THIRD AUTUMN COURSE ON MATHEMATICAL ECOLOGY

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"Soviet Contribution to Mathematical Ecology"

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These are preliminary lecture notes, intended only for distribution to participants.

Soviet Contribution to Mathematical Ecology

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Introduction

The main task of my presentation is to show how the
mathematical ecology was developped in specific condition
of my country. Our western colleagues know about it in-
sufficiently, sorry, may be because of a linguistic barrier
and, may be, because of other reasons.

Traditionally, in my country the mathematical ecology
was developped in frameworks of the pure and applied
mathematics. This was the reason of the strong mathematiza-
tion of it and that the problems of mathematical ecology
were mostly considered as mathematical problems.
Besides that the Russian school of mathematical ecology
has its close "genetic" connection to classical work of
V. Volterra, V. Kostitzin, A. Kolmogorov, J. Petrovsky.
Thus russian works are traditional in this sense.

In my short presentation I can not talk about all
results which were obtained by our school and my choice
of examples will be sufficiently subjective, but I hope
that it will be sufficiently illustrative and represen-
tative.

1. "Prey-Predator" System as a Classical Object of
    Mathematical Ecology

> "When we study the History
> of Science we discover two
> mutual contrary phenomena:
> either behind an apparent
> complexity a simplicity is
> hidden or, on the contrary,
> an evident simplicity con-
> ceals within itself an extra-
> ordinary complexity".
>
> H. Poincaré

Let's consider the model of "prey-predator" system:

$$\frac{dx}{dt} = \alpha x - V(x)y$$

$$\frac{dy}{dt} = kV(x)y - my \,, \tag{1}$$

where $x(t)$ and $y(t)$ are population sizes of a prey and a predator respectively, $\alpha(x)$ is a Malthusian function for a prey, $V(x)$ is a trophic function /or functional response in the American literature/, m is the mortality rate for a predator and k is an "efficiency coefficient". Replacing the variables: $\alpha t \Rightarrow t$, $x/x^* \Rightarrow x$, $y/y^* \Rightarrow y$, $V/V_\infty \Rightarrow V$, $m/\alpha \Rightarrow \mu$ where (x^*, y^*) is a non-zero equilibrium of (1) , we obtain:

$$\frac{dx}{dt} = x - V(x)y$$

$$\frac{dy}{dt} = \mu y \left[V(x) - 1 \right] \,. \tag{2}$$

In (2) the type of equilibrium is determined by the value of $v = V'_x(1)$. This equilibrium is a topological knot, if $v < 1$ that it is unstable and if $v > 1$, stable. During the transition through $v = 1$ we have the Andronov-Hopf bifurcation and in "the general position" case a limit cycle is born out of this equilibrium. It seems there are no problems here.

On the other hand in mathematical ecology there is a very popular parametrization for a trophic function

$$V(x) = \frac{V_\infty x^n}{K^n + x^n} \,, \quad n = 1,2,\ldots \tag{3}$$

especially in the case n = 2, or, in new variables:

$$V(x) = x^2 \big/ (1 - b + bx^2), \quad b = V^*/V_\infty$$

The bifurcation value of b is $b_c = \frac{1}{2}$. Hence the trophic function which gives the equilibrium of "centrum" type, is $V_c = 2x^2/(1 + x^2)$. In this case the system (2) is brought to the Abel equation of $2^{\underline{nd}}$ type and it has the integral

$$\begin{cases} y + Cy^{1/\mu} = (1-\mu)\dfrac{x}{V_c(x)}, & \mu \neq 1 \\ y \ln(Cy) = x/V_c(x), & \mu = 1 \end{cases} \qquad (4)$$

/Note that the integral of such type exists for the trophic function (3), i.e. for the more general case./ Hence the limit cycles can not appear out of the equilibrium /an existance of Abel equation integral is a sufficient condition for this/.

We can show that the periodic regime can not appear out of closed trajectories of centrum, too. Hence the system (2) with trophic function (3) is "non-crude" /in Andronov sense/ and it has not limit cycles. But if the trophic function "to move about", for example, to present it in the form

$$V(x) = x^2 / \left[1 - b + bx^2 + (b-\tfrac{1}{2})F(x)\right], \qquad (5)$$

where $F(x)$ is a finite function, $F(1) = 0$, $F(0) < -(1 + x^2)$, $F(\infty) < x^2$ /see fig. 1/, that we can organize a birth of cycle out of closed trajectories. As $F(x)$ we can get $F(x) = A\left[(x-1)/(x+1)\right]^{\ell}$. Then the birth of cycle my be achieved by the choice of constant A.

