A PREDATOR-PREY SYSTEM INVOLVING FIVE LIMIT CYCLES

EDUARDO SÁEZ, EDUARDO STANGE AND IVÁN SZÁNTÓ

ABSTRACT. In this paper we consider the multiparameter system introduced in [9], which corresponds to an extension of the classic minimal Daphnia-algae model. It is shown that there is a neighborhood in the parameter space where the system in the realistic quadrant has a unique equilibrium point which is a repelling weak focus of order four enclosed by a global attractor hyperbolic limit cycle. For a small enough change of the parameters in this neighborhood, bifurcation occurs from the weak focus four infinitesimal Hopf limit cycles (alternating the type of stability) such that the last bifurcated limit cycle is an attractor. Moreover, for certain values of parameters, we concluded that this applied model has five concentric limit cycles, three of them being stable hyperbolic limit cycles. This gives a positive answer to a question raised in [2, 4].

1. Introduction. In **[9]**, the authors study an extension of the classic minimal Daphnia-algae model where (A) is the population of algae and (Z) is the population for large herbivorous zooplankton:

(1)
$$\begin{cases} \frac{dA}{dt} = rA(1 - \frac{A}{K}) - \frac{gA}{A + h_A}Z + i(K - A), \\ \frac{dZ}{dt} = e\frac{gA}{A + h_A}Z - mZ - F\frac{Z^2}{Z^2 + h_Z^2}. \end{cases}$$

The parameters and functions of the model have the following meanings:

²⁰¹⁰ AMS Mathematics subject classification. Primary 34C, 58F14, 58F21, 92D25.

 $Keywords\ and\ phrases.$ Stability, limit cycles, bifurcations, predator-prey models.

The first and third authors were financed partially by USM grant Nos. 120905 and 120906, and the second author was financed partially by DIPUV, grant No. 022006.

Received by the editors on January 13, 2012, and in revised form on August 13, 2012.

DOI:10.1216/RMJ-2014-44-6-2057 Copyright ©2014 Rocky Mountain Mathematics Consortium

r	=	Maximum growth rate of algae
K	=	Carrying capacity of algae
g	=	Maximun grazing rate of zooplankton
h_A	=	Half-saturation functional respose of zooplankton
i	=	Diffusive inflow of algae
e	=	Food transfer efficiency of zooplankton
m	=	Loss term of zooplankton
h_Z	=	Half-saturation functional response of fish
F	=	The planktivorous capacity the depredation of the
		zooplankton.

Studies of the dynamics of these models are essentially numerical with geometric and biological interpretations, and an overview of the theory of competition of species in ecological communities can be seen in [7]. More precisely, in [1], the congruity of plant-herbivore systems and predator-prey systems is introduced, the former classified according to the interaction between the plants and animals and exploring the dynamics behavior of examples for each category of this classification, while in [5, 6] over 20 years of study of data from populations of Daphnia and algae in a wide variety of field situations is analyzed, proving that these systems display three types of dynamic behavior: both populations stable; both populations cyclic; and Daphnia cyclic but algae stable. Furthermore, this study analyzes the behavior of the reproduction, growth and the mortality of Daphnia with a low rate of food supply.

In [9], an expansion is introduced of a classical minimal *Daphnia-algae* model to account for effects of fish as a top predator. The model predicts that the critical fish density for Daphnia collapse is higher in systems with higher ambient nutrient concentrations and also shows how intrinsic predator-prey oscillations in the planktonic system can facilitate the switch to the algal-dominated regime where Daphnia is controlled by fish.

In this work, we are interested in describing the dynamics of the model suggested in [9], with results and techniques of the qualitative theory of dynamical systems. In [9], based on this theory, the results are demonstrated by the existence of homoclinic bifurcations, while the central interest in this paper is to prove that the model has a high number of cycle limits (Hopf bifurcations) which means the existence of

distinct and diverse stability regions for the coexistence of the species involved.

To simplify the study of the dynamics of the model, we change the parameters and coordinates in order to obtain a more suitable system (normal form) as follows: $\{A \to x, Z \to y, h_A \to a, h_Z \to b\}$, where x, y denote the new coordinates and h_A, h_Z are the values of average saturation of the algae and herbivorous zooplankton, respectively. Then the vector field (1) is C^{∞} -equivalent:

(2)
$$X_{\mu}: \begin{cases} \dot{x} = \frac{r}{K}x(K-x) - yg\frac{x}{x+a} + i(K-x), \\ \dot{y} = egy\frac{x}{x+a} - my - F\frac{y^2}{y^2 + b^2} \end{cases}$$

where the parameters are: $\mu = (r, K, g, a, i, m, F, b) \in \mathbb{R}^8_+$.

