

MSC 2010: 34C05, 92D25

Extinction and coexistence of predators

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Abstracts. We study conditions for extinction and coexistence of predators in a general family of systems with many predators feeding on the same prey. We call the system degenerated in the case some predators go extinct and the essential dynamics occurs in a lower dimensional subspace.

Keywords: predator, prey, extinction, dissipativity, periodic solution.

1. Introduction

We consider the $(n + 1)$ -dimensional system

$$\dot{x}_i = \phi_i(s)x_i, \quad \dot{s} = h(s) - \sum_{i=1}^n \psi_i(s)x_i, \quad i = 1, 2, \dots, n. \quad (1.1)$$

A_1 : All the considered functions are of the class $C^2[0, \infty)$ and the variables x_i and s are non-negative: $x_i \geq 0$, $s \geq 0$.

A_2 : $\psi_i(0) = 0$, $\psi'_i(s) > 0$ for $s > 0$.

Here and further we will suppose that i takes values from the set $\{1, 2, \dots, n\}$.

A_3 : $\phi'_i(s) > 0$ for $s > 0$ and there exists $\lambda_i > 0$ such that $\phi_i(\lambda_i) = 0$.

A_4 : $h(0) = h(1) = 0$, $h'(1) < 0$ and $h''(s) < 0$ for $s > 0$.

A_5 : $0 < \lambda_n < \dots < \lambda_2 < \lambda_1 < 1$.

These and analogous systems for different assumptions on the right hand sides have been considered by many authors [1]-[5] of both mathematical and application view point. We note that our reference list cannot be full. It should be too large.

Analogous systems are considered from another point of view in [6, 7]. However the questions of dissipativity and existing of inner set are on the first place here also.

Systems with the following special choice of functions

$$h(s) = \gamma s(K - s), \quad \psi_i(s) = \alpha_i \frac{s}{s + a_i}, \quad \phi_i(s) = m_i \psi_i(s) - d_i, \quad (1.2)$$

where all introduced parameters are positive, have been examined more extensively.

It is important to say, that this special choice of model is interesting from the mathematical point of view even in the three dimensional case. For instance, in [8, 9] the questions, connected with the problem of the limit cycle uniqueness in the coordinate planes are considered. This problem is connected with the stability of the planes and, consequently, with the problem of the inner set existing.

Such systems can have chaotic regimes. They were studied in detail in [11, 12]. Particularly bifurcation diagrams with a chain of period doubling bifurcations for system (1.1) with (1.2) were given. The functions

$$h(s) = s(1 - s), \quad \phi_i(s) = \frac{s - \lambda_i}{s + a_i}, \quad \psi_i(s) = \frac{s}{s + a_i} \quad (1.3)$$

were chosen as an example. In this paper system 1.1 with these functions will be called *standard system*. We consider a broad class of systems of type (1.1), including right hand sides of type (1.2) and standard system as main example.

The conditions assumed for the system are divided into two groups. In the first group we have assumptions of general type (A_1 - A_5). In the other group we have assumptions of technical type arising in the formulation of statements (D_6 - D_7 and A_6 - A_7). It is easy to verify that all standard systems are included.

It follows from A_1 - A_5 that the system has $n + 1$ equilibria:

$O(0, \dots, 0, 0)$ which is a saddle with n -dimensional stable manifold $s = 0$ and one dimensional unstable manifold: $x_i = 0$ ($i = 1, \dots, n$), $0 < s < 1$.

$O'(0, \dots, 0, 1)$ which is a saddle with one dimensional stable manifold $x_i = 0$ ($i = 1, \dots, n$) and n -dimensional unstable manifold, which we will denote by $W^u(O')$.

One point in each hyperplane: $O_i: s = \lambda_i, x_j = 0, j \neq i, x_i = \frac{h(\lambda_i)}{\psi_i(\lambda_i)}$.

