The recent years witnessed a real outburst in the number of works on mathematical modelling in ecology. Of course, one may suppose that this is the result of a sharp rise of interest in ecological problems in general and the popularity of the subject. But this is only one aspect. The other reason is that ecology represents a branch of biology (probably, together with genetics and the theory of evolution) that uses mathematical methods on such a wide scale that we may now speak about the birth of a new science — mathematical ecology.

What does mathematics get from this synthesis?

Firstly, ecology gives new fields for applying classical mathematical methods.

Secondly, ecology draws the attention of mathematicians to many problems the interest in which previously subsided due to the lack of either encouraging results or useful practical applications.

Finally, ecology offers new possibilities of posing mathematical problems.

Mathematics in turn provides a method of research without which many investigators of theoretical ecology would be in danger of falling into obscure sophistications, loquacious but fruitless.

To substantiate the above claims we shall illustrate each point by concrete examples.

1. “Predator–prey” system—a classical object of mathematical ecology

One of the most popular models in mathematical ecology is the model of a two-population system, one of which being food for the other. Such an interaction is widely spread in nature, it is called “predator–prey” interaction. The model itself is described by a system of two ordinary differen-
tial equations of the form

\[
\frac{dx}{dt} = a(x)x - V(x)y,
\]

\[
\frac{dy}{dt} = kV(x)y - my,
\]  

(1.1)

where \(x(t)\) and \(y(t)\) are the numbers of preys and predators, respectively, and the functions \(a(x)\) and \(V(x)\) must satisfy some conditions to be ecologically sensible. Evidently, system (1.1) represents a wide field of applications of the methods of qualitative theory of differential equations. Let us review in brief some results obtained (see for example [7], [8]).

One of the basic problems of ecology is: "Can the predator control the prey population?" Since \(a(x)\) is a function describing the prey self-regulation, when we investigate this problem it is natural to assume that \(a \rightarrow \text{const}\), i.e., in the absence of the predator the prey population grows according to the Malthus principle. In this case the dynamics of the system significantly depends on the form of the trophic function, the rate of prey consumption by the predator. All the variety of trophic functions can be divided into two classes (see Fig. 1). Class I is characteristic for invertebrate predators, whereas Class II — for organisms, exhibiting a rather complex behaviour (e.g., the ability to learn). Many vertebrates manifest such a behaviour. We shall refer to the predators of Class I and Class II as "silly" and "clever" respectively.

An analysis of system (1.1) for \(V(x)\) belonging to these two classes has shown that the "silly" predator cannot control the prey population,

![Fig. 1. Trophic functions classes: I — “silly” predator, II — “clever” predator.](image)
i.e., the non-trivial equilibrium \( \{x^*, y^*\} \) of system (1.1) is always globally unstable. If the predator is "clever" (i.e., \( V(x) \) belongs to Class II), then the behaviour of the system is much more interesting. In this case either a stable non-trivial equilibrium is observed or there arise limit cycles in its neighbourhood. Let \( S_C \) stand for the region bounded by the Volterra oval

\[
\left( \frac{e^x}{X} \right)^a \cdot \left( \frac{e^y}{Y} \right)^a = C, \quad X = x/x^*, \quad Y = y/y^*
\]

with the centre at the point \( \{x^*, y^*\} \). Let us assume that, in a neighbourhood of \( x^* \),

\[
\left| w(x) = \frac{V(x)x^*}{V(x^*)x} \right| \sim 1.
\]

Hence \( |w(x) - 1| \sim \epsilon \). Consider the integral

\[
\Psi = \int \int_{S_C} \left[ \frac{V(x)}{x} \right] \, dx \, dy.
\]

Then if there exists a \( C^* \) such that

\[
\Psi(C^*) = 0, \quad \Psi'(C^*) \neq 0,
\]

then there exist \( \mu, A > 0 \) such that:

(a) for every \( \epsilon < A \), system (1.1) with \( \alpha = \text{const} \), has a limit cycle in the \( \mu \)-neighbourhood of the Volterra oval with a constant \( C^* \); the limit cycle tends to the oval as \( \epsilon \to 0 \).

(b) this cycle is stable when \( \Psi''(C^*) > 0 \) and unstable when \( \Psi'(C^*) < 0 \).