In order to get a C^{∞} -equivalent polynomial vector field, we consider the rescaling $\{x \to ax, y \to by, F \to bF, e \to e/g\}$. Then system (2) is reduced to the system:

(3)
$$\begin{cases} \dot{x} = rx(1 - \frac{ax}{K}) - \frac{bg}{a}\frac{xy}{x+1} + i(\frac{K}{a} - x), \\ \dot{y} = e\frac{xy}{x+1} - my - F\frac{y^2}{y^2 + 1}. \end{cases}$$

Considering again the rescaling $\{b\to ba/g, K\to aK\}$ we obtain the $C^\infty\text{-equivalent vector field}$

(4)
$$\begin{cases} \dot{x} = rx(1-\frac{x}{K}) - b\frac{xy}{x+1} + i(K-x), \\ \dot{y} = e\frac{xy}{x+1} - my - F\frac{y^2}{y^2+1}. \end{cases}$$

Changing the time $\{t \to t\frac{K}{r}\}$ and considering the change of parameters (using the same symbols for the new parameters) $\{\frac{bK}{r} \to b, \frac{iK}{r} \to i, \frac{eK}{r} \to e, \frac{mK}{r} \to m, \frac{FK}{r} \to F\}$ and, once again changing the time $\{t \to t(x+1)(y^2+1)\}$, finally a C^{∞} -equivalent six-parameters polynomial vector field is obtained: (5)

$$Y_{\mu}: \begin{cases} \dot{x} &= (y^2+1)[x(K-x)(x+1)-bxy+i(K-x)(x+1)], \\ \dot{y} &= ey[x(y^2+1)-m(x+1)(y^2+1)-Fy(x+1)] \end{cases}$$

where $(x, y) \in \overline{\Omega} = \{(x, y) | x, y \ge 0\}$ and the parameters are given by $\mu = (K, b, i, e, m, F) \in \mathbb{R}^6_+$.

In particular,

$$Y_{\mu}(0,y) = iK(y^2+1)\frac{\partial}{\partial x} - y[m(y^2+1) + Fy]\frac{\partial}{\partial y}$$

System (5) is not a Kolmogorov system, because the axis x = 0 is not an invariant straight line of Y_{μ} . In fact, by definition i > 0, then the vector field transversally crosses into the first quadrant at every point of this straight line.

Furthermore, since

$$Y_{\mu}(x,0) = (K-x)(x+1)(x+i)\frac{\partial}{\partial x},$$

then $Y_{\mu}(K,0) = 0$ and (K,0) is the only singularity of field Y_{μ} in the invariant semi-axis $y = 0, x \ge 0$.

In order to show more clearly the results of the dynamic model, in the parameter space mF, we will consider the following auxiliary functions: $\begin{cases} l_1(m,F) &= F - 2m \\ l_2(m,F) &= F + 2m - 2 \end{cases}$, and we define the subset of \mathbb{R}^2 as

$$\Re = l_1^{-1}(0,\infty) \cap l_2^{-1}(-\infty,0).$$

 F
 l_2
 l_2
 R
 $\frac{1}{2}$
 $\frac{1}{2}$
 $\frac{1}{2}$
FIGURE 1.

In the case of uniqueness of the singularities of the vector field in the

open domain Ω , the coordinates of that singularity will be denoted by (A, B). Let us consider the change of parameters

(6)
$$\begin{cases} F = -\frac{(1+B^2)[A(m-1)+m]}{(1+A)B}, & A(m-1)-A < 0\\ b = -\frac{(1+A)(A+i)(A-K)}{AB}, & A < K. \end{cases}$$

Then, introducing into system (5) the change of parameters shown in (6) and also changing the time $\{t \to AB(1+A)t\}$, we have a C^{∞} -equivalent system to the system (5) (and consequently to the system (1)):

(7)
$$Z_{\eta}: \begin{cases} \dot{x} = (1+A)(1+y^2)[AB(K-x)(1+x)(i+x) + (1+A)(A+i)(A-K)xy], \\ \dot{y} = -Aey[(1+A)B(m+(-1+m)x) - (1+B^2)(A(-1+m)+m)(1+x)y + (1+A)B(m+(-1+m)x)y^2]. \end{cases}$$

2. Main results.

Lemma 2.1. Let $(m, F) \in \Re \cap \mathbb{R}^2_+$.

- (i) If m/(1-m) < K, then the vector field Z_η has at least one singularity (A, B) ∈ Ω. Furthermore, the singularity (K, 0) is hyperbolic saddle point with unstable manifold oriented to the realistic quadrant Ω.
- (ii) If $\frac{m}{1-m} = K$, then the vector field Z_{η} has no singularities in Ω and the singularity of (i) collapses with the singularity (K, 0).
- (iii) If $\frac{m}{1-m} > K$, then the vector field Z_{η} has no singularities in Ω . Furthermore, the singularity (K, 0) is an hyperbolic attractor point.

Lemma 2.2. Let $(m, F) \in \Re \cap \mathbb{R}^2_+$, $\frac{m}{1-m} < K$ and (A, B) the singularity of Lemma 2.1 (i). Then there exists a neighborhood in the parameter space of vector field Z_η such that the singularity $(A, B) \in \Omega$ is a repelling weak focus whose order is at least 4.

For $K_1, c > 0$, we define the subset in \mathbb{R}^2

$$R_{K_1,c} = \{(x,y) \in \mathbb{R}^2 \mid x \ge 0, \ 0 \le y \le c(K_1 - x)\}.$$

Lemma 2.3. Let $\frac{m}{1-m} < K$. Then there are constants K_1 , c > 0, with c sufficiently large, so that if $A < K < K_1$ then $R_{K_1,c} \subset \overline{\Omega}$ is a compact invariant set by the vector field Z_{η} containing the singularity (A, B) of Lemma 2.1 (i).

Theorem 2.4. Let $(m, F) \in \Re \cap \mathbb{R}^2_+$ and $\frac{m}{1-m} < K$. Then there exists a neighborhood in the parameter space of vector field Z_η such that the system (7) have five concentric limit cycles, four infinitesimal limit cycles and one non-infinitesimal attractor limit cycle (global). Also three of the five limit cycles are stable.