The Jacobian matrix has the form

$$\begin{pmatrix} \phi_1 & 0 & \dots & \phi_1' x_1 \\ 0 & \phi_2 & \dots & \phi_2' x_2 \\ \cdot & \cdot & \dots & \cdot \\ -\psi_1 & -\psi_2 & \dots & h' - \sum_{i=1}^n \psi_i' x_i \end{pmatrix}. \quad (1.4)$$

2. Dissipativity

A compact set in a phase space is called a *Levinson set*, if it is positively invariant and has a base of globally absorbing neighbourhoods.

A typical problem is to construct a good Levinson set. Below we give one result in this direction. Let $T(O')$ be the tangent plane to the unstable manifold $W^u(O')$ in the point O' . We introduce also a couple of technical conditions:

D_1 : If $s < 1$, then $h(s)\psi_1(1) \geq -h'(s)(1 - s)\psi_1(s)$.

D_2 : If $s < 1$, then $\phi_i(s)\psi_i(1) - \phi_i(1)\psi_i(s) < 0$.

Let us note that the conditions D_1, D_2 are satisfied for standard system (1.3).

Now let V_0 is the simplex determined by the vertices $O, O', \bar{q}_1, \bar{q}_2, \dots, \bar{q}_n$, where

$$\bar{q}_i = (0, \dots, q_i, \dots), \quad q_i = \frac{\phi_i(1) - h'(1)}{\psi_i(1)}, \quad i = 1, 2, \dots, n. \quad (2.1)$$

Theorem 1. *Let us consider system (1.1) satisfying conditions A_1 - A_5 and D_1 - D_2 .*

The trajectories intersect the tangent plane $T(O')$ transversally, except at O' . Moreover at any point, except at O' , the trajectories intersect this plane in the direction inside a simplex V_0 , which is a Levinson set.

Proof. The Jacobian matrix at the point O' has the form

$$\begin{pmatrix} \phi_1(1) & 0 & \dots & 0 \\ 0 & \phi_2(1) & \dots & 0 \\ \vdots & \vdots & \ddots & \vdots \\ -\psi_1(1) & -\psi_2(1) & \dots & h'(1) \end{pmatrix}. \quad (2.2)$$

where all the numbers on the diagonal are positive except $h'(1)$. The tangent plane is defined by the equation

$$\frac{x_1}{q_1} + \frac{x_2}{q_2} + \dots + \frac{x_n}{q_n} + s = 1, \quad (2.3)$$

where q_i are defined by (2.1), so that the vector orthogonal to this plane and directed outside the simplex can be written as

$$\left(\frac{1}{q_1}, \frac{1}{q_2}, \dots, \frac{1}{q_n}, 1 \right). \quad (2.4)$$

At any point of this plane the scalar product (let us denote it by A) of this vector with the vector of the system (1.1) is given by

$$\begin{aligned} A &= \left\langle \left(\frac{1}{q_1}, \dots, \frac{1}{q_n}, 1 \right), \left(\phi_1(s)x_1, \dots, \phi_n(s)x_n, h(s) - \sum_{i=1}^n \psi_i(s)x_i \right) \right\rangle = \\ &= \sum_{i=1}^n \frac{\phi_i(s)}{q_i} x_i + h(s) - \sum_{i=1}^n \psi_i(s)x_i. \end{aligned}$$

Consider now the family of the parallel planes

$$\frac{x_1}{q_1} + \frac{x_2}{q_2} + \dots + \frac{x_n}{q_n} + s = V, \quad (2.5)$$

where $V \geq 1$. It can be checked directly, that if $s = 1$ then $A < 0$ except at O' , where $A = 0$. In other points we get

$$A = h(s) + \sum_{i=1}^n \left[\frac{\phi_i(s)}{q_i} - \psi_i(s) \right] x_i =$$

$$\begin{aligned}
&= \frac{h(s)}{1-s}(1-V) + \frac{h(s)}{1-s}(V-s) + \sum_{i=1}^n \frac{x_i}{q_i} [\phi_i(s) - q_i\psi_i(s)] = \\
&= \frac{h(s)}{1-s}(1-V) + \sum_{i=1}^n \frac{x_i}{q_i} \left[\frac{h(s)}{1-s} + \phi_i(s) - q_i\psi_i(s) \right] < \\
&< \sum_{i=1}^n \frac{x_i}{q_i} \left[-\frac{h'(1)\psi_i(s)}{\psi_i(1)} - q_i\psi_i(s) + \phi_i(s) \right] =
\end{aligned}$$