Note that the factor $(b - \frac{1}{2})$ at $F(x)$ was introduced in order to the Abel integral was not destroyed.

If now remove this factor, i.e. destroy the Abel integral
we can realize the birthe of $(\ell-1)$ cycles out of equilib-
rium by means of the Andronov-Hopf bifurcation. In other
words "the movement about" of trophic function in the
system (2) makes it "crude" and the bifurcation of b can
bear limit cycles as out of equilibrium so out of closed
trajectories /so many how we want/.

It is very interesting that the representation (3)
of trophic function gives us the whole class of structu-
rally unstable phase portraits. Really the probability
to put in a "non-crude" situation is very low but we
has put in because of the such representation is very
popular. None the less we can use it, for example, in
the following cases:

a/ when we consider "prey-predator" system under an
impact of stochastic perturbations /so called "parametric
excitement"/. In this case the perturbations destroy this
"non-crude" structurally unstable situation and in result
of we have got the whole system of /stable and unstable/
stochastic limit cycles.

b/ when for the analyse of dynamic behaviour of system
we use some asymptotic methods /for example, Krylov-Bogolubov
method/. Also the use of asymptotics leads to the destruc-
tion of "non-crude" situation and we obtain more and less
accurate results, as a rule /in details see [1], [2] /.

2. Systems of Competing Species.

Let's consider the simplest model of two species which
compete for one resource:

$$\frac{dx}{dt} = x(\varepsilon_1 - \alpha_{11}x - \alpha_{12}y)$$
$$\frac{dy}{dt} = y(\varepsilon_2 - \alpha_{21}x - \alpha_{22}y). \tag{6}$$

where $x(t)$ and $y(t)$ are the population sizes of competing species. After a transformation of coordinates we have got

$$\frac{dx}{dt} = x(1 - x - \gamma_1 y)$$

$$\frac{dy}{dt} = ky(1 - y - \gamma_2 x). \tag{7}$$

This system has been investigated in details, there are not limit cycles and the equilibria have the form: $\sigma_0 = (0,0)$, $\sigma_1 = (1,0)$, $\sigma_2 = (0,1)$, $\sigma_3 = \left(\frac{1-\gamma_1}{1-\gamma_1\gamma_2}, \frac{1-\gamma_2}{1-\gamma_1\gamma_2}\right)$.
Their stability depends on the values of γ_1 and γ_2
/see fig. 2/. Suppose now that γ_1 and γ_2 evolve slowly
/compared with changes of x and y/, so that

$$\frac{d\gamma_1}{dt} = \varepsilon g_1(x,y,\gamma_1,\gamma_2), \quad \frac{d\gamma_2}{dt} = \varepsilon g_2(x,y,\gamma_1,\gamma_2), \tag{8}$$

where $\varepsilon \ll 1$. Let's consider the evolution of the expanded
system (7) + (8). What will take place here?

Let the system moves along a phase trajectory which
passes through an arbitrary point $\xi(t_0) = \sigma_0$. After the
initial fast movement the point $\sigma \in \xi$ puts into the neigh-
borhood of an equilibrium manifold and then a slow move-
ment occurs in this neighborhood corresponding to change
of parameters γ_1 and γ_2 within a domain ω_i /see fig 3/.
When the curve $f(\xi)$ which is the projection of ξ onto
$\Gamma = \{\gamma_1, \gamma_2\}$, crosses the boundaries between ω_i, the
equilibrium to which x and y are close may disappear or
become unstable. In such a case, however, the system imme-
diately gets into the layers above other stable points,
where it will move fastly, to move again slowly in the
neighborhood of another equilibrium manifold. You can
see it on the fig. 3.

Let the system move from point $(\gamma_1^i, \gamma_2^i) \in \omega_2$ into ω_1
along the path ξ_1 ($f(\xi_1)$ is the projection of ξ_1).