The transformation of variables in (1.1)

\[
\xi = \ln(x/x^*), \quad \eta = \ln(y/y^*), \quad \tau = \alpha t
\]

gives

\[
\frac{d\xi}{d\tau} = 1 - w(\xi) e^\eta, \quad \frac{d\eta}{d\tau} = 2 [w(\xi) e^\xi - 1], \quad \delta = \frac{m}{\alpha}.
\] (1.2)

Let \( w(\xi) = 1 + \epsilon \varphi(\xi) \) where \( \epsilon \) is a small parameter. Actually, \( \epsilon \varphi(\xi) \) represents the deviation of the more realistic trophic function from a hypothetic one of the Volterra (linear) type. The application of the Krylov–Bogolubov method to the system gives the following results ([5], [7], [8]):
Let

\[ a = \varphi'(0), \quad b = \frac{1}{\delta} (\delta \varphi' + \varphi'''), \quad c = \frac{1}{192} (\delta^2 \varphi' + 2 \delta \varphi'' + \varphi'') \]

Then depending on the signs of \( a, b, c, D \) we get different variants of the system’s behaviour (\( r \) being the amplitude of the limit cycle).

1. \( a, b, c > 0 \) or \( a, c > 0; b, D < 0 \): \( r = 0 \) — stable equilibrium with no limit cycles.
2. \( a, b > 0, c < 0 \) or \( a > 0; b, c < 0 \): \( r = 0 \) — stable equilibrium with an unstable limit cycle \( r = r_2 \).
3. \( a, c, D > 0; b < 0 \): \( r = 0 \) — stable equilibrium, \( r = r_1 \) — stable cycle, \( r = r_2 \) — unstable cycle \( (r_1 > r_2) \).
4. \( a, b, c < 0 \) or \( a, c, D < 0; b > 0 \): \( r = 0 \) — unstable equilibrium, \( r = r_2 \) — stable cycle with self-exciting from zero.
5. \( a, b < 0; c > 0 \) or \( a < 0; b, c > 0 \): \( r = 0 \) — unstable equilibrium, \( r = r_1 \) — stable cycle with self-exciting.
6. \( a, c < 0; b, D > 0 \): \( r = 0 \) — unstable equilibrium, \( r = r_1 \) — stable cycle with self-exciting, \( r = r_2 \) — unstable cycle \( (r_2 > r_1) \).

Suppose now that system (1.2) is in a random environment. Then the equations for the amplitude and phase are

\[
\frac{dr}{d\tau} = -\frac{er}{2} (a + br^2 + cr^4) + \sigma_1 n_1,
\]

\[
\frac{d\Phi}{d\tau} = \sqrt{\delta} + \frac{e}{2} (a + br^2 + cr^4) + \sigma_2 n_2,
\]

where \( n_1 \) and \( n_2 \) are \( \delta \)-correlated white noises of constant intensity.

The expression for the stationary density of the probability of the amplitude is

\[
P_0(r) = \text{const} \cdot r \cdot \exp \left\{ -\frac{r^2}{\sigma_1^2} \left( a + \frac{b}{2} r^2 + \frac{c}{3} r^4 \right) \right\}.
\]

The phase is distributed uniformly (if we neglect the phase overlap). The function will have either one maximum in the neighbourhood of the equilibrium or a stable cycle, or two maxima, the latter case being possible only in the presence of two limit cycles: an unstable inner one and a stable outer
one. Consequently, the predator–prey system in random environment over large time intervals reveals four types of behaviour, namely:

1. The trajectories of the system leave the neighbourhood of the equilibrium, either quickly if there is no stable cycle in the neighbourhood or slowly if there are a stable inner cycle and an unstable outer cycle; the system will remain in the neighbourhood of the stable cycle for some time.

2. The diffusion of the trajectories around the stable equilibrium takes place if there are no limit cycles. The most probable values of the amplitudes of random oscillations lie in the neighbourhood of the stable point.

3. If the equilibrium is unstable and the stable limit cycle exists, then it becomes fuzzy, the stationary distribution being unimodal and its maximum lying to the right of the limit cycle amplitude.

4. The diffusion of the trajectories with the most probable values of the amplitude of the random oscillations lies in the neighbourhood of the stable equilibrium and the stable outer limit cycle (intensity of perturbations is sufficiently low).