– we use D_1 here –

$$\begin{aligned}
&= \sum_{i=1}^n \frac{x_i}{q_i} \left[-\frac{\psi_i(s)}{\psi_i(1)} (-\phi_i(1) + h'(1) - h'(1)) + \phi_i(s) \right] = \\
&= \sum_{i=1}^n \frac{x_i}{q_i} \left[-\frac{\phi_i(s)\psi_i(1) - \phi_i(1)\psi_i(s)}{\psi_i(1)} \right].
\end{aligned}$$

By assumption D_2 the proof is complete. \square

An example. Now, as in [2] we consider the system

$$\dot{x} = (m\phi(s) - d)x, \quad \dot{s} = h(s) - \psi(s)x, \quad (2.6)$$

with

$$h(s) = s(1-s), \quad \psi(s) = \frac{s}{s+a}, \quad m = 1, \quad a = 0.5, \quad d = 0.25.$$

Hence,

$$h'(1) = -1, \quad \phi(1) = 7/12, \quad \psi(1) = 2/3 \quad \Rightarrow \quad q = 19/8.$$

Therefore the Levinson simplex in this case is defined by the straight line $s = 1 - 8x/19$. The estimate in [2] gives the region bounded by lines $s = 1$, $x + s = 5$.

3. Degeneracy

Definition 1. An invariant set of system 1.1 will be called an *inner set* if its closure does not intersect with the boundary of R_{n+1}^+ . If a system does not have inner sets it will be called *degenerated*.

Definition 2. The vector function $F = F(s) = (F_1, \dots, F_n)$ is called *linearly determined on the interval* $I = [a, b]$, or the function collection F_1, \dots, F_n is called *linearly determined on I* , if there exists a vector $k = (k_1, \dots, k_n)$ such that $\langle k, F(s) \rangle \leq 0$ for all $s \in I$ and the inequality does not degenerate to equality on any subinterval $I_1 \subset I$. A collection F_1, \dots, F_n which is not linearly determined will be called *linearly connected*.

Further we will consider only functions defined on the interval $I = [0, 1]$.

Theorem 2. *If the function $\phi = (\phi_1, \dots, \phi_n)$ is linearly determined on I , then system (1.1) is degenerated.*

Proof. We suppose the opposite, that is, that there exists a trajectory $(\xi, \zeta) = (\xi_1, \dots, \xi_n, \zeta)$, with closure wholly included in $V = \text{int}R_{n+1}^+$.

We consider the function $L(x, s) = \ln(x_1^{k_1} \cdots x_n^{k_n})$ on V , where $k = (k_1, \dots, k_n)$ is the vector making ϕ determined. The derivative of L along the trajectory (ξ, ζ) equals $\dot{L} = \langle k, \phi(\zeta(t)) \rangle \leq 0$ and, consequently, L is a Lyapunov function. The limit set of the trajectory (ξ, ζ) is contained in the set $W = \{(x, s) | \dot{L} = 0\}$. (This can be proved by standard methods. See for instance [10].)

But any connected component of W is contained in one hyperplane $s = \text{const} > 0$, which cannot contain whole trajectories except singular points. Because V does not contain any equilibrium the theorem is proved. \square

We will now look at conditions for linear connectedness.

