T_0 = & -\frac{\sqrt{b_1 d_1 k}}{k},
\end{aligned}$$

$$\begin{aligned}
T_1 = & -\frac{(a_1 - d_1)d_1r}{a_1b_1} \cos^3 \theta - \frac{2(d_1 - a_1)\sqrt{b_1d_1kw}}{a_1b_1k} \cos^2 \theta - \\
& \frac{\sqrt{b_1d_1k}(ka_1^2 - 2d_1ka_1 + b_1d_1 + d_1^2k)r}{a_1b_1^2k} \cos^2 \theta \sin \theta - \frac{(a_1 - d_1)w^2}{a_1kr} \cos \theta + \\
& \frac{(b_1ka_1^3 - 2b_1d_1ka_1^2 + 2b_2d_1ka_1^2 + 2b_1^2d_1a_1 + b_1d_1^2ka_1 - 4b_2d_1^2ka_1 + 2b_2d_1^3k)w}{a_1k(b_2ka_1^2 + b_1^2a_1 - 2b_2d_1ka_1 + b_2d_1^2k)} \cos \theta \sin \theta + \\
& \frac{(a_1 - d_1)^2r}{a_1b_1} \cos \theta \sin^2 \theta - \frac{L}{M} \sin^2 \theta - \frac{\sqrt{b_1d_1kw}^2}{a_1k^2r} \sin \theta, \\
W_1 = & \frac{a_2b_1b_2(a_1 - d_1)^3(a_1 + d_1)kw}{(b_2ka_1^2 + b_1^2a_1 - 2b_2d_1ka_1 + b_2d_1^2k)^2} \sin \theta, \\
W_2 = & mw - \frac{a_2b_1^2b_2(a_1 - d_1)^4(a_1 + d_1)^2kw}{(b_2ka_1^2 + b_1^2a_1 - 2b_2d_1ka_1 + b_2d_1^2k)^3} \sin^2 \theta.
\end{aligned}$$

where

$$\begin{aligned}
J = & k(2b_2^3k^3d_1^7 - 12a_1b_2^3k^3d_1^6 + 30a_1^2b_2^3k^3d_1^5 + 6a_1b_1^2b_2^2k^2d_1^5 - 40a_1^3b_2^3k^3d_1^4 - \\
& 24a_1^2b_1^2b_2^2k^2d_1^4 + 30a_1^4b_2^3k^3d_1^3 + 36a_1^3b_1^2b_2^2k^2d_1^3 + a_1^2a_2b_1^3b_2k^2d_1^3 + 6a_1^2b_1^4b_2kd_1^3 - \\
& 12a_1^5b_2^3k^3d_1^2 - 24a_1^4b_1^2b_2^2k^2d_1^2 - 3a_1^3a_2b_1^3b_2k^2d_1^2 - 12a_1^3b_1^4b_2kd_1^2 + 2a_1^3b_1^6d_1 + \\
& 2a_1^6b_2^3k^3d_1 + 6a_1^5b_1^2b_2^2k^2d_1 + 3a_1^4a_2b_1^3b_2k^2d_1 + 6a_1^4b_1^4b_2kd_1 - a_1^5a_2b_1^3b_2k^2)r^2w \\
& (a_1 - d_1)^3, \\
K = & a_1^2b_1^2\sqrt{b_1d_1k}(b_2ka_1^2 + b_1^2a_1 - 2b_2d_1ka_1 + b_2d_1^2k)^3, \\
L = & (a_1 - d_1)^2\sqrt{b_1d_1k}(b_2^2k^2a_1^4 + a_2b_1b_2k^2a_1^3 - 4b_2^2d_1k^2a_1^3 + 2b_1^2b_2ka_1^3 + b_1^4a_1^2 + \\
& 6b_2^2d_1^2k^2a_1^2 - 2a_2b_1b_2d_1k^2a_1^2 - 4b_1^2b_2d_1ka_1^2 - 4b_2^2d_1^3k^2a_1 + a_2b_1b_2d_1^2k^2a_1 + \\
& 2b_1^2b_2d_1^2ka_1 + b_2^2d_1^4k^2)w, \\
M = & a_1b_1d_1k(b_2ka_1^2 + b_1^2a_1 - 2b_2d_1ka_1 + b_2d_1^2k)^2.
\end{aligned}$$