3. Proof of the main results.

Proof of Lemma 2.1. The auxiliary straight lines l_1, l_2 and the *F*-axis of the statement of Lemma 2.1 form the triangle \Re (see Figure 1).

It is clear that, if $(m, F) \in \Re$, then these parameters are bounded by $0 < m < \frac{1}{2}$ and 0 < F < 2.

In vector field (5), let us consider the first and second component:

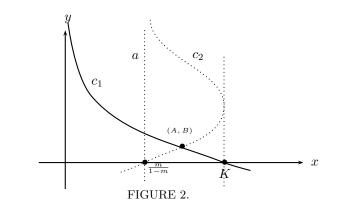
(i) $\pi_1(Y_{\mu}) = 0 \iff x(K-x)(x+1) - bxy + i(K-x)(x+1) = 0.$ If x > 0, the equation x(K-x)(x+1) - bxy + i(K-x)(x+1) = 0 implicitly defines $c_1 : y = \frac{(x+i)(K-x)(x+1)}{bx}.$

In the same way, $\pi_2(Y_\mu) = 0 \Leftrightarrow x(y^2 + 1) - m(x+1)(y^2 + 1) - Fy(x+1) = 0.$

If y > 0, the cubic curve $x(y^2 + 1) - m(x + 1)(y^2 + 1) - Fy(x + 1) = 0$

implicitly defines $c_2 : x = \frac{m(y^2+1)+Fy}{(y^2+1)(1-m)-Fy}$ because, for all $(m,F) \in \Re, (y^2+1)(1-m)-Fy > 0.$

It is clear that the straight line $a: x = \frac{m}{1-m}$ is an asymptote of the above cubic and, since we assume that $\frac{m}{1-m} < K$, then there exists at least one singularity (A, B) of Y_{μ} in Ω (see Figure 2). Now, as vector fields (5) and (7) are C^{∞} -equivalent in Ω by identity transformation, we conclude that the vector field (7) has at least the singularity $(A, B) \in \Omega$.



(8)

Moreover,
$$DY_{\mu}(K,0) = \begin{pmatrix} -(1+K)(i+K) & -bK \\ 0 & e(K(1-m)-m) \end{pmatrix}$$
.

As K(1-m) - m > 0 and $m < \frac{1}{2}$, the singularity (K, 0) is a hyperbolic saddle whose unstable manifold is oriented to Ω .

(ii) If
$$\frac{m}{1-m} = K$$
, then $(\pi_1(Y_\mu))^{-1}(0) \cap (\pi_2(Y_\mu))^{-1}(0) \cap \overline{\Omega} = \{(K,0)\}.$

(iii) If $\frac{m}{1-m} > K$, then $(\pi_1(Y_\mu))^{-1}(0) \cap (\pi_2(Y_\mu))^{-1}(0) \cap \overline{\Omega} = \Phi$. Moreover, from (8), the singularity (K, 0) is a hyperbolic attractor node.

Proof of Lemma 2.2. Let us consider vector field (7). By direct calculation,

$$DZ_{\eta}(A,B) = \begin{pmatrix} A10 & A01 \\ B10 & B01 \end{pmatrix}, \text{ where}$$

$$A10 = -(1+A)B(1+B^2)(A^2+2A^3+A^2i-A^2K+iK)$$

$$A01 = A(1+A)^2(1+B^2)(A+i)(A-K)$$

$$B10 = AB^2(1+B^2)e$$

$$B01 = -A(1+A)(-1+B)B(1+B)e(-A+m+Am)$$

$$\text{Trace} = -(1+A)B(1+B^2)(A^2+2A^3+A^2i-A^2K+iK)$$

$$-A(1+A)(-1+B)B(1+B)e(-A+m+Am)$$

$$Det = -A^{2}(1+A)^{2}B^{2}(1+B^{2})^{2}e(A+i)(A-K)$$

+ $A(1+A)^{2}(-1+B)$
 $B^{2}(1+B)(1+B^{2})e(A^{2}+2A^{3}+A^{2}i-A^{2}K+iK)$
 $(-A+m+Am)$

In particular, for B = 1, we have

Trace =
$$-2(1+A)(A^2+2A^3+A^2i-A^2K+iK)$$

Det = $4A^2(1+A)^2e(A+i)(K-A)$

Since B = 1 and Det > 0, by continuity of the vector field with respect to the parameter B, it is shown that in a small enough neighborhood of B = 1 the singularity (A, B) of (7) is a focus.