Statement 1. *In the case $n = 1$, the function ϕ is linearly connected if and only if system (1.1) is degenerated.*

Statement 2. *Suppose $n > 1$. If there exists a linearly determined subcollection $\phi_{j_1}, \dots, \phi_{j_k}$, $k < n$ for the collection $\phi = (\phi_1, \dots, \phi_n)$, then the collection ϕ is linearly determined.*

Thus we can assumed that the functions are numbered according to condition A_5 . Remark also that $\phi_i(0) < 0$, $\phi_i(1) > 0$.

In connection to ϕ we consider the functions

$$f = (f_1, \dots, f_n), \quad g = (g_1, \dots, g_n), \quad f_i(s) = \frac{\phi_i(s)}{\phi_i(0)}, \quad g_i(s) = \frac{\phi_i(s)}{\phi_i(1)}, \quad i = 1, \dots, n.$$

Definition 3. We will say that *scalar the functions $p = p(s)$ and $q = q(s)$ intersect at some point of the interval I* , if in any neighbourhood of this point there exist s_1 and s_2 , such that $p(s_1) - q(s_1) < 0$ and $p(s_2) - q(s_2) > 0$.

We will say that *the functions p and q intersect on the interval I* , if either there exists a point, where they intersect, or a subinterval $I_1 \subset I$, where they are linearly dependent.

Statement 3. *If the collection $\phi = (\phi_1, \dots, \phi_n)$ is linearly connected, then any functions of the collections ϕ, f and g intersect pairwise.*

Proof. We assume the opposite. For example, that the functions f_1 and f_2 do not intersect. This means that $f_1(s) - f_2(s) \neq 0$ on I . If $f_1(s) - f_2(s) \leq 0$ then

$$k_1\phi_1(s) + k_2\phi_2(s) \geq 0, \quad \forall s \in I, \quad \text{where} \quad k_1 = -\frac{1}{\phi_1(0)}, \quad k_2 = \frac{1}{\phi_2(0)}$$

and the inequality does not degenerate to equality on any interval.

Choosing $k_i = 0$ for $i > 2$, when $n > 2$, we get $\langle k, \phi(s) \rangle \geq 0$, which is a contradiction. Statement is proved. \square

In order to get explicit conditions for the linear connectedness of ϕ , we introduce more assumptions.

A_6 : The equation $k_i\phi_i = k_j\phi_j$ does not have more than two solutions on I for any indices i, j , $i \neq j$, and any constants k_i and k_j , such that at least one of them is non-zero.

A_7 : The equation $c_i\phi_i + c_j\phi_j + c_k\phi_k = 0$ does not have more than three solutions on the interval I for any indices i, j, k and for any constants c_i, c_j, c_k , such that at least one of them is non-zero.

It is easily verified that the standard functions $\phi_i = \frac{s - \lambda_i}{s + a_i}$ satisfy these conditions. We also notice that if all numbers a_i are different, then the collection of functions of type (1.3) are not linearly dependent on any subinterval.

We introduce the notations $\alpha_i = g_i(0)$, $\beta_i = f_i(1) = \alpha_i^{-1}$.

Theorem 3. *We assume that the functions ϕ satisfy the conditions $A_1 - A_6$.*

If ϕ is linearly connected on I , then

- 1) $\beta_1 < \beta_2 < \dots < \beta_n, \quad \alpha_1 > \alpha_2 > \dots > \alpha_n.$

- 2) *The functions f_i , $i = 1, \dots, n$, intersect pairwise exactly one time on $(0, 1)$, and if θ_{ij} is the intersection point of f_i and f_j ($i < j$), then $\theta_{ij} \in (\lambda_i, 1)$.*

Analogously, the functions g_i , $i = 1, \dots, n$, intersect pairwise exactly one time on $(0, 1)$, and if τ_{ij} is the intersection point of the functions g_i and g_j ($i < j$), then $\tau_{ij} \in (0, \lambda_j)$.

- 3) *If $n > 2$, and the function ϕ satisfy condition A_7 and θ_{ik} and θ_{jk} are the intersection points of f_i and f_j with f_k and $i < j < k$, then $\theta_{ik} > \theta_{jk}$.*

Analogously, if τ_{ik} and τ_{jk} are intersection points of g_i , g_j with g_k , and $i < j < k$, then $\tau_{ik} > \tau_{jk}$.