Now let us try to answer another question: how much does the population dynamics of the system depend upon the ethological (behavioural) characteristics of the prey? The question is of importance as we have found out that the dynamics of the system depends essentially upon the fine structure of the trophic function, the latter in turn being a result of the predator's hunting strategy.

Now we pass to the behaviour of the prey. The simplest hypothesis about the “reasonableness” of the behaviour of the prey is the hypothesis of a collective behaviour (mutual aid) improving (up to a certain limit)
characteristics of the prey population, for example the relative rate of its growth. If we accept this hypothesis, the function \(a(x)\) must take the form given in Fig. 2. But making this aspect of the problem more complex, we simplify the other one: \(V(x) = \beta x\), i.e., the trophic function is of the Volterra type. Then (1.1) may be written in the form

\[
\frac{dx}{dt} = x[a(x) - \beta y], \quad \frac{dy}{dt} = y(k\beta x - m). \tag{1.5}
\]

Denote \(x^* = m/k\beta, y^* = a(x^*)/\beta, \beta_0 = m\kappa/x_0\). Let the parameter \(\beta\) change in a small neighbourhood \(\beta_0\), so that \(\beta^2 > m/4k^2 \cdot \left[\frac{a'(x^*)}{a(x^*)}\right]^2\).

i.e., small variations of \(\beta\) are considered. Since we deal here with a typical Hopf bifurcation, by applying a more or less standard technique we get the following picture of the dynamic behaviour of the system:

(a) for \(\alpha''(x_0)x_0 < -2\alpha''(x_0)\) and for \(\beta > \beta_0\) in the neighbourhood of \(\{x^*, y^*\}\) there appears a stable limit cycle,

(b) for \(\alpha''(x_0)x_0 > -2\alpha''(x_0)\) and for \(\beta < \beta_0\) in the neighbourhood of \(\{x^*, y^*\}\) there appears an unstable limit cycle. It should be noted that \(\beta < \beta_0\) if \(x^* > x_0\). Since the trajectories (1.5) are bounded and point \(\{x_1, 0\}\) is a saddle point, this unstable cycle is certainly surrounded by a stable limit cycle. The question of the existence of a third, a fourth, etc. limit cycles remains open.

Since both the trophic function \(V(x)\) and the prey self-regulation function \(\alpha(x)\) are nothing but the aggregated averaged description of the ethological (behaviour) characteristics of predator and prey, the foregoing results lead us to the following ecological conclusion: the complex ethology manifesting itself at the level of individuals gives rise to a great diversity of the dynamic behaviour of populations, even in such an ecologically simple system as the “predator–prey” one.

It appears that we have succeeded in illustrating the possible applications of classical methods of the qualitative theory to a classical ecological problem. Here we shall not dwell upon the ecological interpretations of the mathematical results obtained. We shall only mention that these conclusions could not have been obtained in other ways. Certainly, there remain numerous other problems which are still to be solved and we hope that we have managed to draw attention to them.
2. Lagrange stability and ecological stability

In the previous section we used well-known mathematical methods for solving ecological problems; now we shall show how ecological "demands" make it possible to treat an old mathematical problem (not considered to be of interest before) in a new light.

We begin with a small ecological essay. One of the most common definitions of stability of the biological community is the requirement to maintain the number of species. It means that, on the one hand, none of the species dies out, and on the other, none of them grows infinitely.

If this happens in a model, the model is inadequate. Let the population sizes of species in the community be non zero and not grow to infinity and suppose that there exists no stable non-trivial equilibrium. Nevertheless, none of the species dies out in such a community. It means that the trajectories of the model are bounded from above and below in the positive orthant. However, if we consider here the Lyapunov stability, the community will be unstable; on the other hand, it will be stable if stability is understood ecologically.

Such a type of stability has long been known and is referred to as the Lagrange stability. However, while Lyapunov's theory is well-developed, we cannot say that about the Lagrange stability, though the latter is more suitable for ecology.

Suppose that the dynamics of a biological community is given by a system of ordinary differential equations:

\[
\frac{dN_i}{dt} = F_i(N_1, \ldots, N_n), \quad i = 1, n
\]

(2.1)

with initial conditions \(N_i(0) = N_i^0\) where \(N_i(t)\) are the sizes of the populations in the community. For our model to be biologically sensible, the following conditions must be fulfilled: \(N_i(t) \geq 0, \ i = 1, n\) for all \(t \geq 0, N_i^0 \geq 0\), meaning that the set \(P^n\) (i.e., the positive orthant of an \(n\)-dimensional space) is an invariant set for system (2.1).