The trace of the matrix $DZ_{\eta}(A, B)$ is zero if

(9)
$$i = (-A^2 - 2A^3 - A^2B^2 - 2A^3B^2 - A^2e + A^2B^2e + A^2K + A^2B^2K + Aem + A^2em - AB^2em - A^2B^2em)/(1 + B^2)(A^2 + K)$$

In order to calculate the weakness of the focus (A, B) of (7), we consider the translation of the focus to the origin of the coordinate system $\{x \to x + A, y \to y + B\}$. Then system (7) is C^{∞} -equivalent to the system (10)

$$\begin{cases} \dot{x} = (1+A)[AB(-A+K-x)(1+A+x)(A+i+x)+(1+A)(A+i) \\ (A-K)(A+x)(B+y)](1+(B+y)^2), \\ \dot{y} = -Ae(B+y)[(1+A)B(m+(-1+m)(A+x)) \\ -(1+B^2)(A(-1+m)+m)(1+A+x)(B+y) \\ +(1+A)B(m+(-1+m)(A+x))(B+y)^2]. \end{cases}$$

The coefficients of the linear part and consequently, the trace and the determinant, are invariant under translation. Introducing the expression of the parameter i given in (9), which cancels the trace (10), we obtain the new coefficients of the linear part:

$$\begin{split} a10 &= A(1+A)(-1+B)B(1+B)e(-A+m+Am)\\ a01 &= -A^2(1+A)^2(A-K)[A+A^2+AB^2+A^2B^2+Ae]\\ &- AB^2e-K-AK-B^2K-AB^2K-em-Aem \end{split}$$

$$+ B^{2}em + AB^{2}em]/(A^{2} + K)$$

$$b10 = AB^{2}(1 + B^{2})e$$

$$b01 = -A(1 + A)(-1 + B)B(1 + B)e(-A + m + Am)$$

and

$$\begin{aligned} \operatorname{Tr} (DZ_{\eta})(0,0) &= 0 \\ \operatorname{Det} (DZ_{\eta})(0,0) &= -A^{2}(1+A)^{2}(-1+B)^{2}B^{2}(1+B)^{2} \\ &\times e^{2}(-A+m+Am)^{2} \\ &+ [A^{3}(1+A)^{2}B^{2}(1+B^{2})e(A-K) \\ &(A+A^{2}+AB^{2}+A^{2}B^{2}+Ae-AB^{2}e \\ &-K-AK-B^{2}K-AB^{2}K \\ &-em-Aem+B^{2}em+AB^{2}em)]/(A^{2}+K) \end{aligned}$$

Now, for B = 1,

a10	=	0
a01	=	$(-2A^2(1+A)^3(A-K)^2)/(A^2+K)$
b10	=	2Ae
b01	=	0
$\operatorname{Tr}(DZ_{\eta})(0,0)$	=	0
$\operatorname{Det}\left(DZ_{\eta}\right)(0,0)$	=	$4A^3(1+A)^3e(A-K)^2/(A^2+K)$

In order to present the matrix of the linear part of system (10) as a Jordan matrix, let us consider, in a sufficiently small neighborhood of B = 1, the change of coordinates

$$\left(\begin{array}{c} x\\ y\end{array}\right) = \left(\begin{array}{c} 0&-L\\ b10&0\end{array}\right) \left(\begin{array}{c} u\\ v\end{array}\right)$$

where $L^2 = \text{Det}(DZ_{\eta})(0,0) > 0$. Explicitly, the equality $L^2 = \text{Det}(DZ_{\eta})(0,0)$ is equivalent to

$$L^{2} = 4A^{3}(1+A)^{3}e(A-K)^{2}/(A^{2}+K).$$

The previous expression is linear in the parameter e and, being a positive number, is the only restriction. This now allows us to change the parameter e of vector field (10) to the new parameter L which only has the restriction $L \in \mathbb{R}^+$. Then the system (10) is reduced to the

system
(11)

$$\begin{cases}
\dot{x} = -A(1+A)(A^3x^2 + Kx^2 + 3AKx^2 - K^2x^2 + A^2x^3 + Kx^3 + A^3y + 2A^4y + A^5y - 2A^2Ky - 4A^3Ky + 2A^4Ky + AK^2y + 2A^2K^2y + A^3K^2y + A^2xy + 2A^3xy + A^4xy - 2AKxy - 4A^2Kxy - 2A^3Kxy + K^2xy + 2AK^2xy + A^2K^2xy) + 2AK^2xy + A^2K^2xy) + (2AK^2xy + A^2K^2xy) + (2AK^2xy + A^2K^2xy) + (2AK^2xy + A^2K^2xy) + (2AK^2xy + A^2K^2xy) + (2A^2(1+y)(-2x - 2xy - Ay^2 - A^2y^2 + mxy^2 + Amxy^2)) + (4A^2(1+A)^3(A-K)^2),
\end{cases}$$

where

$$\begin{array}{rcl} a10 & = & 0 \\ a01 & = & (-2A^2(1+A)^3(A-K)^2)/(A^2+K) \\ b10 & = & (A^2+K)L^2/(2A(1+A)^3(A-K)^2) \\ b01 & = & 0 \\ \operatorname{Tr} (DZ_\eta)(0,0) & = & 0 \\ \operatorname{Det} (DZ_\eta)(0,0) & = & L^2 \end{array}$$

In order to know the weakness of focus at the origin, we have to calculate the Lyapunov quantities, and these are defined through the focal values which are polynomials in the coefficients of the vector field (11). In fact, it is known that there is an analytical function, V, in a neighborhood of the origin, such that the rate of change along orbits, \dot{V} , is of the form $\eta_2 r^2 + \eta_4 r^4 + \cdots$, where $r^2 = x^2 + y^2$ (see [3]). The focal values are the terms η_{2k} . However, since they are polynomials, the ideal they generate has a finite basis, so there is M such that $\eta_{2\ell} = 0$, for $\ell \leq M$, implies that $\eta_{2\ell} = 0$ for all ℓ . The value of M is not known a priori, so it is not clear in advance how many focal values should be calculated. The software Mathematica [10] is used to calculate the first few focal values. These are then 'reduced' in the sense that each is computed modulo the ideal generated by the previous ones: that is, the relations $\eta_2 = \eta_4 = \cdots = \eta_{2k} = 0$ are used to eliminate some of the variables in η_{2k+2} . The reduced focal value η_{2k+2} , with strictly positive factors removed, is known as the Lyapunov quantity.