2.3. The computation of the small amplitude limit cycles. Now we compute the function F_{10} , see Theorem 2, and we obtain

$$\begin{aligned}
F_{10}(r, w) = & \left(\frac{1}{2\pi} \int_0^{2\pi} F_{11}(\theta, r, w) d\theta, \frac{1}{2\pi} \int_0^{2\pi} F_{21}(\theta, r, w) d\theta \right) \\
= & \left(0, -\frac{Nw}{P} \right),
\end{aligned}$$

where

$$N = b_1ka_1^3 - 2b_1d_1ka_1^2 - 2b_2d_1ka_1^2 - 2b_1^2d_1a_1 + b_1d_1^2ka_1 + 4b_2d_1^2ka_1 - 2b_2d_1^3k,$$

$$P = a_1b_2ka_1^2 + b_1^2a_1 - 2b_2d_1ka_1 + b_2d_1^2k.$$

Taking

$$(5) \quad k = \frac{2a_1b_1^2d_1}{(a_1 - d_1)^2(a_1b_1 - 2b_2d_1)},$$

we obtain that the averaged function of first order is identically zero. We must compute the averaged function of second order, for more details see the appendix.

We note that since in the expressions of F_{ij} with $i, j \in \{1, 2\}$ appears \sqrt{k} we need that

$$(6) \quad a_1 b_1 - 2b_2 d_1 > 0.$$

From (13) the averaged function of second order $F_{20}(r, w)$ has the two components:

$$F_{201}(r, w) = \frac{Nr}{2\sqrt{2}a_1^4 b_1^4 d_1} (2(a_1 - d_1)^2 (a_1 b_1 - 2b_2 d_1) (b_1 a_1^3 - b_1 d_1 a_1^2 - 4a_2 b_2 d_1^2) w^2 - a_1^3 b_1^2 d_1 (4a_1 l b_1^2 + d_1 (d_1 - a_1) r^2)),$$

$$F_{202}(r, w) = -\frac{\sqrt{2}}{a_1^5 b_1^5} (a_1 - d_1)^2 (a_1 b_1 - 2b_2 d_1) N^3 w (a_1^4 m_2 b_1^4 - 6a_1 a_2 b_2 d_1^3 r^2 b_1 - 2a_2 b_2 (a_1 - d_1)^2 d_1 (a_1 b_1 - 2b_2 d_1) w^2),$$

where

$$N = \sqrt{\frac{a_1 b_1}{(a_1 - d_1)^2 (a_1 b_1 - 2b_2 d_1)}}.$$

In order to look for the small amplitude limit cycles bifurcating from the origin of system (1), after all the changes of coordinates that we did and according with Theorem 2, we must find the zeros (r_0, w_0) with $r_0 > 0$ of the system

$$(7) \quad F_{201}(r, w) = 0, \quad F_{202}(r, w) = 0.$$

such that the Jacobian

$$(8) \quad \det \begin{pmatrix} \frac{\partial F_{201}}{\partial r} & \frac{\partial F_{201}}{\partial w} \\ \frac{\partial F_{202}}{\partial r} & \frac{\partial F_{202}}{\partial w} \end{pmatrix} \bigg|_{(r,w)=(r_0,w_0)}$$

be nonzero.

It is easy to check that system (7) can have at most 3 solutions satisfying (8) according with the values of the parameters of system (1). More precisely one solution (r_1, w_1) is

$$(9) \quad r_1 = 2b_1 \sqrt{\frac{a_1 l}{(a_1 - d_1) d_1}} = 2b_1 \sqrt{R_1}, \quad w_1 = 0;$$

of course it exists if $R_1 > 0$. The other two possible solutions are $(r_2, \pm w_2)$ where

$$\begin{aligned}
 r_2 &= \frac{a_1 b_1}{d_1} \sqrt{\frac{a_1 b_1 (a_1^2 b_1 (a_1 - d_1) m - 4 a_2 b_2 d_1^2 (l + m))}{a_2 b_2 d_1 (5 b_1 a_1^3 - 5 b_1 d_1 a_1^2 - 24 a_2 b_2 d_1^2)}} = \frac{a_1 b_1}{d_1} \sqrt{R_2}, \\
 w_2 &= \frac{a_1^2 b_1^2}{\sqrt{2}} \sqrt{\frac{24 a_2 b_2 d_1^2 l - a_1^2 b_1 (a_1 - d_1) m}{a_2 b_2 (a_1 - d_1)^2 d_1 (2 b_2 d_1 - a_1 b_1) (-5 b_1 a_1^3 + 5 b_1 d_1 a_1^2 + 24 a_2 b_2 d_1^2)}} \\
 &= \frac{a_1^2 b_1^2}{\sqrt{2}} \sqrt{W_2};
 \end{aligned}
 \tag{10}$$

of course again these last two small amplitude limit cycles will exist if $R_2 > 0$ and $W_2 > 0$.