At the moment of crossing the boundary AB the σ_1 loses
stability, the new stable point σ_3 appears /at the boun-
dary when $\gamma_2 = 1$ $\sigma_1 = \sigma_3$/. The transition from one equilib-
rim to another occurs without fast movement and the chan-
ge of the ecosystem structure proceeds smoothly. The re-
placement of σ_3 by σ_2 proceeds in a similar way when
$f(\xi_1)$ crosses BC. The entire transition $\sigma_1 \to \sigma_3 \to \sigma_2$ is
reversible in the sense that if the system performs a
reverse transition from (γ_1^f, γ_2^f) to (γ_1^i, γ_2^i) and
$f(\bar{\xi}_1) = f(\xi_1)$ $(\bar{\xi}_1$ is a reverse trajectory), then trajec-
tories ξ_1 and $\bar{\xi}_1$ are close to each other in the phase
space $V = \{x, y ; x, y \geq 0\}$.

The situation will be quite different when $f(\xi_2)$ passes
through the domains ω_2, ω_3 and ω_4. Upon crossing BE
the equilibrium σ_1 retains its stability, but at the same
time σ_2 becomes unstable and the unstable saddle σ_3
separates from it. The part of ξ_2 which is projected into
ω_2, is in the neighborhood of equilibrium manifold
corresponding to σ_1, the part which is projected into
ω_3, remaining in the same neighborhood. However, upon
crossing BD σ_1 loses its stability and slow movement along
this manifold changes into fast one, which leads ξ_2 into
the neighborhood of the equilibrium manifold corresponding
to σ_2. In this case the observed variables x and y change
fastly, the ecosystem structure changes in a jump, and the
transition $\sigma_1 \to \sigma_2$ is irreversible. /The irreversibility
is understood in the sense that if there exists a trajecto-
ry ξ_2 leading from (γ_1^f, γ_2^f) to (γ_1^i, γ_2^i), such that $f(\bar{\xi}_2) =$
$= f(\xi_2)$ then a fast movement along $\bar{\xi}_2$ will take place
at E rather than at D, i.e. ξ_2 and $\bar{\xi}_2$ will be not close
in V. This is the hysteresis phenomenon, typical for
non-linear systems.

It is clear that the hysteresis phenomena and some other catastrophes will take place for the more complex "competitive" communities. Slow evolution of parameters caused, for example, by genetic processes or climatic changes, will generates various stuctural ecological "perestroika's", and the non-linear effects of hysteresis type ensuring irreversibility of these "perestroika's".

3. Chaos in Simple Ecological Model.

> "Before all things Chaos had
> appeared in the Universum".
> Hesiodus

Chaotic dynamics and strange attractors are not very exotic in ecology. Let's even remember Rikker's model of one population with non-overlapping generations. One of the simplest ecological model in the class of differential equations is the model of closed triphic chain with 3 levels /see fig. 4/. In this model the occurence of chaos was detected [3]. When we looked for a strange attractor by computer we took the trophic functions V_i in the following forms: $V_0 = \alpha_0 N_0$, $V_1 = V_2 = V_\infty N_i / (K + N_i)$, $i = 1,2$. Since the conservation law here says that $N_0 = C - (N_1 + N_2 + N_3)$ where C = const is a total amount of matter in this ecosystem. Then its the model can be presented in the form:

$$\frac{dN_1}{dt} = N_1 \left[-m_1 + \alpha_0 \left(C - \sum_{i=1}^{3} N_i \right) - \frac{V_\infty N_2}{K + N_1} \right]$$

$$\frac{dN_2}{dt} = N_2 \left[-m_2 + \frac{V_\infty N_1}{K + N_1} - \frac{V_\infty N_3}{K + N_2} \right] \tag{9}$$

$$\frac{dN_3}{dt} = N_3 \left[-m_3 + \frac{V_\infty N_2}{K + N_2} \right] .$$

We succeeded to prove analytically the possibility of the birth of a cycle in result of the Andronov-Hopf bifurcation and the existence of a stable limit cycle for large α_0. Numerically the system (9) was investigated for

$$m_1 = 0.1, \ m_2 = m_3 = 0.2, \ V_\infty = 1, \ K = 5, \ 0.30 \leqslant \alpha_0 \leqslant 0.37,$$

C is the bifurcation parameter. We obtained the following results.