In order to simplify the calculations of the Lyapunov quantities, we

consider the x-axis rescaling

$$\begin{array}{rcl}
x &= & Qu \\
y &= & v \\
Q &= & \frac{2A^2(1+A)^3(K-A)^2}{(A^2+K)L}
\end{array}$$

Thus, system (11) has the form

(12)
$$\begin{cases} \dot{u} = -Lv + a_{20}u^2 + a_{11}uv + a_{02}v^2 + a_{21}u^2v + a_{12}uv^2 \\ + a_{03}v^3 + a_{13}uv^3 + a_{22}u^2v^2, \\ \dot{v} = Lu + b_{11}uv + b_{02}v^2 + b_{12}uv^2 + b_{03}v^3 + b_{13}uv^3 \end{cases}$$

where the coefficients are given by

Moreover,

$$\operatorname{Tr}(DZ_{\eta})(0,0) = 0$$
 and $\operatorname{Det}(DZ_{\eta})(0,0) = L^{2}$.

Let us consider the change of the time $\{t \to \frac{1}{L}t\}$ in (12). Denoting by η_i , $i = 1, 2, 3, \ldots$, the focal value of the monodromic focus of (12) at the origin, as $\operatorname{Tr}(DZ_\eta)(0,0) = 0$, we have $\eta_1 = 0$. Now, it is known that the focal value η_2 depends only on the 3-jet of vector field (12), and this is given by:

$$\eta_2 = (a_{02}a_{11} + a_{12} + a_{11}a_{20} + 3a_{30} + 2a_{02}b_{02} + 3b_{03} - b_{02}b_{11})/8.$$

Replacing the coefficients in system (12) in the expression of η_2 we obtain:

 $\eta_2 = (32A^{15} + 288A^{16} + 1152A^{17} + 2688A^{18} + 4032A^{19} + 4032A^{20} +$ $2688A^{21} + 1152A^{22} + 288A^{23} + 32A^{24} + 32A^{12}K + 384A^{13}K + 1824A^{14}K +$ $4416A^{15}K + 5184A^{16}K - 9408A^{18}K - 14976A^{19}K - 12384A^{20}K - 6016A^{21}K 1632A^{22}K - 192A^{23}K - 192A^{11}K^2 - 2336A^{12}K^2 - 11904A^{13}K^2 - 33696A^{14}K^2 -$ $57984A^{15}K^2 - 60480A^{16}K^2 - 32256A^{17}K^2 + 2496A^{18}K^2 + 16704A^{19}K^2 +$ $93312A^{13}K^3 + 174528A^{14}K^3 + 212352A^{15}K^3 + 165312A^{16}K^3 + 73728A^{17}K^3 +$ $9312A^{18}K^3 - 7872A^{19}K^3 - 4128A^{20}K^3 - 640A^{21}K^3 - 640A^9K^4 - 8160A^{10}K^4 -$ $44160A^{11}K^4 - 135840A^{12}K^4 - 264960A^{13}K^4 - 342720A^{14}K^4 - 295680A^{15}K^4 164160A^{16}K^4 - 51840A^{17}K^4 - 4960A^{18}K^4 + 1920A^{19}K^4 + 480A^{20}K^4 +$ $480A^{8}K^{5} + 6400A^{9}K^{5} + 35808A^{10}K^{5} + 113472A^{11}K^{5} + 228288A^{12}K^{5} +$ $306432A^{13}K^5 + 278208A^{14}K^5 + 167808A^{15}K^5 + 63072A^{16}K^5 + 12288A^{17}K^5 + 12288A^{17}K^5 + 167808A^{15}K^5 + 16880A^{15}K^5 + 16880A^{15}K^5$ $352A^{18}K^5 - 192A^{19}K^5 - 192A^7K^6 - 2784A^8K^6 - 16384A^9K^6 - 53856A^{10}K^6 111744A^{11}K^6 - {154560}A^{12}K^6 - {145152}A^{13}K^6 - {91584}A^{14}K^6 - {37056}A^{15}K^6 8544A^{16}K^6 - 768A^{17}K^6 + 32A^{18}K^6 + 32A^6K^7 + 576A^7K^7 + 3744A^8K^7 +$ $13056A^9K^7 + 28224A^{10}K^7 + 40320A^{11}K^7 + 38976A^{12}K^7 + 25344A^{13}K^7 +$ $10656A^{14}K^7 + 2624A^{15}K^7 + 288A^{16}K^7 - 32A^6K^8 - 288A^7K^8 - 1152A^8K^8 - 288A^7K^8 - 1152A^8K^8 - 1154A^8K^8 - 1154A^8K^8 - 1154A^8K^8 - 1154A^8K^8 - 1154A^8K^8$ $2688A^9K^8 - 4032A^{10}K^8 - 4032A^{11}K^8 - 2688A^{12}K^8 - 1152A^{13}K^8 - 288A^{14}K^8$ $-32 A^{15} K^8-48 A^{14} L-288 A^{15} L-720 A^{16} L-960 A^{17} L-720 A^{18} L-288 A^{19} L 48A^{20}L - 48A^{11}KL - 480A^{12}KL - 1680A^{13}KL - 2688A^{14}KL - 1680A^{15}KL +$ $672A^{16}KL + 1680A^{17}KL + 960A^{18}KL + 192A^{19}KL - 48A^9K^2L - 240A^{10}K^2L +$ $384A^{11}K^{2}L + 4368A^{12}K^{2}L + 10752A^{13}K^{2}L + 12432A^{14}K^{2}L + 6720A^{15}K^{2}L +$ $624A^{16}K^{2}L - 912A^{17}K^{2}L - 288A^{18}K^{2}L + 192A^{8}K^{3}L + 1488A^{9}K^{3}L +$ $3552A^{10}K^{3}L + 1008A^{11}K^{3}L - 9408A^{12}K^{3}L - 17808A^{13}K^{3}L - 14112A^{14}K^{3}L - 14112A^$ $4848A^{15}K^{3}L - 192A^{16}K^{3}L + 192A^{17}K^{3}L - 288A^{7}K^{4}L - 2592A^{8}K^{4}L 8448A^9K^4L - 12432A^{10}K^4L - 6048A^{11}K^4L + 5712A^{12}K^4L + 9408A^{13}K^4L +$ $4752A^{14}K^{4}L + 768A^{15}K^{4}L - 48A^{16}K^{4}L + 192A^{6}K^{5}L + 1968A^{7}K^{5}L +$ $7392A^8K^5L + 13776A^9K^5L + 13440A^{10}K^5L + 5712A^{11}K^5L - 672A^{12}K^5L - 672A^{12}K^5$ $1488A^{13}K^5L - 384A^{14}K^5L - 48A^5K^6L - 624A^6K^6L - 2688A^7K^6L - 5712A^8K^6L - 624A^6K^6L - 624A^6K^$ $6720A^9K^6L - 4368A^{10}K^6L - 1344A^{11}K^6L - 48A^{12}K^6L + 48A^{13}K^6L +$ $48A^{5}K^{7}L + 288A^{6}K^{7}L + 720A^{7}K^{7}L + 960A^{8}K^{7}L + 720A^{9}K^{7}L + 288A^{10}K^{7}L + 720A^{9}K^{7}L + 720A$ $48A^{11}K^{7}L - A^{9}L^{4} - 4A^{7}KL^{4} - 6A^{5}K^{2}L^{4} - 4A^{3}K^{3}L^{4} - AK^{4}L^{4} + A^{8}L^{4}m +$ $A^{9}L^{4}m + 4A^{6}KL^{4}m + 4A^{7}KL^{4}m + 6A^{4}K^{2}L^{4}m + 6A^{5}K^{2}L^{4}m + 4A^{2}K^{3}L^{4}m +$