Let \(\Omega_0^n\) and \(\Omega^n\) be closed finite domains lying within \(P^n\). We shall call a community, described by the model (2.1), ecologically stable, if for any \(\hat{N}^0 = \{N_1^0, \ldots, N_n^0\} \in \Omega_0^n\) there exists \(\Omega^n(\Omega_0^n)\) such that \(\hat{N}(t) = \{N_1(t), \ldots, N_n(t)\} \in \Omega^n\) for all \(t > 0\), or in formal terms:

\[
\forall \hat{N}^0 \in \Omega_0^n \exists \Omega^n(\Omega_0^n) \subseteq \text{Int}P^n: \forall t > 0, \ \hat{N}(t) \in \Omega^n.
\]
Since all $N^0_i$ are positive, then by substituting $\xi_i = \ln(N_i/N^0_i)$ in (2.1), we get
\[ \frac{d\xi_i}{dt} = \varphi_i(\xi_1, \ldots, \xi_n; N^0_1, \ldots, N^0_n), \quad i = 1, n \] (2.2)
with initial conditions $\xi_i(0) = 0, i = 1, n$.

Evidently, for $N_i(t) \to +\infty$ we have $\xi_i(t) \to +\infty$ and for $N_i(t) \to 0$ we have $\xi_i(t) \to -\infty$ (for finite $N^0_i$). Thus the solutions of system (2.2) are defined in the whole phase space $R^n$ (not only in the positive orthant). Since the conditions $\varphi_i(0, \ldots, 0; N^0_1, \ldots, N^0_n) = 0$ are not obligatory, i.e., $\xi^*_i = 0, i = 1, n$ is not the solution to (2.2), we rearrange (2.2) to the form
\[ \frac{d\xi_i}{dt} = \Phi_i(\xi_1, \ldots, \xi_n; N^0_1, \ldots, N^0_n) + B_i, \quad i = 1, n, \] (2.3)
where
\[ \Phi_i = \varphi_i(\xi_1, \ldots, \xi_n; N^0_1, \ldots, N^0_n) - \varphi_i(0, \ldots, 0; N^0_1, \ldots, N^0_n), \]
\[ B_i = \varphi_i(0, \ldots, 0; N^0_1, \ldots, N^0_n). \]

If we now formulate for (2.3) the problem of the Lyapunov stability of the trivial solution $\xi^*_i = 0, i = 1, n$ under permanent perturbations and find the domain of stability in the space of parameters $\{N^0_1, \ldots, N^0_n\}$, then the solution of this problem will imply the solution of the problem of ecological stability in system (2.1). The proof of this statement obviously follows from the Lyapunov stability definition and the properties of the mapping $P^n \Rightarrow R^n$.

Thus we have reduced the analysis of the Lagrange stability to the problem of the Lyapunov stability. By Malkin’s theorem [4] the solution $\xi^*_i = 0, i = 1, n$ is Lyapunov stable if it is asymptotically stable for the system $\xi_i = \Phi_i(\xi_1, \ldots, \xi_n; N^0_1, \ldots, N^0_n), i = 1, n$, with $B_i$ sufficiently small.

Let us clarify all the above by an example. Suppose the population dynamics is given by the equation
\[ \frac{dN}{dt} = rN \left( 1 - \frac{N}{K} \right) (N - k), \quad 0 < k < K \] (2.4)
(this is the so-called population with lower threshold number). The phase picture of this equation is presented in Fig. 3. Evidently $N(t) \to 0$ for
\( N_0 < h \) and the population is destined to extinction, i.e., there is no ecological stability.

