BIFURCATION EFFECTS IN DEGENERATE DIFFERENTIAL MODELS OF SUBPOPULATION DYNAMICS

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ABSTRACT
The model of subpopulation dynamic of the Lotka-Volterra type has been investigated. Stability of stationary points and hyper-planes of the system was in the focus of the article; appearance conditions are found. Bifurcation analysis of system has been realized also.

MATHEMATICAL MODEL

The majority of existing models of population dynamics describe dynamics of whole populations, their interaction and influence of environment for them. The phenomenon of subpopulation dynamics is considered with much less attention. One of reasons is the fact that in most cases subpopulations aren't isolated from each other and exchange by individuals.
For taking into account the subpopulation effects, let's consider the general model of subpopulation dynamics in the form:

$$\dot{x}_i = \sum_{j=1}^{n} A_{ij} \cdot f_j(x_1,\dots,x_n), i = \overline{1,n}, A_{ji} \in [0;1],$$

where x_i is a biomass of i-th subpopulation. In the right hand part of each equation, the "base functions" $f_i(x_1,..,x_n)$ are combined linearly; each of them is "distributed" between all equations in accordance with some coefficients A_{ij} ("cross coefficient").

In [3] the model of subpopulation dynamics was investigated for the case of the logistic base functions. It was also supposed that the total size of the population (the total sum of sizes of all the subpopulations) was limited by some fixed niche capacity. In the current article, individual niche capacities for each subpopulations is considered. Correspondingly, the initial model of subpopulation dynamics can be represented in the following form:

$$\frac{dx_i}{dt} = \sum_{j=1}^{n} A_{ij} \cdot \left(a_j - c_j \cdot \sum_{k=1}^{n} x_k \right) \cdot x_j, i = \overline{1,n}, \quad (1)$$

Here the coefficients A_{ij} describe exchange by specimens between the subpopulations, a_i is a birth rate of i-th subpopulation, c_i is a level of sensitivity of i-th subpopulation to inter-subpopulation competition, n - amount of subpopulations (a_i/c_i - niche capacity for i-th subpopulation). It can be easily shown, that the model can find applications not only in ecology, but also in economy, sociology, etc.
Under a condition

$$\sum_{i=1}^{n} A_{ij} = 1, 0 \le A_{ij} \le 1, \quad (2)$$

the system can be considered as "closed" [5]. The condition (2) reflects the assumption that all population as a whole is closed, i.e. there are no migratory processes both to population and from it.
In the case $n = 2$ the system (1) takes a form:

$$\begin{cases} \dfrac{dx_1}{dt} = \lambda_1 a_1 \left(1 - \dfrac{x_1 + x_2}{a_1/c_1}\right) x_1 + (1-\lambda_2) a_2 \left(1 - \dfrac{x_1 + x_2}{a_2/c_2}\right) x_2 \\ \dfrac{dx_2}{dt} = (1-\lambda_1) a_1 \left(1 - \dfrac{x_1 + x_2}{a_1/c_1}\right) x_1 + \lambda_2 a_2 \left(1 - \dfrac{x_1 + x_2}{a_2/c_2}\right) x_2 \end{cases} . (3)$$

For investigation of system critical points, the Lyapunov's method [4] was used. There are three critical points: $(0;0)$, $(a_1/c_1;0)$, $(0;a_2/c_2)$ and a stationary straight line:

$$x_1 = a_1/c_1 - x_2, \quad (4)$$

which exists under a condition

$$a_1/c_1 = a_2/c_2 . \quad (5)$$

BIFURCATION ANALYSIS OF THE MODEL

Theorem 1: Points of the stationary regular hyper-plane (4) of the system (3), exist under an additional condition (5), are degenerate, i.e. the Jacobi matrix is equal to zero in them.

Proof:
An ij-th element of the Jacobi matrix of the system (3) has a form:

$$J_{ij} = \sum_{j=1}^{2} \left[a_j A_{ij} \left(1 - \frac{(x_1 + x_2)}{a_j/c_j} \right) - c_j x_j \right]. \quad (6)$$

Taking into account the condition (5),

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$$J_{ij} = \sum_{j=1}^{n} \left(-c_j \cdot x_j\right).$$

As J_{ij} doesn't depend directly from i, $J_{pi} = J_{hi}$, $p,h = \overline{1,n}$. So, the column vectors of the Jacobi matrix are linearly dependent, and $\det(J) = 0$.