Proof. Statement 2) follows from the pairwise linearly connectedness of the functions ϕ_i and ϕ_j . We show this for the functions f_1 and f_2 . Clearly these functions must have an intersection and according to A_6 only one. We suppose the intersection is not in $I_1 = (\lambda_1, 1)$. Then $f_2 < f_1$ in I_1 .

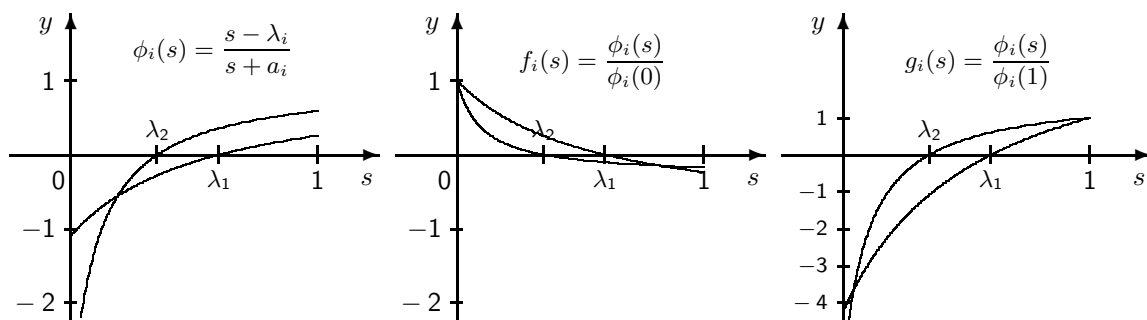


Рис. 1. $\lambda_1 = 0.6$, $\lambda_2 = 0.35$, $a_1 = 0.55$, $a_2 = 0.1$

We consider the minimal $k > 0$ such, that $kf_2(s) \leq f_1(s)$ for all $s \in I_1$. Evidently

$k < 1$. From A_6 and $kf_2(0) < f_1(0)$ and $kf_2(\lambda_2) < f_1(\lambda_2)$ follows that the same inequality is satisfied in $s \in [0, \lambda_2]$.

The inequality is automatically satisfied in the segment $[\lambda_2, \lambda_1]$. We obtain that $kf_2(s) \leq f_1(s)$ everywhere in I , which contradicts the linear connectedness of ϕ . Analogously, 2) is proved for any pair from collection g . Further:

$$\lambda_1 > \lambda_2 \Rightarrow f_1(\lambda_1) > f_2(\lambda_1) \Rightarrow f_1(1) < f_2(1) \Rightarrow \beta_1 < \beta_2.$$

We get similar inequalities for the functions g_1, g_2 from which follows $\alpha_1 > \alpha_2$. Thus 1) is proved.

We now prove 3) for any three functions from collection f . For example, for f_1, f_2, f_3 . We assume the opposite, that is, $\theta_{13} < \theta_{23}$. We define $c^0 = f_2(\lambda_3)/f_1(\lambda_3)$. Clearly, $0 < c^0 < 1$. We consider the function $l_c(s) = f_2(s) - cf_1(s) - (1 - c)f_3(s)$. It is clear, that $l_c(0) = 0$ and $l_c(\theta_{13}) < 0$ for any $c \in [0, 1]$. Moreover, $l_{c^0}(\lambda_3) = 0$.

We consider the intervals on which $l_{c^0}(s) > 0$ (if such do not exist, proof is finished). According to A_7 the function $l_{c^0}(s)$ does not have more than three zeros and thus there are no more than three of such intervals, and if they are two, then their closure contains λ_3 .

In this case there exists a $c < c^0$ such that again there are two of these intervals, but $l_c(\lambda_3) < 0$, and thus their closure does not contain λ_3 .