We represented on the plane $\{C, \alpha_0\}$ the curves $C_\infty(\alpha_0)$ and $C_3^o(\alpha_0)$ /see fig. 5/ which are the bifurcation curves, i.e. for $C = C_1^o$ in the result of the Andronov-Hopf bifurcation the stable limit cycle appears, for $C = C_2^o$ two cycles appear etc. At points $C_1, C_2, \ldots$ bifurcation doubling takes place, i.e. for $C = C_1$, the cycle /one or two/ loses a stability etc... Finally, in the hatched domain the "pre-turbulent" regime /pre-stochasticity/ takes place, i.e. in this domain the strange attractor /resulting from an infinite chain of the Feigenbaum's doubling/ and the stable limit cycle coexist. The complete stochasticity is oberved for $C > C_3^o$, i.e. when the stable cycle vanishes. It is interesting that the pre-stochastic regime is typical for the Lorenz system, however, there the stochastization process is distinguished from the Feigenbaum's mechanism of cycle doubling. Hence, we have obtained the new type of strange attractor which lies between Lorenz's and Feigenbaum's classical attractors.

4. Lagrange Stability and Ecological Stability.

On of the most popular definition of stability in ecology is the requirement to keep the number of species. It means that on the hand not one species eliminates, on the other, not one species grows infinitely. It means that the trajectories of community must be limited above and below in the positive orthant.

However, if in this orthant there are several equilibria and some of them are unstable, then with point of view of Lyapunov stability this community is unstable. But it is stable with point of view of ecological stability concept /if all trajectories were limited within the positive orthant/. The latter type of stability has long been known and is refered to as Lagrange stability. I think that this concept is more suitable for ecology. However there is not now the effective methods for the solution of Lanrange stability problems. Here we try to do it for the special case of positive orthant.

Let the dynamics of a biological community is given by

$$\frac{dN}{dt} = F(N),$$

$$N(0) = N_0, \quad N(t) \in P^n \quad \text{for all } t \geq 0. \tag{10}$$

The vector N with components N_i, where $N_i(t)$ is the population size of ith species, has to lie within the positive orthant of n-dimensional phase space, i.e. P^n /P^n is an invariant set for (10)/.

Let Ω_0^n and Ω^n be closed finite domains lying within P^n. We shall speak that the community is ecologically stable, if for any $N^\circ \in \Omega_0^n$ such the $\Omega^n(\Omega_0^n)$ exists that $N \in \Omega^n$ for all $t > 0$. /If you want you can find the similarity and distinction between this determinition and the classical Lyapunov determinition for stability./

The substitution $\xi_i = \ln(N_i/N_i^\circ)$ into (10) gives:

$$\frac{d\xi}{dt} = \varphi(\xi, N^\circ),$$

$$\xi(0) = 0. \tag{11}$$

Thus in a result of this substitution we have got, firsty, instead of one system (10) with the set of initial conditions the whole family of systems depending on N^0 as a parameter, but with the one initial condition and, secondly, the solutions of (11) are determined in the whole phase space $\mathbb{R}^n_\xi$ /not only in the positive orthant/.

Evidently that $\xi^* = 0$ is a trivial solution for the system

$$\frac{d\tilde{\xi}}{dt} = \varphi(\tilde{\xi}, N^0) - \varphi(0, N^0) = \psi(\tilde{\xi}, N^0) \qquad (12)$$

Then we can consider the problem of stability for the solution $\xi^* = 0$ of system (11) as the problem of Lyapunov stability under permanent perturbations $B = \varphi(0, N^0)$. You can see that

$$\frac{d\xi}{dt} = \varphi(\xi, N^0) = \psi(\xi, N^0) + B \qquad (11')$$

Accordingly with the Chetaev-Malkin theorem the state $\xi^* = 0$ is stable /in Lyapunov's sense/ if it is stable asymptotically for the system (12), and B are sufficienty small. What does this mean? This means that the all trajectories which are started within some small neighborhood of state $\xi^* = 0$, will be limited in $\mathbb{R}^n_\xi$. If we remember now that the negative infinity in $\mathbb{R}^n_\xi$ corresponds to the boundaries of P^n /and the positive infinity in $\mathbb{R}^n_\xi$ corresponds to the one in P^n/ then we can stay that the stable trajectory of (11) for the determined value of parameter N^0 will be corresponded the limited trajectory of (10) which is started in the point N^0. Finally, if now we find the stability domain in the space of parameters N^0 is this way we can build up such the set of initial conditions that the all trajectories which are started within it, will be limited within P^n. This set is none other that the set $\tilde{\Omega}_0$.