The theorem is proved.

All stationary sets of the system can be easily explained. The stationary point in the origins or with one zero coordinate reflects the situation when both subpopulations are absent at all or one population has zero size and the other one totally fill the niche. In the conditions of lack of resources the subpopulations divide the ecological niche. In the case of equality of niche sizes for all the subpopulations, they can coexist with different size ratio among themselves. The equilibrium ratio will depend on initial conditions.

Elements of the Jacobi matrix of system (3) look like:

$$J_{11} = \lambda_1\left(a_1 - c_1\left(2x_1 + x_2\right)\right) + c_2 x_2\left(\lambda_2 - 1\right),$$
$$J_{12} = \left(1-\lambda_2\right)\left(a_2 - c_2\left(2x_2 + x_1\right)\right) - \lambda_1 c_1 x_1,$$
$$J_{21} = \left(1-\lambda_1\right)\left(a_1 - c_1\left(2x_1 + x_2\right)\right) - \lambda_2 c_2 x_2,$$
$$J_{22} = \lambda_2\left(a_2 - c_2\left(2x_2 + x_1\right)\right) + c_1 x_1\left(\lambda_1 - 1\right).$$

In the origin of coordinates the matrix is:

$$J\big|_{(0;0)} = \begin{pmatrix} \lambda_1 \cdot a_1 & \left(1-\lambda_2\right)\cdot a_2 \\ \left(1-\lambda_1\right)\cdot a_1 & \lambda_2 \cdot a_2 \end{pmatrix}, \quad (7)$$

and in nonzero critical points $\left(a_1/c_1;0\right)$ and $\left(0;a_2/c_2\right)$ it has the forms:

$$J\big|_{(a_1/c_1;0)} = \begin{pmatrix} -\lambda_1 a_1 & \left(1-\lambda_2\right)\left(a_2 - \dfrac{a_1 c_2}{c_1}\right) - \lambda_1 a_1 \\ \left(\lambda_1 - 1\right)a_1 & \lambda_2\left(a_2 - \dfrac{a_1 c_2}{c_1}\right) + a_1\left(\lambda_1 - 1\right) \end{pmatrix}, \quad (8)$$

and

$$J\big|_{(0;a_2/c_2)} = \begin{pmatrix} \lambda_1\left(a_1 - \dfrac{a_2 c_1}{c_2}\right) + a_2\left(\lambda_2 - 1\right) & \left(\lambda_2 - 1\right)a_2 \\ \left(1-\lambda_1\right)\left(a_1 - \dfrac{a_2 c_1}{c_2}\right) - \lambda_2 a_2 & -\lambda_2 a_2 \end{pmatrix}. \quad (9)$$

respectively.

In the Table 1 coefficients of the characteristic equation of system (3) (for each critical point) are presented.

Table 1: Factors of the characteristic equation of system (3) in special points

Stationary point	$b = -Tr(J)$	$c = Det(J)$
$(0;0)$	$-\left(\lambda_1 a_1 + \lambda_2 a_2\right);$	$a_1 a_2\left(\lambda_1 + \lambda_2 - 1\right)$
$\left(\dfrac{a_1}{c_1};0\right)$	$a_1 - \lambda_2\left(a_2 - \dfrac{c_2 a_1}{c_1}\right)$	$a_1\left(1-\lambda_1-\lambda_2\right)\times$ $\times\left(a_2 - \dfrac{c_2 a_1}{c_1}\right)$
$\left(0;\dfrac{a_2}{c_2}\right)$	$a_2 - \lambda_1\left(a_1 - \dfrac{c_1 a_2}{c_2}\right)$	$a_2\left(1-\lambda_1-\lambda_2\right)\times$ $\times\left(a_1 - \dfrac{c_1 a_2}{c_2}\right)$

Theorem 2: The system (3), under the conditions

$$\left[\begin{array}{l} a_1 = 0 \\ a_2 = 0 \\ \lambda_1 + \lambda_2 = 1 \\ \begin{cases} a_1 a_2\left(\lambda_1 + \lambda_2 - 1\right) > 0 \\ \lambda_1 a_1 + \lambda_2 a_2 = 0 \end{cases} \end{array}\right.$$

is degenerate in a vicinity of the origin.