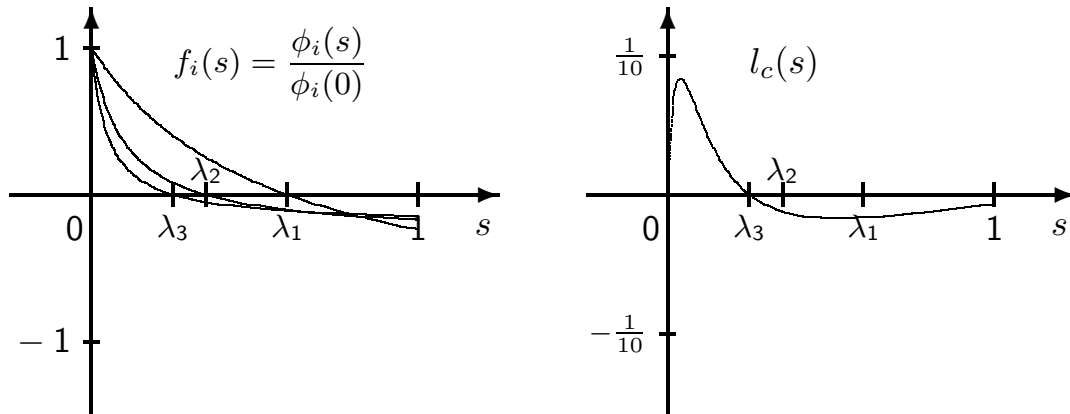


Рис. 2. $\lambda_1 = 0.6, \lambda_2 = 0.35, \lambda_3 = 0.25, a_1 = 0.55, a_2 = 0.1, a_3 = 0.05$

Consequently l_c does not have less than four zeros, which contradicts assumption. It remains to consider the case, when there are only one interval of positiveness. We note that this should be satisfied for all $c \in [0, c^0]$. Moreover the interval of positiveness intersect for nearby values of parameters. Consequently the interval should be on the left for $c = 0$, because the interval is to left of θ_{13} for $c = c^0$.

On the other side, the inequality $l_0(1) > 0$ is satisfied and we get a contradiction proving 3). Theorem is proved. \square

We now consider sufficient conditions.

Theorem 4. *Suppose function ϕ satisfies conditions $A_1 - A_5$. Then*

in the case when $n = 2$, one of the conditions $\beta_1 > \beta_2$ or $\alpha_1 > \alpha_2$ is sufficient for linear connectedness;

for the case $n = 3$, one of conditions $\beta_1 > \beta_2 > \beta_3$, $\theta_{13} > \theta_{23}$ or $\alpha_1 > \alpha_2 > \alpha_3$, $\tau_{13} < \tau_{23}$ is sufficient for linear connectedness.

Proof. Let $n = 2$ and $\beta_1 > \beta_2$. We suppose that the function f is linearly determined, that is that $k_1 f_1(s) + k_2 f_2(s) \leq 0$ for some vector k , $|k| \neq 0$. Substituting $s = 0$, λ_2 , λ_1 , 1 , we get a contradiction with the inequality for k , which proves this part of the theorem.

Let $n = 3$ and $\beta_1 > \beta_2 > \beta_3$. We assume that the function f is linearly determined, that is that $k_1 f_1(s) + k_2 f_2(s) + k_3 f_3(s) \leq 0$ for some vector k , $|k| \neq 0$. Substituting $s = 0$, we get $k_1 + k_2 + k_3 \geq 0$. Substituting $s = \theta_{23}$, we get $k_1 \mu + k_2 + k_3 \leq 0$, where $\mu = f_1(\theta_{23})/f_2(\theta_{23}) < 1$, from which follows $k_1 > 0$.

Analogously, substituting θ_{12} , we get $k_3 > 0$ and, automatically, $k_2 < 0$.