Thus we have reduced the problem of ecological /Lagrange/ stability to the problem of Lyapunov stability. For latter there are constructive methods of solution.

The simplest example. Suppose the dynamics of one population is described by

$$\frac{dN}{dt} = \tau N \left(1 - \frac{N}{K}\right)(N - k), \quad o < k < K . \qquad (10')$$

Evidently $N(t) \to 0$ for $N_0 < k$ /there is not ecostability here/, for $N_0 > k$ this population is ecostable /see fig. 6/. After the substitution $\xi = \ell_n (N/N_0)$ we have got $\dot{\xi} = \psi + B$, where

$$\psi = \frac{\tau N_0}{K} \left(K + k - 2N_0\right)\xi + O(\xi), \quad B = \tau\left(1 - \frac{N_0}{K}\right)(N_0 - k).$$

According to Chetaev-Malkin theorem the trivial solution $\xi^* = 0$ is stable /in Lyapunov sense/ under permanent perturbation B for $N_0 > \frac{K + k}{2}$. Consequently we can state that the domain Ω_0': $\frac{k + k}{2} < N_0 < \infty$ is the domain of ecostability. You see that the real domain of ecostablity $(k < N_0 < \infty)$ is larger that Ω_0', why? The fact is that the Chetaev-Malkin theorem gives us only sufficient conditions of stability but no necessary ones.

Clearly, the requirement for the non-tirvial equlibrium N^* of (10) /if the latter exists/ to be stable is of a necessary condition for ecostability in general. However, there exists quite a large class of ecological models in which the conditions of ecostability and the existence of a positive equilibrium /stable in Lyapunov sense/ turn out to be equivalent. This class contains the so-called conservative and dissipative /according to Volterra/ communities. A very interest classification of various types of stability based on "the community matrix", carries out [4].

5. Competition for Resource, "Self-Thinning" Problem and Schroedinger Systems

Let's pass from the point systems to the space-distributed ones, and consider the next model. Suppose we have the biomass distribution $N(x,t)$ and the consumed resource distribution $R(x,t)$, $-\infty < x < +\infty$. Let the uptake rate of resource located in ξ by unit of biomass located in x , is equal to

$$\mathcal{P}(|x - \xi|) \, V[R(\xi,t)] \qquad (13)$$

where V is a trophic function, $\mathcal{P}$ is some function which describes "long-action" between the resource and consumer /for example, a normal distribution density with the center in x and variation σ^2 /. Then

$$\frac{\partial R}{\partial t} = Q - \int_{-\infty}^{\infty} \mathcal{P}(|x-\xi|) V[R(x,t)] N(\xi,t) d\xi ,$$

$$\frac{\partial N}{\partial t} = k \int_{-\infty}^{\infty} \mathcal{P}(|x-\xi|) V[R(\xi,t)] N(x,t) d\xi - mN . \qquad (14)$$

Here Q is the input flow of resource, k is "the efficiency coefficient", m is the mortality. Let σ^2 is sufficienty small then the asymptotic analogy of (14) will be

$$\frac{\partial R}{\partial t} = Q - V(R)\left\{ N + \frac{\sigma^2}{2} \frac{\partial^2 N}{\partial x^2} \right\},$$

$$\frac{\partial N}{\partial t} = kN\left\{ V(R) + \frac{\sigma^2}{2}\left[V''\left(\frac{\partial R}{\partial x}\right)^2 + V' \frac{\partial^2 R}{\partial x^2} \right]\right\} - mN . \qquad (15)$$

Let $V(R) = \alpha R$. To linearize of this system in the vinicity of spatially uniform stationary solution $R^* = m/k\alpha$, $N^* = kQ/m$ we get ($\vec{z} = \{ z_1 = R - R^*,$ $z_2 = N - N^* \}$) :

$$\frac{\partial \vec{z}}{\partial t} = A\vec{z} + D\frac{\partial^2 \vec{z}}{\partial x^2} , \tag{16}$$

where

$$A = \begin{Vmatrix} -\alpha k Q/m & -m/k \\ \alpha k^2 Q/m & 0 \end{Vmatrix} \qquad D = \begin{Vmatrix} 0 & -m\sigma^2/2k \\ \alpha k^2 Q\sigma^2/2m & 0 \end{Vmatrix}$$

Since the eigenvalues of D are pure imaginery the system (15) is not parabolic according to Petrovsky. Used an analogy with quantum mechanics we refer to these systems as "the Schroedinger systems", the solutions of its can possess rather interesting properties. In particulary there may exist spatially periodic solutions and spatial chaos. If we come back to the origin system (14) of integral- -differential equations we can prove that this system has the spatially periodic discontinuous solutions belonging the type of finite functions. Such the solutions may describe the so-called "pathchiness" or "self-thinning" processes in plant communities when from an initial continuous /every- where compact/ distribution of biomass there arises a stable discrete structure /in details see [2]/.