2068

$$4A^{3}K^{3}L^{4}m + K^{4}L^{4}m + AK^{4}L^{4}m)/(32A^{2}(1+A)^{2}(A-K)^{2}(A^{2}+K)^{3}L^{3})$$

The numerator of η_2 is linear in the parameter m and defines implicitly a value of m being one of the zeros of η_2 . This results in (14)

$$m = \frac{A/(1+A) - 32A^{6}(1+A)^{8}(A-K)^{6}(A^{3}+K+3AK-K^{2})}{(A^{2}+K)^{4}L^{4} + 48A^{5}(1+A)^{5}(A-K)^{4}(A^{3}+K+3AK-K^{2})}{(A^{2}+K)^{3}L^{3}}.$$

With the restrictions of the parameters K and A (and looking at Figure 2), in order to obtain a numerical simulation, we can choose the numerical values $K = 1, A = \frac{1}{3}$. Then the expression of m is reduced to

$$m = 1/4 - 234881024/(8968066875L^4) + 917504/(7381125L^3).$$

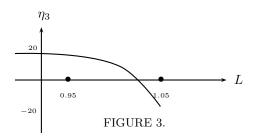
Since $L \in \mathbb{R}^+$ and $m \approx \frac{1}{4} < \frac{1}{2}$, for example, we can choose values compatible with the model L = 1 and $m \approx 0.348$. Now, as m = m(A, K, L) is a continuous function in the parameter space, the numerical simulation shows that, for certain values of the parameters, there is an open set such that expression (14) will zero the focal value η_2 . Hence the origin of system (12) is at least a weak focus of second order.

With the Mathematica software, we can compute the third Lyapunov focal value η_3 of (12)