On the other side, for $s = \theta_{13}$ we get $(k_1 + k_3)f_1(\theta_{13}) + k_2 f_2(\theta_{13}) \leq 0$. But then $0 < f_1(\theta_{13}) < f_2(\theta_{13})$, leads to a contradiction proving the theorem. \square

4. Standard three dimensional system (n=2)

We use here some ideas and methods of [12], where sufficient conditions for degeneracy of the standard system were obtained.

Explicit formulas for degeneracy in the standard system were obtained in [?]-[12] for $n = 2$ and moreover theorem 2 was proved for this system. Concretely it was shown that, when $\lambda_2 < \lambda_1$, if one of the following conditions

- 1) $a_1 < a_2$,
- 2) $a_1 \lambda_2 - a_2 \lambda_1 \leq 0$,
- 3) $a_1 a_2 (\lambda_1 - \lambda_2) + \lambda_1 \lambda_2 (a_1 - a_2) \geq a_1 \lambda_2 - a_2 \lambda_1$,

is satisfied then one of the coordinate plane is globally attracting in $\text{int}R_3^+$.

We introduce the notations

$$\gamma = \frac{\lambda_2 a_1}{\lambda_1 a_2}, \quad \alpha = \frac{1 - \lambda_2}{1 + a_2} \cdot \frac{1 + a_1}{1 - \lambda_1}.$$

In case $\lambda_1 > \lambda_2$ it follows directly from theorems 3-4 that the function

$$\phi(s) = (\phi_1(s), \phi(s)) = \left(\frac{s - \lambda_1}{s + a_1}, \frac{s - \lambda_2}{s + a_2} \right)$$

is linearly connected if $\gamma > \alpha$.

We show that then $\alpha > 1$. We first prove that $a_1 > a_2$. Indeed, let $a_1 \leq a_2$. Then

$$\frac{\lambda_2}{1 - \lambda_2} \cdot \frac{a_1}{1 + a_1} \leq \frac{\lambda_1}{1 - \lambda_1} \cdot \frac{a_2}{1 + a_2} \Leftrightarrow \frac{\lambda_2 a_1}{\lambda_1 a_2} \leq \frac{1 - \lambda_2}{1 - \lambda_1} \cdot \frac{1 + a_1}{1 + a_2}.$$

We got a contradiction.

Further:

$$\lambda_1 > \lambda_2, \quad a_1 > a_2 \Rightarrow \frac{1 - \lambda_2}{1 - \lambda_1} > 1 \ \& \ \frac{1 + a_1}{1 + a_2} > 1 \Rightarrow \alpha > 1.$$

Thus the condition $\lambda_1 > \lambda_2$ is equivalent to $\gamma > \alpha > 1$ in the case of linear connectedness.

Simple transforms show that the complement to these inequalities coincides with the set of parameters given by 1) – 3).

5. Conclusion

We have obtained conditions for dissipativity and degeneracy (meaning extinction of some predators) for a general family of predator-prey systems with many predators and one prey. Considering degeneracy we have only used the properties of the equations of the predators. Using the equation for the prey will give better results. Finally we include figure 3 for the standard three dimensional system showing results of numerical experiments for the regions of degeneracy of one predators and for existence of inner solutions. In region 1 predator x_2 goes extinct and x_1 in region 4. An inner solution exists in regions 2 and 3 and on the boundary between them there is a period doubling bifurcation. The regions are shown in the parameter plane of parameters λ_1 and λ_2 keeping a_1 and a_2 fixed.