On the other hand, the equilibrium \( N^* = K \) is asymptotically stable. Let us see whether we can prove the ecostability of this population, by using the method described above. Substituting \( \xi = \ln \left( \frac{N}{N_0} \right) \) we get

\[
\frac{d\xi}{dt} = r \left( 1 - \frac{N_0 e^\xi}{K} \right) \left( N_0 e^\xi - h \right) = \Phi(\xi, N_0) + B,
\]

\( \Phi(\xi, N_0) = \frac{rN_0}{K} (K + h - 2N_0) \xi + o(\xi), \)

where

\[
B = r \left( 1 - \frac{N_0}{K} \right) (N_0 - h).
\]

It is obvious that the solution \( \xi^* = 0 \) for \( \dot{\xi} = \Phi(\xi, N_0) \) is asymptotically stable for \( N_0 > \frac{1}{2}(K + h) \). Besides, if, for example, the Malthusian parameter \( r \) is small, then \( B \) is small, too. Then, according to the Malkin theorem, the trivial solution \( \xi^* = 0 \) is stable (in Lyapunov's sense) under a permanent perturbation \( B \). Consequently, we can state that for \( N_0 > \frac{1}{2}(K + h) \), the function \( N(t) \) will be bounded from above and below for all \( t > 0 \), i.e., the population will be ecologically stable.

Note that by using this method we have obtained a stronger restriction, namely the population is ecologically stable for all \( N_0 > h \). This condition is after all natural, since the Lyapunov stability conditions are the sufficient ones.

Clearly, the requirement for the non-trivial equilibrium \( \bar{N}^* \) in (2.1) (if it exists) to be stable, is not, in general, a necessary condition for the ecostability. However, there exists quite a wide class of ecological models.
in which the conditions of ecological stability and the existence of a positive stable equilibrium in Lyapunov's sense turn out to be equivalent. This class contains the communities called conservative and dissipative (according to Volterra) [7], [8]. We mean here systems of the type

\[ \frac{dN_i}{dt} = N_i \left( c_i - \sum_j \gamma_{ij} N_j \right), \quad i, j = 1, n \]

in which there is a single positive equilibrium \( \vec{N}^* = \{N_1, \ldots, N_n\} \) and the quadratic form \( \sum_i \sum_j a_{ij} N_i N_j; \quad i, j = 1, n \) (where \( a_{ij} > 0 \)) is either identically zero or positive definite.

3. Competition for resource, the self-thinning out problem and "Schrödinger" systems

In this section we shall try to show how the attempts to solve some ecological problems result in new non-traditional formulations of mathematical problems.

Suppose we have the biomass distribution \( N(x, t) \) and the consumed resource (nutrients) distribution \( R(x, t), -\infty < x < +\infty \). We assume that the uptake rate of the resource, located at point \( \xi \) by the unit of biomass, located at point \( x \), is equal to

\[ P(|x - \xi|) V[R(\xi, t)]. \]

Here \( P(|x - \xi|) \) can be represented by the density of the normal distribution with the centre at the point \( x \) and variation \( \sigma^2 \). Then the equations of this model will take the form

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

\[ \frac{\partial N(x, t)}{\partial t} = k \int_{-\infty}^{+\infty} P(|x - \xi|) V[R(\xi, t)] N(x, t) d\xi - m N(x, t). \] (3.1)

Here \( Q \) is the input flow of resource, \( k \) is the efficiency, and \( m \) is a coefficient of natural mortality. Considering \( \sigma \ll L \), where \( L \) stands for the specific scale in the problem (which corresponds to the assumption that the radius of the effective interaction between the consumer and the resource is small),
we bring (3.1) to its asymptotic analogy:

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

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

(3.2)

This system is interesting in itself but to understand better what it really is we shall take \( V(R) = aR \) and linearize it in the neighbourhood of a spatially homogeneous stationary solution \( \{ R^*, N^* \} \) where \( R^* = m/\alpha \), \( N^* = kQ/m \). Denoting \( Z_1 = R - R^* \) and \( Z_2 = N - N^* \) and considering \( Q, m, k \) to be constant, we get

\[
\frac{\partial \tilde{Z}}{\partial t} = A \tilde{Z} + D \frac{\partial^2 \tilde{Z}}{\partial x^2}, \quad \tilde{Z} = \{ Z_1, Z_2 \},
\]

(3.3)

where

\[
A = \begin{bmatrix}
-akQ/m & -m/k \\
ak^2Q/m & 0
\end{bmatrix}, \quad D = \begin{bmatrix}
0 & -m\sigma^2/2k \\
ak^2Q\sigma^2/2m & 0
\end{bmatrix}.
\]

Since the eigenvalues of the matrix \( D \) are purely imaginary, system (3.3) is not parabolic, according to Petrovsky. Similar equations arise in quantum mechanics and therefore we shall refer to these systems (3.1)–(3.3) as “Schrödinger” ones. Practically there is no theory of such systems, whereas their solutions (if they exist) may have fairly interesting properties. In particular, there may exist spatially periodic discontinuous solutions belonging to the type of finite functions. Such solutions describe the so-called “self-thinning out” processes in plant communities when from an initial everywhere continuous distribution of biomass there arises a stable discrete structure. However, these are only hypotheses and this new mathematical object — “Schrödinger systems” — should be subjected to profound investigation.