6. Geography of Mathematical Ecology in USSR

Above I have tryed to show style and methods which were typical for the soviet schools of mathematical ecology. Here I say some words about several soviet laboratories and scientific groups.

1. Department of Mathematical Modelling in Ecology and Medicine, Computing Center of USSR Acad. Sci. /Moscow/, Yu. M. Svirezhev, D. O. Logofet, G. A. Alexandrov, M. A. Semenov, A. A. Voinov and others.

The main topics: stability of ecosystems and biological
communities, non-linear waves and dissipative stuctures
in the models of space-distributed ecosystems, catastrophes,
chaos and strange attractors - complex dynamics of simple
models, stochastical models, problems of optimal harvesting.
Simulation modelling of global biospheric processes. Thermo-
dynamics and ecology. Modelling of fresh water-body systems
and agroecosystems. Mathematical genetics /see [1 - 5],
[12], [13]/

2. Scientific Computing Center of USSR Acad. Sci. Bio-
logical Center /Puschino, near Moscow/. A. D. Basykin,
A. M. Molchanov, A. I. Khibnik, Yu. A. Kuznetsov. The main
topics: application of qualitative methods of differential
equations to the analyse of ecological models /see [9]/.

3. Laboratory of Monitoring of All-Union Committee for
Meteorology and Environment Control /Moscow/. S. M. Semenov,
F. N. Semevsky. The main topics: application of general
theory of dynamic systems to ecological models, [6].

4. Laboratory of Bioenergetics, Geographical faculty
of Lomonosov Moscow State University. V. V. Alekseev,
I. I. Kryshev, Yu. A. Loskutov. The main topics: statistical
mechanics of ecological systems, strange attractors in multi-
species communities.

5. Institute of Agrophysics, All-Union Acad. of Agricul-
tural Sciences /Leningrad/. R. A. Poluektov, Yu. A. Pykh,
I. A. Vol., L. R. Ginzburg and A. Gimmelfarb are working
in USA now. The main topics: stability problems in the
models of ecology and population genetics. Stochastical
models. Crop simulation modelling /see [7], [11]/.

6. Institute of Applied Mathematics and Mechanics of
Rostov-Don State University. A. M. Gorstko, G. A. Markman,
Yu. A. Dombrovsky.

The main topics: optimal control of ecological systems, dissipative structures in ecology. Simulation modelling of marine ecosystems.

7. Mathematics Faculty of Jaroslavl State University. Yu. C. Kolesov. "Time-Lag" ecological models /see [16]/.

8. Center for Ecological Studies of Lithuanien Acad. Sci. /Lithuania/. D. I. Shvitra. "Time-Lag" ecological models /see [16]/.

. 9. Theoretical Department of Institute of the Southern Seas Biology, Ukrainen Acad. Sci. /Sevastopol/. V. Belyaev, N. Abrosov. The main topics: role of physical processes in ecology, models of competitive communities, simulation modelling of marine ecosystems.

10. Krasnoyarsk Center of Siberian Branch USSR Acad. Sci. Intsitute of Biophysics, N. S. Abrosov, N. S. Pechurkin, A. S. Dergemendgi, R. G. Khlebopros, L. V. Nedorezov. The main topics: modelling of microbial communities, competitive ecosystems, the application and development of Limiting Factors Principle /L-systems/. Models of insect populations /see [8], [14] /.

11. Institute of Authomatics and Informatics of Far-Eastern Branch USSR Acad. Sci. /Vladivostok/. A. I. Abakumov, E. J. Frisman. The main topics: models with non-overlapping generations, optimal harvesting /see [10], [15]/.

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    "Population Dynamics of Forest Insect", "Nauka",
    Novosibirsk, 1984.

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    "Disrete Models of Population Dynamics and Optimi-
    zation of Catchment", "Nauka", Moscow, 1979.