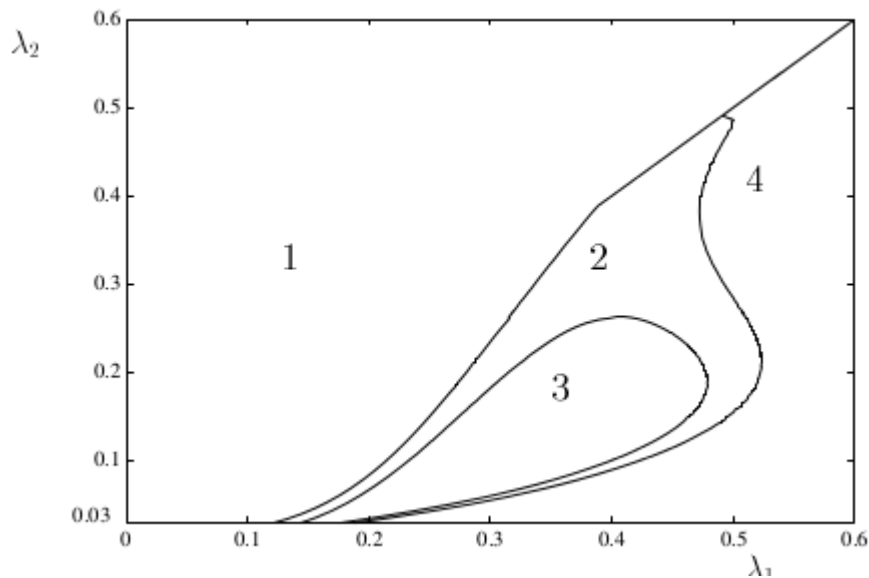


Рис. 3. Regions of extinction and coexistence for $a_1 = 0.2, a_2 = 0.02$

We observe that condition 1) in previous section implies condition 2) which implies condition 3) and condition 3) implies $x_1 \rightarrow 0$. Condition 3) in the figure gives a subregion of region 4. We also observe that changing the order of variables we get

analogous conditions in the case when $\lambda_1 < \lambda_2$ and then corresponding condition 1) gives $x_2 \rightarrow 0$ for $a_1 > a_2$. This corresponds to a subregion of region 1.

References

1. *Hofbauer J., Sigmund K.* The theory of evolution and dynamical systems. Cambridge - New York: Cambridge Univ. Press, 1988.
2. *Pospišil Z.* Remark on the Dissipativity of an N Prey – One Predator System. *Math. Biosci.*, 1996, 31, 173-183.
3. *Yang F., Ruan S.* A generalization of the Butler-McGehee lemma and its applications in persistence theory. *Differential and Integral Equations.* – 1996 – 9, 6, 1321-1330.
4. *Smith H.L., Waltman P.* The theory of the chemostat: dynamics of microbial competition. Cambridge: Cambridge Univ. Press, 1995.
5. *Alebraheem Jawdat, Abu-Hasan Yahya.* Persistence of Predators in a Two Predators-One Prey Model with Non-Periodic Solution. *Applied Mathematical Sciences.* – 2012. – Vol. 6, no.19, 943 - 956.
6. *Geritz S., Gyllenberg M.* A mechanistic derivation of the DeAngelis-Beddington functional response. *J. Theoret. Biol.* – 2012. – 314, pp. 106–108.
7. *Hirsch M.W., Smith H.L.* Competitive and Cooperative Systems: a mini-review. – 2003. – Springer.
8. *Nåsell I.* Extinction and Quasi-stationarity in the Verhulst Logistic Model. // *J. theor. Biol.* – 2001. – 211, 11-27.
9. *Torsten Lindström T., Cheng Yuanji* Uniqueness of limit cycles for a limiting case of the chemostat: does it justify the use of logistic growth rates? // *Electronic Journal of Qualitative Theory of Differential Equations.* – 2015. – No. 47, 1–14.
10. *Demidovich B.P.* Lectures on mathematical theory of stability (in Russian). Moscow: Nauka, 1969.
11. *Eirola T., Osipov A.V., Söderbacka G.* On chaotic coexistence for the systems of "two predators – one prey" type. // Intern. Congress on Computer Systems and Appl. Math., – 1993. – St. Petersburg, 19-23 July, 1993.
12. *Eirola T., Osipov A.V., Söderbacka G.* On the appearance of the chaotic regime in one dynamical system of "two predators – one prey" type. (in Russian). In compendium: "Actualnye problemy sovremennoj matematiki (ed. – A.V. Osipov). – 1996. – I, 39-70.

Получена 03.03.2016