Proof: the origin is a critical point of the system (3). The Jacobi matrix has in it the form (7). The determinant of a characteristic matrix $Det(J) = a_1 a_2\left(\lambda_1 + \lambda_2 - 1\right)$ under theorem conditions it is equal to zero.

Roots of the characteristic equation are complex under the condition $Tr^2(J) - 4Det(J) < 0$, and the condition of equality to zero of their real part is $Tr(J) = \lambda_1 a_1 + \lambda_2 a_2 = 0$. So, a general condition of zero real part for the case of complex roots is

$$\begin{cases} a_1 a_2\left(\lambda_1 + \lambda_2 - 1\right) > 0 \\ \lambda_1 a_1 + \lambda_2 a_2 = 0 \end{cases}.$$

The theorem is proved.

Theorem 3: The origin is the saddle stationary point of the system (3) under the condition:

$$a_1 a_2\left(\lambda_1 + \lambda_2 - 1\right) < 0.$$

If

$$0 < a_1 a_2\left(\lambda_1 + \lambda_2 - 1\right) < 0{,}25\left(\lambda_1 a_1 + \lambda_2 a_2\right)^2,$$

the point is a knot, and under the condition

$$a_1 a_2\left(\lambda_1 + \lambda_2 - 1\right) > 0{,}25\left(\lambda_1 a_1 + \lambda_2 a_2\right)^2$$

it is a focus.

In the last two cases the point is stable if $\lambda_1 a_1 + \lambda_2 a_2 < 0$,

and unstable if

$$\lambda_1 a_1 + \lambda_2 a_2 > 0.$$

Proof: The Jacobi matrix of the system (3) has in the origin the form (7), and its characteristic equation is

$$t^2 - \left(\lambda_1 a_1 + \lambda_2 a_2\right)t + a_1 a_2\left(\lambda_1 + \lambda_2 - 1\right) = 0.$$

Under the condition

$$Det(J) = a_1 a_2\left(\lambda_1 + \lambda_2 - 1\right) < 0$$

determinant of the characteristic equation

$$D(J) = Tr(J)^2 - 4Det(J).$$

Is positive, and the product of the equation roots (according to the Vieta theorem) is less than a zero. The critical point, by definition, has the saddle type.

Let's assume that $Det(J) > 0$. The determinant $D(J)$ of the characteristic equation has the form:

$$D(J) = (\lambda_1 a_1 + \lambda_2 a_2)^2 - 4a_1 a_2 (\lambda_1 + \lambda_2 - 1).$$

Under the condition:

$$a_1 a_2 (\lambda_1 + \lambda_2 - 1) > 0{,}25(\lambda_1 a_1 + \lambda_2 a_2)^2 ,$$

The stationary point is elliptic; the real part of the complex roots is $\lambda_1 a_1 + \lambda_2 a_2$. Under the condition $\lambda_1 a_1 + \lambda_2 a_2 < 0$, the origin has the "stable focus" type; and under the condition $\lambda_1 a_1 + \lambda_2 a_2 > 0$ it is "unstable focus". If

$$a_1 a_2 (\lambda_1 + \lambda_2 - 1) < \frac{(\lambda_1 a_1 + \lambda_2 a_2)^2}{4},$$

the stationary point is hyperbolic. According to the assumption $Det(J) > 0$, the roots of the characteristic equation have an identical sign, therefore under a condition $\lambda_1 a_1 + \lambda_2 a_2 < 0$ the point has type "steady knot", and under a condition $\lambda_1 a_1 + \lambda_2 a_2 > 0$ it is "unstable knot".

The theorem is proved.