4. Models of spatially distributed ecosystems—ecologically active media

Account of the movements of individuals over the areal forces us to consider a spatial generalization of the “predator–prey” or “resource–consumer” models. So this naturally gives rise to the concept of an ecologically active medium, in which there may occur either the propagation of nonlinear population waves or the rise of stationary stable distributions of popula-
tions nonhomogeneous in the space (even in a homogeneous environment),
the so-called dissipative or spatial structure (SS) [1], [3].

Since random migration of individuals is quite well described by
the diffusion terms (where the “diffusion” coefficients are uniquely defined
by the radii of individual activity), the models of spatially distributed
ecosystems are systems of the quasi-linear parabolic type

$$\frac{\partial N_i}{\partial t} = D_i \Delta N_i + f_i(N_1, \ldots, N_n), \quad i = 1, n, \quad (4.1)$$

where $N_i(\vec{x}, t)$ are the population densities for the $i$th species at point
$\vec{x} = \{x_1, \ldots, x_m\} \in \Omega$, $\Omega$ being the total areal of the ecosystem. The func­
tions $f_i$ stand for the local interactions of populations. On the boundary $\Gamma$
of the domain, the boundary conditions are to be specified to provide
a correct solvability of the initial value problem, for instance the condition
of the non-permeability of the boundary

$$\frac{\partial N_i}{\partial \vec{n}} \bigg|_{\Gamma} = 0, \quad \vec{n} \text{ is a normal to } \Gamma. \quad (4.2)$$

For $n = 1$ there are classical results indicating the absence of SS in convex
domain under conditions (4.2). Now we shall quote the result generalizing
the above assertion [4].

Let $f(N)$ be such that there are no two roots of equation $f(N) = 0,$
$N_1^* < N_2^*$ such that $F(N) = \int_{N_1^*}^{N_2^*} f(N) dN$ for $N \in (N_1^*, N_2^*)$ and $F(N_2^*) = 0.$
Then no stationary bounded solution of the equation

$$\frac{\partial N}{\partial t} = \Delta N + f(N), \quad \vec{x} \in \mathbb{R},$$

except the constant one is stable. The stability is understood here in the
sense of the norm $C(\mathbb{R})$.

It follows that the search for SS should begin either on areas of a more
exotic configuration (e.g., non-convex) or for interacting populations
($n \geq 2$). The most natural approach is based on the investigation of the
character of stationary bifurcation of the solution under variations of
$D_i$ in (4.1). Let $n = 2.$ Then (4.1) and (4.2), in the neighbourhood of the
nontrivial stationary distribution \( \{N^*_1, N^*_2\} \), take the form \( (\dot{u} = N_i - N^*_i) \):

\[
\frac{\partial \hat{u}}{\partial t} = D(\lambda) \Delta \hat{u} + A \hat{u} + g(\hat{u}), \quad \left. \frac{\partial \hat{u}}{\partial n} \right|_r = 0,
\]

(4.3)

where \( A = [a_{ij}] \) is the matrix of the linearized system, \( D = \text{diag} \{1, \lambda\} \), \( g(\hat{u}) \) is a nonlinear component, considered to be small. It turns out that necessary and almost always sufficient conditions for the existence of a critical value \( \lambda_0 > 0 \), in the neighbourhood of which there exists a family of stationary spatially nonhomogenous solutions of (4.3) are the following:

(1) \( \det A > 0 \),
(2) \( \text{tr} A < 0 \),
(3) \( a_{11} < 0 \)

if \( a_{22} > 0 \) or \( a_{11} > |\lambda_1| \), where \( \lambda_i, i = 0, 1, \ldots \) is the \( i \)th eigenvalue of the Laplace operator in the domain \( \Omega \).