When the parameters of system (1) are such that we have 3 small amplitude limit cycles, then the one which has initial conditions on the plane $w = 0$ (see Theorem 2) remains in this plane because it is invariant by the flow of the system. Again since this plane is invariant, the other two small amplitude limit cycles which have initial conditions on half-spaces $w > 0$ and $w < 0$ remain in such half-spaces. Of course the invariant plane $w = 0$ corresponds to the plane $z = 0$ in the initial coordinates.

According with the statement (b) of Theorem 2 we can compute the type of stability of these small amplitude limit cycles computing the eigenvalues of the matrix (8). More precisely, let λ_1 and λ_2 be the two eigenvalues of the matrix (8) evaluated on a zero (r_0, w_0) of system (7), then the small amplitude limit cycle associated to the zero (r_0, w_0)

- (I) is a local repeller if $\text{Re}(\lambda_1), \text{Re}(\lambda_2) > 0$,
- (II) is a local attractor if $\text{Re}(\lambda_1), \text{Re}(\lambda_2) < 0$,
- (III) has two invariant manifolds, one stable and the other unstable, which locally are formed by two 2-dimensional cylinders.

We note that conditions (4) with $\varepsilon = 0$, (5) and (6) are necessary in order to apply the second order averaging theory. More precisely we need that system (1) satisfies the conditions

$$\begin{aligned}
 d_2 &= \frac{a_1 a 2 b_1^2 d_1}{a_1^2 b_2 d_1 k + b_2 d_1^3 k + a_1 d_1 (b_1^2 - 2 b_2 d_1 k)}, \\
 \rho &= \frac{b_1 (a_1 + d_1)}{(a_1 - d_1) k}, \\
 k &= \frac{2 a_1 b_1^2 d_1}{(a_1 - d_1)^2 (a_1 b_1 - 2 b_2 d_1)}, \\
 0 &< a_1 b_1 - 2 b_2 d_1,
 \end{aligned}
 \tag{11}$$

in order that we can apply the averaging theory of second order for studying its small amplitude limit cycles.

In short we have proved the next result.

Theorem 1. *The following statements hold.*

- (a) *The tritrophic food chain model given by system (1) satisfying the four conditions (11) has a triple Hopf bifurcation at the singular point p_3 if R_1 , R_2 and W_2 are positive (these last three expressions are defined in (9) and (10)).*
- (b) *More precisely, under the assumptions of statement (a) three small amplitude limit cycles bifurcate from p_3 with initial conditions in the coordinates (U, V, W) given by $(\varepsilon r_1, 0, \varepsilon w_1)$ and $(\varepsilon r_2, 0, \pm \varepsilon w_2)$, where the values of r_i and w_i are given in (9) and (10). Moreover in the variables (x, y, z) the small amplitude limit cycle coming from the initial conditions $(\varepsilon r_1, 0, \varepsilon w_1)$ lies on the plane $z = 0$, the one coming from the initial conditions $(\varepsilon r_2, 0, \varepsilon w_2)$ lies in the half-space $z > 0$, and the remainder one lies in the half-space $z < 0$.*
- (c) *Under the assumptions of statement (a) the kind of stability of the small amplitude limit cycles is determined by the eigenvalues of the matrix (8) as it is explained in (I), (II) and (III).*

3. AN EXAMPLE

When $\varepsilon = 0$ the relations (11) for the values

$$a_1 = 5, \quad a_2 = 0.1, \quad b_1 = 3, \quad b_2 = 2, \quad d_1 = 0.4,$$

become

$$d_2 = 0.09, \quad \rho = 27.74, \quad k = 0.13, \quad a_1 b_1 - 2b_2 d_1 = 13.4.$$

These values are compatible with the biological conditions. Moreover the parameters l and m are free. Taking $l = 400$ and $m = 1$ we obtain that the eigenvalues of the matrix in the expression (8) are

$$\begin{aligned} -154.96 \quad \text{and} \quad -0.32 \quad \text{for} \quad (r_1, w_1) &= (221.16, 0), \\ -135.14 \quad \text{and} \quad -0.29 \quad \text{for} \quad (r_2, w_2) &= (207.24, 39), \\ -135.14 \quad \text{and} \quad -0.29 \quad \text{for} \quad (r_2, w_2) &= (207.24, -39). \end{aligned}$$

Therefore the three small amplitude limit cycles are local attractors for these values of the parameters.