Similarly to the proof of the theorem 2 and 3, one can prove the following statements:

Theorem 4: The system (3), under the condition

$$\left[\begin{array}{l} a_1 = 0 \\ (1 - \lambda_1 - \lambda_2) = 0 \\ (a_2 - c_2 a_1 / c_1) = 0 \\ \begin{cases} a_1 (1 - \lambda_1 - \lambda_2)(a_2 - c_2 a_1 / c_1) > 0 \\ \lambda_2 (a_2 - c_2 a_1 / c_1) - a_1 = 0 \end{cases} \end{array}\right.$$

is degenerate in a vicinity of $(a_1 / c_1; 0)$.

Theorem 5: The point $(a_1 / c_1; 0)$ has the saddle type has systems (3) under the condition $a_1 (1 - \lambda_1 - \lambda_2)(a_2 - c_2 a_1 / c_1) < 0$. If

$$0 < a_1 (1 - \lambda_1 - \lambda_2)(a_2 - c_2 a_1 / c_1) <$$
$$< (\lambda_2 (a_2 - c_2 a_1 / c_1) - a_1)^2 / 4$$

th point has the hub type; and if

$$a_1 (1 - \lambda_1 - \lambda_2)(a_2 - c_2 a_1 / c_1) >$$
$$> (\lambda_2 (a_2 - c_2 a_1 / c_1) - a_1)^2 / 4$$

It is "focus". In the last two cases the point is steady under a condition

$$\lambda_2 (a_2 - c_2 a_1 / c_1) - a_1 < 0,$$

It is unstable if $\lambda_2 (a_2 - c_2 a_1 / c_1) - a_1 > 0$.

Theorem 6: The system (3) under the condition

$$\left[\begin{array}{l} a_2 = 0 \\ (1 - \lambda_1 - \lambda_2) = 0 \\ (a_1 - c_1 a_2 / c_2) = 0 \\ \begin{cases} a_2 (1 - \lambda_1 - \lambda_2)(a_1 - c_1 a_2 / c_2) > 0 \\ \lambda_1 (a_1 - c_1 a_2 / c_2) - a_2 = 0 \end{cases} \end{array}\right.$$

is degenerate in a vicinity of the critical point $(0; a_2 / c_2)$.

Theorem 7: The critical point $(0; a_2 / c_2)$ of the system (3) is a saddle under the condition $a_2 (1 - \lambda_1 - \lambda_2)(a_1 - c_1 a_2 / c_2) < 0$. If

$$0 < a_2 (1 - \lambda_1 - \lambda_2)(a_1 - c_1 a_2 / c_2) <$$
$$< (\lambda_1 (a_1 - c_1 a_2 / c_2) - a_2)^2 / 4$$

the point has the hub type; and if

$$a_2 (1 - \lambda_1 - \lambda_2)(a_1 - c_1 a_2 / c_2) >$$
$$> (\lambda_1 (a_1 - c_1 a_2 / c_2) - a_2)^2 / 4 ,$$

it is "focus". In the last two cases the point is steady under the condition $\lambda_1 (a_1 - c_1 a_2 / c_2) - a_2 < 0$, and it is unstable if $\lambda_1 (a_1 - c_1 a_2 / c_2) - a_2 > 0$.

All possible cases of the system topology are represented in the Table 2 and Fig. 1-9.

Table 2: Different topology of the system (3) phase portrait

Design-ations	Type of point (0;0)	Type of point $(a_1 / c_1; 0)$	Type of point $(0; a_2 / c_2)$
1	Stable	Stable	Saddle
2	Stable	Saddle	Stable
3	Stable	Saddle	Saddle
4	Stable	Saddle	Unstable
5	Stable	Unstable	Saddle
6	Saddle	Stable	Stable
7	Saddle	Stable	Saddle
8	Saddle	Stable	Unstable
9	Saddle	Saddle	Stable
10	Saddle	Saddle	Unstable
11	Saddle	Unstable	Stable
12	Saddle	Unstable	Saddle
13	Saddle	Unstable	Unstable
14	Unstable	Stable	Saddle
15	Unstable	Saddle	Stable
16	Unstable	Saddle	Saddle
17	Unstable	Saddle	Unstable
18	Unstable	Unstable	Saddle

In Fig. 1-9 one can see bifurcation charts of system (3) in different parametrical spaces of dimension 2 with fixed values of other parameters. It is important to note, that the bifurcation charts are presented in two variants (with different signs of $(\lambda_1 + \lambda_2 - 1)$).