If the domain \( \Omega \) is not too symmetrical, one of the two semibranches of this family corresponds to the stable solution, i.e., to SS. If this is not the case (e.g., the domain \( \Omega \) is one-dimensional) then additional verification of stability is needed.

Among the systems of the (4.1)-type a special place is held by those having some \( D_i \) equal to 0. Such systems are not parabolic in Petrovsky's sense and that is why this case gives rise to complex mathematical problems connected with the existence and stability of solutions. Here is one of the results on linear stability of a stationary spatially homogeneous solution.

Let system (4.1), linearized in the neighbourhood of that solution, have the form \( (\dot{u} = N_i - N^*_i) \):

\[
\frac{\partial \hat{u}}{\partial t} = D \Delta \hat{u} + A \hat{u}, \quad \hat{u}(\vec{x}, t) \in \mathbb{R}^n, \quad \vec{w} \in \mathbb{R}^m,
\]

(4.4)

where \( A \) and \( D \) are real \( n \times n \) matrices, \( D \) being diagonal with non-negative elements. If there is a \( \delta > 0 \) such that for each \( s \geq 0 \) the eigenvalues of the matrix \( A + \delta E - Ds \) lie in the left half-plane, then the trivial solution of (4.4) is stable with respect to the perturbations \( \hat{u}_0(\vec{x}) \in \mathcal{O}^\infty(\mathbb{R}^n) \).

Note, that from the ecological point of view such an approach is by no means exotic since \( D_i = 0 \) correspond to species of plants. As an example let us consider the "resource-consumer" system with immovable resource.

\[
\begin{align*}
\frac{\partial N}{\partial t} &= \dot{Q} - V(R)N, \\
\frac{\partial R}{\partial t} &= D \Delta N + [kV(R) - m]N.
\end{align*}
\]

(4.5)
Here $R(x,t)$ and $N(x,t)$ are the densities of the resource and consumer respectively, given in the one-dimensional infinite areal. Applying the previous statement to system (4.5) one can easily prove the linear stability of the stationary distribution

$$N^* = kQ/m, \quad R^* = V^{-1}(m/k).$$

In the case of a local outbreak of the consumer population this distribution is settled following the wave, propagating at a velocity $v = 2\sqrt{D[kV(\infty) - m]}$. If $Q = 0$ (i.e., the resource is unrenewable) and the initial resource density is $R_0$, then the outbreak of the consumer population generates a single wave, spreading at a velocity of $v = 2\sqrt{D[kV(R_0) - m]}$ [1].

However, if the areal contains so-called “dead zones”, i.e., regions $x$ in which $R_0(x) = 0$, then the wave velocity in the zone will be close to the value

$$v_z = [kV(\infty) - m] \cdot \sqrt{D/kV(\infty)}.$$

What is curious is that $v_z$ does not depend on the size of the zone.

And what is the picture if the resource is being restored according to the Malthusian or logistic law, i.e., if

$$Q(R) = a(R)R, \quad a(0) > 0, \quad a'(R) < 0, \quad a(R^*) = 0?$$

This model is nothing but a spatial generalization of the “predator–prey” system. It turns out that for appropriate parameter values in automodel variables $\xi = x + vt$ there exist periodic solutions. In real variables they are represented by “wave packets” or “wave pattern” — successions of running waves. This means that the local outbreak of the consumer arising at a certain time starts to work as a generator of waves propagating over an ecologically active medium occupied by the consumer. The minimum velocity of those waves is

$$v_{\text{min}} = 2\sqrt{D[kV(R^*) - m]}. $$

The topic is discussed in detail in our paper [6].

In this section we have attempted to show how the study of nonlinear waves (the dissipative structures may also be included in this class) in models of spatially distributed ecosystems gives rise to a new class of problems which are of both theoretical and practical interest. The main problem here is to prove the convergence of the solution to a stationary wave (being at rest or running) for a sufficiently wide class of initial
conditions. This problem is solved only for very simple models (cf. the classical works of Kolmogorov, Petrovsky and Piskunov), thus representing a wide field of action. Another important class of problems is the generation and propagation of waves in active two-dimensional ecological media in a plane areal.

It seems that nothing has been done in this direction, except for a lot of computer experiments.