16. Kolesov Yu. S., Shvitra D. I. "Self-Oscillations
    in Systems with Time-Lag", Vilnus, 1979. Also I
    would recommend the annual collection works: "The
    problems of ecological monitoring and modelling of
    ecosystems", Hydrometeoizdat", Leningrad, which
    were issued since 1978, and the collection works:
    "Dynamics of Biological Populations", which were
    issued by Gorky State University.
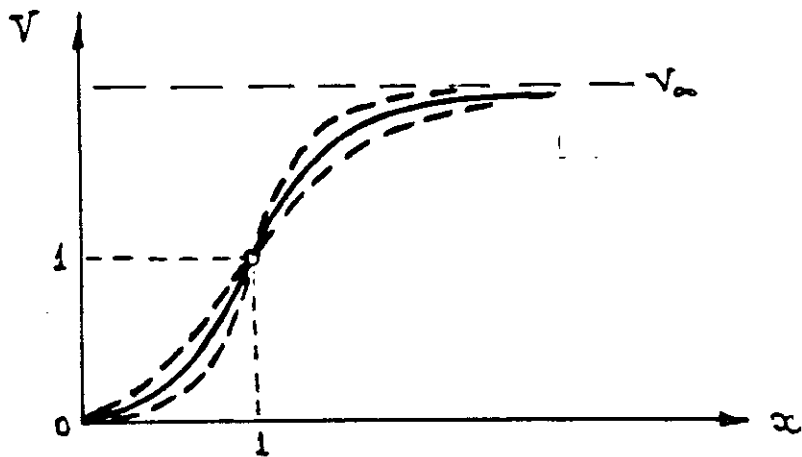
Fig. 1. The small „movement aboutⁿ of trophic function
— before , --- after.
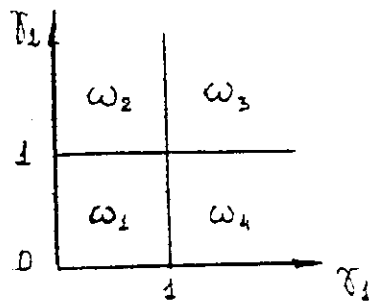
a)
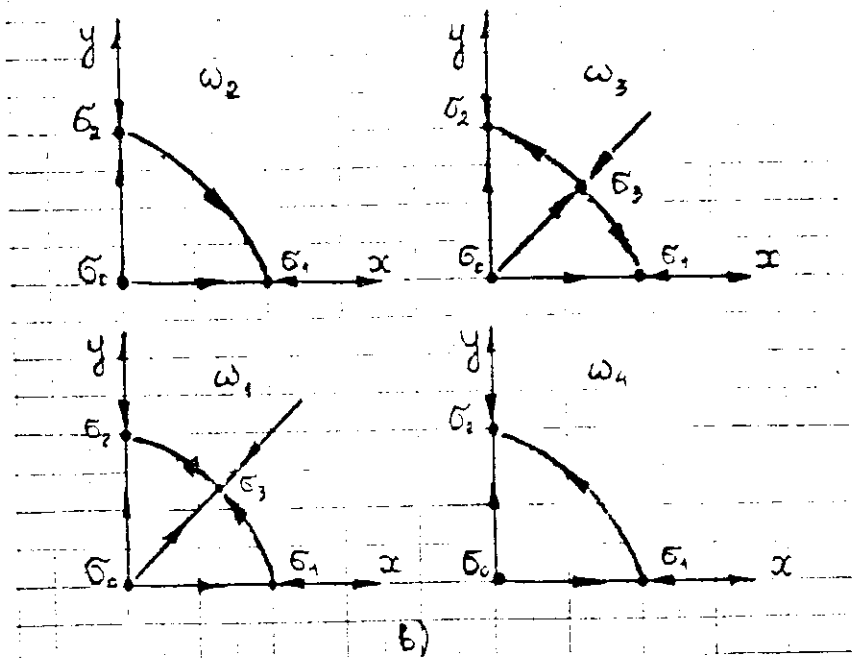
b)