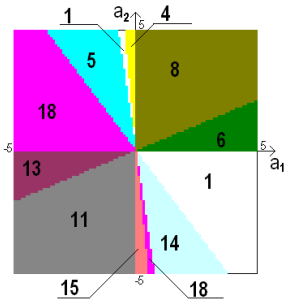


Figure.1.The bifurcation diagram of system (3) with parameters $\lambda_1 = 0.7;\ \lambda_2 = 0.2;\ c_1/c_2 = -0.1;$

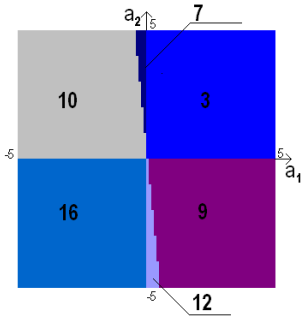


Figure.2. The bifurcation diagram of system (3) with parameters $\lambda_1 = 0.7;\ \lambda_2 = 0.8;\ c_1/c_2 = -0.1;$

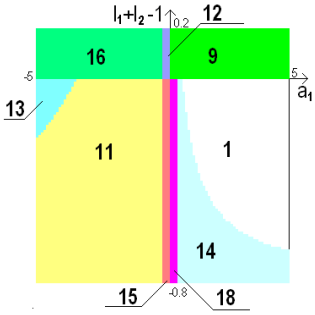


Figure.3. The bifurcation diagram of system (3) with parameters $a_2 = -3;\ c_1/c_2 = -0.1;$

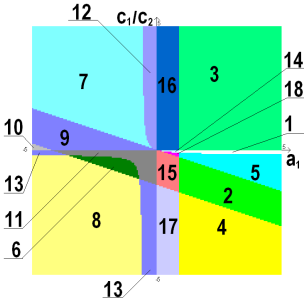


Figure.4. The bifurcation diagram of system (3) with parameters $a_2 = -3;\ \lambda_1 = 0.7;\ \lambda_2 = 0.2;$

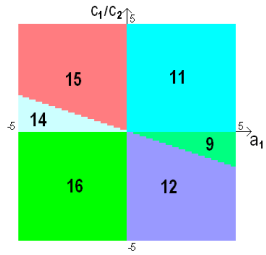


Figure.5. The bifurcation diagram of system (3) with parameters $a_2 = -3;\ \lambda_1 = 0.7;\ \lambda_2 = 0.8;$

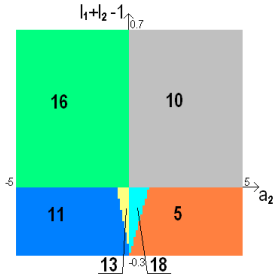


Figure.6. The bifurcation diagram of system (3) with parameters $a_1 = 1; c_1/c_2 = -0.1;$

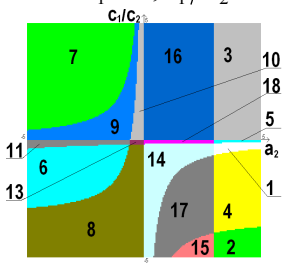


Figure.7. The bifurcation diagram of system (3) with parameters $a_1 = 1;\ \lambda_1 = 0.7;\ \lambda_2 = 0.2;$

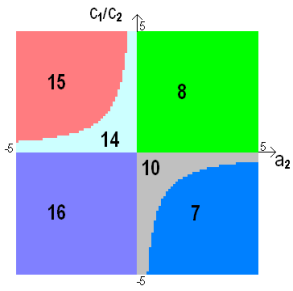


Figure.8. The bifurcation diagram of system (3) with parameters $a_1 = -2;\ \lambda_1 = 0.7;\ \lambda_2 = 0.8;$

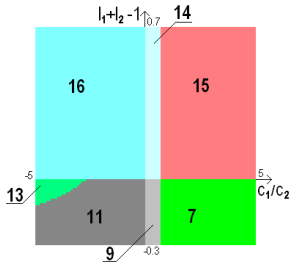


Figure.9. The bifurcation diagram of system (3) with parameters $a_1 = 1;\ a_2 = -3;$