5. Strange attractors in simple ecosystems

Recently it has become quite popular to look for examples of complex dynamic behaviour in systems of ordinary differential equations which are known as strange attractors. Such behaviour does not appear to be very exotic in ecology. Consider the model of a simple ecosystem: a closed trophic chain with three levels. If $N_0$ is the resource concentration (e.g., nutrients) and $N_i$ are the biomasses in the trophic levels, then this chain is described by the equations

$$\frac{dN_i}{dt} = V_{i-1}(N_{i-1})N_i - V_i(N_i)N_{i+1} - m_iN_i,$$

$$i = 1, 2, 3, \quad N_4 = 0, \quad N_0 = C - (N_1 + N_2 + N_3). \quad (5.1)$$

Here $V_i(N_i)$ are trophic functions, $C = \text{const}$ is the total amount of matter in the system. Let

$$V_0 = a_0N_0, \quad V_i(N_i) = \frac{aN_i}{1 + bN_i}, \quad i = 1, 2, 3.$$ 

For this case B. I. Yatsalo and myself succeeded to prove analytically the possibility of generating a cycle as a result of the Hopf bifurcation and also the existence of a stable limit cycle for large $a_0 \sim 1/\varepsilon$. The system was studied numerically for $m_1 = 0.1$, $m_2 = m_3 = 0.2$, $a = b = 0.2$ and for different values of the parameters $C$ and $a_0$ ($0.2 < a_0 < 0.38$). The system develops in the following way: for $C = C_1 = C_3(a_0)$ the Hopf bifurcation results in the stable limit cycle $\gamma_1 = \gamma_1(C)$; for $C = C_2$ two cycles are generated: the stable $\gamma_2$ and the unstable $\gamma_3$ (i.e., for $C \to C_2^+$ they unite through $+1$); for $C = C_3$ the cycles unite and vanish. Consequently the bifurcation doubling takes place at points $C_1$, $C_2$, $C_3$, i.e., for $C = C_1$ the cycle $\gamma_2$ loses stability, its multiplicator passes through $-1$ and in the
neighbourhood there arises a stable cycle with a double period which goes through the same bifurcation at $C = C_2$, etc., where $C_n \rightarrow C_\infty = C_\infty(a_0)$. Taking $a_0 = 0.34$ we get the following values of the parameters: $C_1^0 = 9.447$, $C_2^0 = 30.55$, $C_3^0 = 36.251$, $C_1 = 33.04$, $C_2 = 34.835$, $C_3 = 35.41$, $C_4 = 35.541$, ..., $C_\infty \approx 35.58$.

Feigenbaum's constant calculated according to the above values of $C_3$, $C_4$, $C_5$ is
\[ k = \frac{C_4 - C_3}{C_5 - C_4} = 4.5 + \beta, \quad 0 < \beta < 0.1 \]
and so it is close to the theoretical one:
\[ k_T = \lim_{n \rightarrow \infty} \frac{C_n - C_{n-1}}{C_{n+1} - C_n} \approx 4.66. \]

The analysis of curves $C_\infty(a_0)$ and $C_3^0(a_0)$ gives a very interesting result (see Fig. 4): in the hatched domain "the pre-turbulent regime" (pre-stochasticity) exists when there are both a strange attractor resulting from an infinite chain of the Feigenbaum doubling and a stable limit cycle. Complete stochasticity is observed for $C > C_3^0$, i.e., when the stable cycle vanishes. It is interesting that stochasticity was previously observed in the classical Lorentz system, but there the strange attractor did not appear as a result of bifurcation doubling. What has been said above, indicates the possibility of the generation of strange attractors of a new type, even in simple ecosystems.

Fig. 4. Existence domains of different dynamic regimes for the closed trophic chain.
Conclusions

In this report abstaining from superfluous mathematical strictness, we have tried to show what an extensive field of action the new science of mathematical ecology offers to mathematicians.

Since previously the main clients of mathematics were the physical sciences, it was physics that to a great extent determined the interest in this or that field of mathematics. With the rise of a need for mathematical ecology many mathematical methods, developed for physics, turned out to be inapplicable. The need for new methods (or non-traditional applications of the old ones) entailed the formulation of new problems. Mathematical physics took shape as a science in the 19th century, whereas the 20th century may be considered as marking the birth of mathematical ecology, ecology being the science about our home, the home we live in.

References