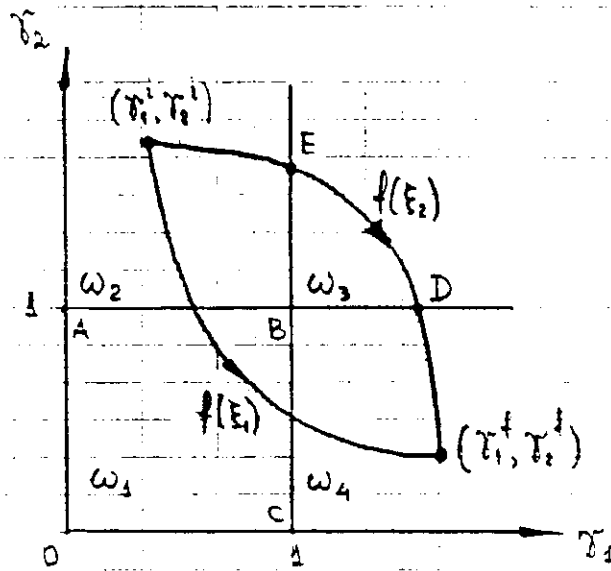Fig. 2. The stability domains and phase portraits of system (7)

Fig. 3. The projection of phase trajectories of the system (7) + (8) on Γ: various types of „slow" dynamics.
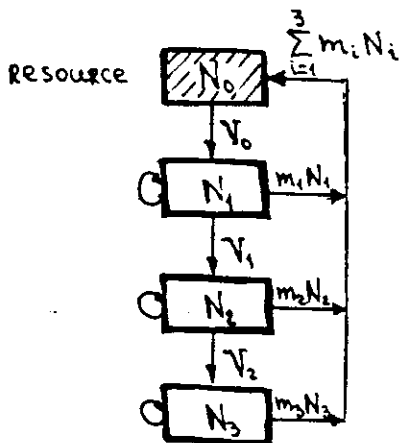

Fig. 4. Closed trophic chain with 3 levels.
N_i is the biomass of ith level; V_0, V_i, $i = 1,2$ are the corresponding trophic functions; m_i are the mortality coeffi-cients.

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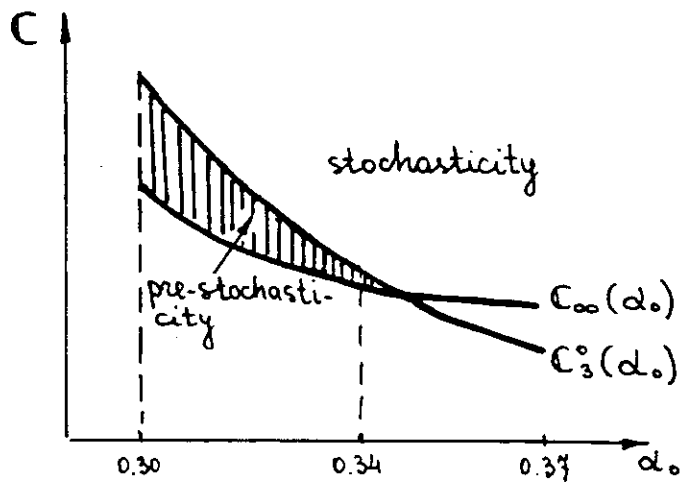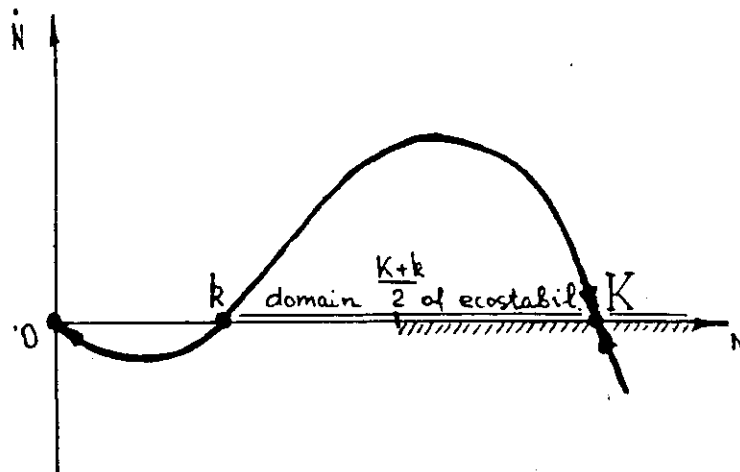Fig. 5. The domains of various dynamic regimes of the system (9).

Fig. 6. Phase portrait of equation (10').

$=\!=$ domain of ecostability

/////// estimation of this domain
(by means of the Chetaev-malkin theorem)