Invariant analysis of the system shows that topology of the system is determined by values of four parameters: a_1, a_2, $(\lambda_1 + \lambda_2 - 1)$ и c_1 / c_2. It is important: are positive or negative values of parameters a_1, a_2, $(\lambda_1 + \lambda_2 - 1)$; is value of c_1 / c_2 less than zero, belongs to the interval [0; 1], or more than zero. Maximal quantity of different phase portrait topologies is equal to $3 \times 3 \times 3 = 27$. More precise analysis shows that there are only 18 topologies; 9 cases (tab. 3) are theoretically impossible.

Table 3: Impossible topologies of the system phase portraits

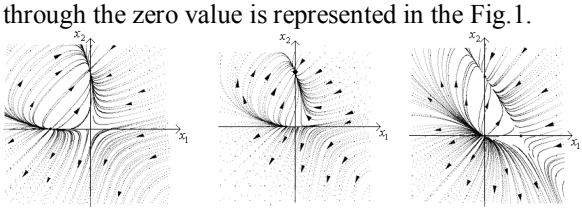
№	Type of point $(0;0)$	Type of point $(a_1/c_1;0)$	Type of point $(0;a_2/c_2)$
1	Stable	Stable	Stable
2	Stable	Stable	Unstable
3	Stable	Unstable	Stable
4	Stable	Unstable	Unstable
5	Saddle	Saddle	Saddle
6	Unstable	Stable	Stable
7	Unstable	Stable	Unstable
8	Unstable	Unstable	Stable
9	Unstable	Unstable	Unstable

Excluding x_1 / x_2 symmetrical cases, the system (3) is characterised by 11 types of non-equivalent phase portraits (Tab. 4) only.

Table 4: Non-equivalent phase portraits of system (3)

№	Type of point $(0;0)$	Type of point $(a_1/c_1;0)$	Type of point $(0;a_2/c_2)$
1	Stable	Stable	Saddle
2	Stable	Saddle	Unstable
3	Stable	Saddle	Saddle
4	Saddle	Stable	Stable
5	Saddle	Stable	Saddle
6	Saddle	Stable	Unstable
7	Saddle	Saddle	Unstable
8	Saddle	Unstable	Unstable
9	Unstable	Stable	Saddle
10	Unstable	Saddle	Saddle
11	Unstable	Saddle	Unstable

As an illustration, typical bifurcation, based on change of value of the birth rate of the first subpopulation, through the zero value is represented in the Fig.1.



a) b) c)

Figure.10. The phase portrait of the system (3) with parameters $a_2 = 1{,}5$; $\lambda_1 = 0{,}8$; $\lambda_2 = 0{,}75$; $c_1 = c_2 = 0{,}01$; and a) $a_1 = -1$;b) $a_1 = 0$;c) $a_1 = 1$.

CONCLUSION:

A new degenerate model of subpopulations dynamics has been proposed. It can be used, particularly, for description of dynamics of genetically not isolated populations. It is assumed, that some specimens, born within one subpopulation, has probability to join another subpopulation by its genotype. Such probability is defined by many factors, including present and past isolation of the subsystems, character of genetic variance within the subpopulations and so on.

The model is a sketch model, similarly to Lotka-Volterra one, which is, on one hand, rather simple for its analytical research, but is quite adequate qualitatively, with possibility to use results of analytic investigation in practice.

For the analysed system, three possible equilibrium states and one stationary hyper-plane exist. Its potential bifurcations are determined by signs of special characteristic indexes of the system.

Adequacy of the model is confirmed by number of phase portraits and charts, which illustrate conditions of qualitative changes in behaviour of the system.

Bifurcation properties of the model were in the focus of the research. The bifurcations have obtained rather natural applied interpretations; and it was possible to estimate qualitatively factors, which influence on dynamics of the system. As usual, bifurcation analysis gives opportunity to find critical values of parameters, a tend to which can point for danger of essential reordering the system or even its destroying. Such analysis for ecological models, particularly, models of population dynamics, can give a tool for preventing unexpected ecological catastrophes.

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