$$\begin{split} \eta_3 &= (-10a_{02}^3a_{11} + 17a_{02}a_{03}a_{11} - 23a_{02}a_{11}^3 - 10a_{02}^2a_{12} - 3a_{03}a_{12} - 23a_{11}^2a_{12} + \\ 20a_{02}a_{13} - 76a_{02}^2a_{11}a_{20} + 13a_{03}a_{11}a_{20} - 23a_{11}^3a_{20} - 46a_{02}a_{12}a_{20} + 28a_{13}a_{20} - \\ 142a_{02}a_{11}a_{20}^2 - 64a_{12}a_{20}^2 - 76a_{11}a_{20}^3 + 4a_{11}a_{22} - 90a_{02}^2a_{30} - 45a_{03}a_{30} - \\ 77a_{11}^2a_{30} - 234a_{02}a_{20}a_{30} - 228a_{20}^2a_{30} - 20a_{02}^3b_{02} + 34a_{02}a_{03}b_{02} - 159a_{02}a_{11}^2b_{02} - \\ 105a_{11}a_{12}b_{02} - 132a_{02}^2a_{20}b_{02} + 32a_{03}a_{20}b_{02} - 109a_{11}^2a_{20}b_{02} - 192a_{02}a_{20}^2b_{02} - \\ 24a_{20}^3b_{02} - 16a_{22}b_{02} - 287a_{11}a_{30}b_{02} - 350a_{02}a_{11}b_{02}^2 - 148a_{12}b_{02}^2 - 144a_{11}a_{20}b_{02}^2 - \\ 392a_{30}b_{02}^2 - 248a_{02}b_{02}^3 + 24a_{20}b_{02}^3 - 13a_{02}^2a_{11}b_{11} + 8a_{03}a_{11}b_{11} - 13a_{02}a_{12}b_{11} + \\ 8a_{13}b_{11} - 42a_{02}a_{11}a_{20}b_{11} - 17a_{12}a_{20}b_{11} - 29a_{11}a_{20}^2b_{11} - 75a_{02}a_{30}b_{11} - 87a_{20}a_{30}b_{11} \\ - 16a_{02}^2b_{02}b_{11} + 19a_{03}b_{02}b_{11} + 27a_{11}^2b_{02}b_{11} + 28a_{02}a_{02}b_{02}b_{11} + 96a_{20}^2b_{02}b_{11} + \\ 101a_{11}b_{02}^2b_{11} + 124b_{02}^3b_{11} - 3a_{02}a_{11}b_{11}^2 - 3a_{12}b_{11}^2 - 9a_{30}b_{11}^2 + \\ 27a_{02}b_{02}b_{11}^2 + 370a_{20}b_{02}b_{11}^2 - b_{02}b_{11}^3 - 3a_{02}a_{11}b_{12} - 3a_{12}b_{12} - 7a_{11}a_{20}b_{12} - \\ 21a_{30}b_{12} - 46a_{02}b_{02}b_{12} - 40a_{20}b_{02}b_{12} + 23b_{02}b_{11}b_{12} - 36b_{02}b_{13})/192 \end{split}$$

where the coefficients are obtained from (13) and from the expression (14) of the parameter m. The focal value η_3 is an expression too large

to be present here. However, if we use the previous numerical data, we can show that the graph corresponding to the numerator of η_3 as a function of the parameter L is as shown in Figure 3.

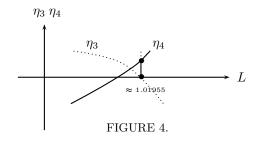


Then, in an open set of the parameter space, there are values of parameters K, A, L with $m < \frac{1}{3}$ such that η_2 and η_3 vanish simultaneously. Then the origin of (12) is at least a weak focus of order 3.

To investigate a higher weakness, it is necessary to compute η_4 . Again, using Mathematica software, the focal value η_4 is an expression too large to be shown in this work. To calculate the Lyapunov focal values, see [8].

The coefficient in terms of the parameter of the vector field are obtained from (13) and (14).

However, if we use the previous values of the numerical simulation K = 1 and $A = \frac{1}{3}$, the graph of η_4 as a function only of the parameter L, compared with Figure 3, is shown as in Figure 4. Both graphs are locally transverse to the axis L, and the behavior will be stable under small perturbations.



The values of the numerical simulation are:

- i) $L \approx 0.209412 \Rightarrow \eta_3|_L \approx 0$ and $\eta_4|_L < 0$
- ii) $L \approx 1.01955 \Rightarrow \eta_3|_L \approx 0$ and $\eta_4|_L > 0$.

Thus, for case (ii), there is a neighborhood in the parameter space such that the origin is a repelling weak focus of order 4. \Box

Proof of Lemma 2.3. We consider system (7) and the triangle $R_{K_1,c}$ defined above. The straight line $l: y = c(K_1 - x)$ is part of the border of $R_{K_1,c}$, where $K_1, c > 0$. The gradient of vector field Z_η on the straight line l corresponds to

$$\nabla l = c \frac{\partial}{\partial x} + \frac{\partial}{\partial y}.$$

The inner product $\langle Z_{\eta}, \nabla l \rangle |_l$ is given by

$$\begin{split} \left< Z_{\eta}, \nabla l \right> \Big|_{l} &= -(Ace(K_{1}-x)((1+A)Bm - (1+B^{2})c(A(-1+m)+m) \\ &\times (K_{1}-x) + (1+A)Bc^{2}m(K_{1}-x)^{2} + (1+A)B(-1+m)x \\ &- (1+B^{2})c(A(-1+m)+m)(K_{1}-x)x \\ &+ (1+A)Bc^{2}(-1+m)(K_{1}-x)^{2}x)) \\ &+ (1+A)c(1+c^{2}(K_{1}-x)^{2}) \\ &\times (ABiK + AB(-i+K+iK)x \\ &+ (1+A)c(A+i)(A-K)(K_{1}-x)x \\ &+ AB(-1-i+K)x^{2} - ABx^{3}). \end{split}$$

The previous expression is a cubic polynomial in the parameter c, where the coefficient of the cubic term is given by: $\operatorname{coef}(c^3) = c(1+A)^2(A+i)(A-K)(K_1-x)^3x$. Since A < K, $K < K_1$ and $x < K_1$ in the triangle, for large values of the parameter c, we have $\langle Z_{\eta}, \nabla l \rangle |_l < 0$.