4. THE APPENDIX: AVERAGING THEORY OF SECOND ORDER

We shall use the following result.

Theorem 2 (Second order averaging method). *We consider the following differential system*

$$(12) \quad \frac{dx}{dt} = \varepsilon F_1(t, x) + \varepsilon^2 F_2(t, x) + \varepsilon^3 R(t, x, \varepsilon),$$

where $F_1, F_2 : \mathbb{R} \times D \rightarrow \mathbb{R}^n$, $R : \mathbb{R} \times D \times (-\varepsilon_f, \varepsilon_f) \rightarrow \mathbb{R}^n$ are continuous functions, T -periodic in the first variable, and D is an open subset of \mathbb{R}^n . We assume that

- (i) $F_1(t, \cdot) \in C^1(D)$ for all $t \in \mathbb{R}$, F_1 , F_2 , R and $D_x F_1$ are locally Lipschitz with respect to x , and R is differentiable with respect to ε . We define F_{10} , $F_{20} : D \rightarrow \mathbb{R}^n$ as

$$F_{10}(z) = \frac{1}{T} \int_0^T F_1(s, z) ds,$$

$$(13) \quad F_{20}(z) = \frac{1}{T} \int_0^T \left[D_z F_1(s, z) \cdot \int_0^s F_1(t, z) dt + F_2(s, z) \right] ds,$$

and assume moreover that

- (ii) for $V \subset D$ an open and bounded set and for each $\varepsilon \in (-\varepsilon_f, \varepsilon_f) \setminus \{0\}$, there exists $a_\varepsilon \in V$ such that $F_{10}(a_\varepsilon) + \varepsilon F_{20}(a_\varepsilon) = 0$ and $d_B(F_{10} + \varepsilon F_{20}, V, a_\varepsilon) \neq 0$.

Then the following statements hold.

- (a) For $|\varepsilon| > 0$ sufficiently small there exists a T -periodic solution $\varphi(t, \varepsilon)$ of system (12) such that $\varphi(0, \varepsilon) = a_\varepsilon$.
 (b) If the function $F_{10} + \varepsilon F_{20}$ is C^1 the stability or instability of the limit cycle $\varphi(t, \varepsilon)$ is given by the stability or instability of the singular point a_ε of the averaged system

$$\frac{dx}{dt} = \varepsilon F_{10}(x) + \varepsilon^2 F_{20}(x),$$

corresponding to system (12). In fact, the singular point a_ε of the averaged system has the stability behavior of the Poincaré map associated to the limit cycle $\phi(t, \varepsilon)$.

The proof of statement (a) can be found in [2], and of statement (b) is standard, see for instance [24, 23, 18].

The expression $d_B(F_{10} + \varepsilon F_{20}, V, a_\varepsilon) \neq 0$ means that the Brouwer degree of the function $F_{10} + \varepsilon F_{20} : V \rightarrow \mathbb{R}^n$ at the fixed point a_ε is not zero. For instance it is sufficient that the Jacobian of the function $F_{10} + \varepsilon F_{20}$ at a_ε is not zero in order that the mentioned Brouwer degree be nonzero.

If F_{10} is not identically zero, then the zeros of $F_{10} + \varepsilon F_{20}$ are mainly the zeros of F_{10} for ε sufficiently small. In this case the previous result provides the *averaging theory of first order*.

If F_{10} is identically zero and F_{20} is not identically zero, then the zeros of $F_{10} + \varepsilon F_{20}$ are mainly the zeros of F_{20} for ε sufficiently small. In this case the previous result provides the *averaging theory of second order*.