From (5), we see that the vector field crosses the axis x = 0 transversally in the positive sense with respect to the coordinates system. Finally the positive axis y = 0 is a straight line invariant of the vector field. This shows that the compact region $R_{K_{1,c}}$ containing the singularity (A, B) is an invariant set of vector field (7).

Proof of Theorem 2.4. Recall that the vector field (7) has the form

$$Z_{\eta}(x,y) = (1+A)(1+y^2)P(x,y)\frac{\partial}{\partial x} - AeyQ(x,y)\frac{\partial}{\partial y},$$

where

$$P(x,y) = AB(K-x)(1+x)(i+x) + (1+A)(A+i)(A-K)xy$$

and

$$Q(x,y) = (1+A)B(m+(-1+m)x)(1+y^2) - (1+B^2)(A(-1+m)+m)(1+x)y.$$

By Lemma 2.1, system (7) has a singularity at Ω . Considering the numerical values B = 1, K = 1, $A = \frac{1}{3}$ and L = 1, we have $m \approx \frac{87}{250}$. Then it is clear that the system zeros the factors P(x, y) and Q(x, y) of the components of vector field (7) in Ω and $P^{-1}(0) \cap Q^{-1}(0) \cap \Omega \approx \{(0.714687, 0.410065)\}$. By the continuity of vector field (7) with respect to the parameters, the numerical calculation shows that there is a neighborhood in the parameter space such that the singularity (A, B) is unique.

From (5), we have that the vector field crosses the axis x = 0 transversally in the positive sense with respect to the coordinate system. The x-axis is invariant, and the origin of vector field (5) is not a singularity.

By Lemma 2.1 (i), the singularity (K, 0) is a hyperbolic saddle. By Lemma 2.2, the singularity (A, B) is a repelling weak focus of order 4 and the omega limit set of the unstable manifold of the singularity (K, 0) is contained in the invariant region guaranteed by Lemma (2.3). Hence, by the Poincaré-Bendixson theorem, there is a hyperbolic attracting limit cycle that encloses the singularity (A, B). Now, by small perturbations of the vector field, we can change the stability of the weak focus and then four Hopf infinitesimal hyperbolic limit cycles will be created simultaneously enclosed by at least one global stable limit cycle. Since the focus is now a hyperbolic attractor fixed point, the first of the bifurcated limit cycle (and also the third) will be repelling and the second and the fourth will be hyperbolic attracting limit cycles. This, together with the global limit cycle shows that the system supports five hyperbolic limit cycles, three of them being stable. This is a concrete example of an applied model with at least three stable limit cycles, a question raised in [2, 4].

4. Discussion. Under the hypothesis of Theorem 2.4, the only singularity (K, 0) in the invariant axis y = 0, $x \ge 0$ is a hyperbolic saddle with unstable manifold to the realistic quadrant where there is no extinction phenomenon.

With the existence of three stable limit cycles, it follows that the model depends on initial conditions and supports three possible equilibrium periodic states.

REFERENCES

1. G. Caughley and J.H. Lawton, *Plant-herbivore systems*, in *Theretical ecology, principles and applications*, R.M. May, ed., Blackwell Scientific Publications, Oxford, UK, 1981.

2. C.S. Coleman, *Hilbert's* 16th problem: *How many cycles?*, in *Differential equations models*, Vol. 1., W. Lucas, ed., Springer-Verlag, New York, 1978.

3. N.G. Lloyd, *Limit cycles of polynomial systems-some recent developments*, in *New direction in dynamical systems*, Cambridge University Press, Cambridge, 1988.

4. N.G. Lloyd, J.M. Pearson, E. Sáez and I. Szántó, *Limit cycles of a cubic Kolmogorov system*, Appl. Math. Lett. 9 (1996), 15–18.

5. E. McCauley and W.W. Murdoch, Cyclic and stable populations: plankton as paradigm, Amer. Nat. 129 (1987), 97–121.

6. E. McCauley, W.E. Murdoch and R.M. Nisbet, Growth, reproduction and mortality of Daphnia pule Leydig: Life at low food, Funct. Ecol. 4 (1990), 505-514.

7. J. Roughgarden, Competition and theory in community ecology, Amer. Nat. **122** (1983), 583–601.

 E. Sáez, http://docencia.mat.utfsm.cl/ esaez/index.html/cliapunov.pdf, 2000.

9. M. Scheffer, S. Rinaldi and Y.A. Kuznetsov, *Effects of fish on plankton dynamics: A theoretical analysis*, Canad. J. Fish. Aq. Sci. **57** (2000), 1208–1219.

10. Stephen Wolfram, The Mathematica book, 5th ed., Wolfram Media, 2003.

Departamento de Matemática, Universidad Técnica Federico Santa María, Casilla 110-V, Valparaíso, Chile

Email address: eduardo.saez@usm.cl

Departamento de Matemáticas, Universidad de Valparaíso, Casilla 5030, Valparaíso, Chile

Email address: eduardo.stange@uv.cl

Departamento de Matemática, Universidad Técnica Federico Santa María, Casilla 110-V, Valparaíso, Chile

Email address: ivan.szanto@usm.cl