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REFERENCES

- [1] A. BAZYKIN, *Nonlinear Dynamics of Interacting Populations*, World Scientific, River Edge, NJ, 1998.
- [2] A. BUICĂ AND J. LLIBRE, *Averaging methods for finding periodic orbits via Brouwer degree*, Bull. Sci. Math. **128** (2004), 7–22.
- [3] K. CHENG, *Uniqueness of a limit cycle of a predator–prey system*, SIAM J. Math. Anal. **12** (1981), 541–548.
- [4] B. DENG, *Food chain chaos with canard explosion*, Chaos **14** (2004), 1083–1092.
- [5] B. DENG AND G. HINES, *Food chain chaos due to Shilnikov’s orbit*, Chaos **12** (2002), 533–538.
- [6] B. DENG AND G. HINES, *Food chain chaos due to transcritical point*, Chaos **13** (2003), 578–585.

- [7] O. DIEKMANN, R. DURRETT, K.P. HADELER, P. MAINI, H.-L. SMITH, V. CAPASSO, *Mathematics inspired by Biology*, Lect. Notes in Maths 1714, Springer, Berlin, 2000.
- [8] H. FREEDMAN AND J. SO, *Global stability and persistence of simple food chains*, Math. Biosci. **76** (1985), 69-86.
- [9] H. FREEDMAN AND P. WALTMAN, *Mathematical analysis of some three-species food-chain models*, Math. Biosci. **33** (1977), 257-276.
- [10] T. GARD, *Persistence in food chains with general interactions*, Math. Biosci. **51** (1980), 165-174.
- [11] K.P. HADELER AND H. FREEDMAN, *Predator-prey populations with parasitic infection* Journal of Mathematical Biology, vol. 27, n6, (1989), 609-631.
- [12] A. HASTINGS AND T. POWELL, *Chaos in a three-species food chain*, Ecol. **72** (1991), 896-903.
- [13] A. KLEBANOFF AND A. HASTINGS, *Chaos in three species food chains*, J. Math. Biol. **32** (1994), 427-451.
- [14] B.W. KOOI, M.P. BOER, S.A.L.M. KOOLJMAN, *Consequences of population models for the dynamics of food chains*, Math. Biosci. **153** (1998) 99-124.
- [15] Y.A. KUZNETSOV AND S. RINALDI, *Remarks on food chain dynamics* Math. Biosci. **124** (1996) 1-33.
- [16] YU. A. KUZNETSOV, O. DE FEO AND D. RINALDI, *Belyakov homoclinic bifurcations in a tritrophic food chain model*, SIAM J. Appl. Math. **62** (2001), 462-487.
- [17] A. LOTKA, *Elements of Physical Biology*, Williams and Wilkins, Baltimore, MD, 1925.
- [18] J. LLIBRE, *Averaging theory and limit cycles for quadratic systems*, Radovi Matematički **11** (2002), 215-228.
- [19] R. MAY, *Limit cycles in predator-prey communities*, Science **177** (1972), 900-902.
- [20] J.D. MURRAY, *Mathematical biology. I. An introduction*, third edition, Interdisciplinary Applied Mathematics **17**, Springer-Verlag, New York, 2002.
- [21] S. MURATORI AND S. RINALDI, *A dynamical system with Hopf bifurcations and catastrophes*, Appl. Math. Comp. **29** (1989), 1-15.
- [22] S. MURATORI AND S. RINALDI, *Low- and high-frequency oscillations in three-dimensional food chain systems* SIAM J. Appl. Math. **52** (1992), 1688-1706.
- [23] J. A. SANDERS AND F. VERHULST, *Averaging Methods in Nonlinear Dynamical Systems*, Applied Mathematical Sci., Vol. **59**, Springer-Verlag, New York, 1985.
- [24] F. VERHULST, *Nonlinear Differential Equations and Dynamical Systems*, Universitext, Springer-Verlag, Berlin, 1996.
- [25] A. VIDAL, *Stable periodic orbits associated with bursting oscillations in population dynamics in Positive Systems*, Lecture Notes in control and Information Science, vol. **341**, Springer, 2006, 439-446.
- [26] A. VIDAL, *Periodic orbits of tritrophic slow-fast systems and double homoclinic bifurcations*, Discrete and Continuous Dynamical Systems, 2007, Dynamical Systems and Differential Equations. Proceedings of the 6th AIMS International Conference, suppl., pp. 1021-1030.
- [27] V. VOLTERRA, *Variazioni e fluttuazioni del numero di individui in specie animali conviventi*, Mem. Accad. Lincei **2** (1926), 31-113.

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