

Biophysics of communities of living organisms

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This article reviews theoretical and experimental studies on fundamental problems of ecology. Theoretical study of the dynamics of ecosystems was initiated by the studies of V. Volterra, A. Lotka, A. N. Kolmogorov, and A. A. Lyapunov. These have been primarily models of point systems of the predator-prey type and models of competitive interrelationships between populations. The conclusions of the theory are illustrated by the experimental data of G. F. Gause, Nicholson, et al. It is shown how one might introduce the Lagrangian and Hamiltonian formalism to describe multispecies ecosystems. Considerable space is given to describing closed ecosystems whose development is limited by a biogenic element that constitutes the ecological minimum. It is shown that auto-oscillations can arise in such systems, while the stability of such ecosystems is determined by the diversity of species and some other factors, in particular, the specialization of species. Since real ecosystems consist of a large number of species, it becomes necessary to apply the methods of statistical mechanics to study these systems. Yet one cannot use the Gibbs method, owing to lack of ergodicity. The possibility is discussed of selecting macroparameters for describing ecosystems and constructing a Fokker-Planck equation for the populations.

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INTRODUCTION

Interest is now rising in fundamental problems of ecology in connection with the intensive effect of the productive activity of humans on the environment, and these problems can be solved only by the combined efforts of scientists of different specialties: physicists, biologists, chemists, etc.

The famous American theoretical physicist F. Dyson has spoken quite definitely of the need for participation of physicists in solving problems involving protection of the environment in his article "The Future of Physics."^[1] Academician P. L. Kapitza calls the ecological problem one of the most important among the global problems of the immediate future.^[2]

The global nature of disturbed equilibria existing in nature is already evident. The amount of energy that humans produce every year in the form of heat from burning various types of fuels already amounts to 0.01% of all the radiant energy that falls on the Earth from the Sun.^[3] The central problem of climatology is becoming that of determining the limiting admissible amount of heat that can be produced on Earth. This limit would seem to be several percent of the energy coming from the Sun, and it can be reached in the first half of the 21st Century.

Pollution of the environment by industrial, agricultural, and domestic effluents is also acquiring a global character. The sharp disproportion between the chemi-

cal composition of living organisms (which predominantly consist of the light chemical elements at the top of the periodic table: H, O, N, S, P, and C) and that of manufactured goods (in which mainly the elements in the middle and the bottom of the periodic table are used) causes the biosphere to become polluted with heavy metals. That is, the natural relationship of the chemical elements in the biosphere is upset.

Tens of thousands of new chemical compounds have been synthesized in recent years, and they have entered the biosphere in enormous amounts in the form of fungicides, insecticides, industrial and domestic wastes. Many of them, e.g., DDT, are concentrated in organisms, following the food chains.

The development of nuclear power poses its own problems that involve the protection of the environment. Water, soil, and air become polluted with radioactive elements through the operation of nuclear industrial enterprises and accidents in nuclear-powered ships. As we know, many chemical elements, including the radioactive isotopes, are concentrated by organisms with accumulation coefficients that reach tens and hundreds of thousands.^[4] This threatens radioactive contamination of humans through their food.

Communities of living organisms (or biocenoses) are most sensitive toward anthropogenic factors. The biocenoses, along with the environmental non-living matter that they use, constitute ecosystems or biogeoceno-

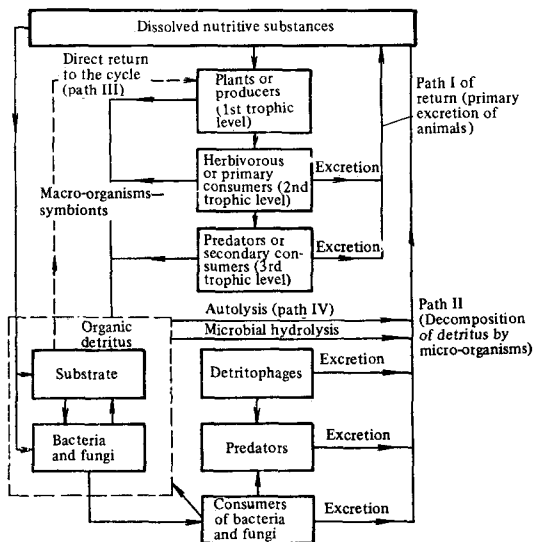


FIG. 1. Fundamental pathways of return of nutritive substances into the cycle.

ses. Study of the structures of the biogeocenoses that have been formed during billions of years of evolution has shown that in nature the problem of purifying the environment of the wastes of living organisms is successfully solved by the almost closed recycling of matter.

Figure 1 shows a diagram of the circulation of matter in a biogeocenosis.^[5] We can distinguish two very important pathways of return of food materials into the cycle: 1) primary excretion by organisms, and 2) decomposition of detritus by micro-organisms. The first way predominates in planktonic communities, and the latter in the steppes and forests of the temperate zone. Finally, there can be a third and a fourth way: direct transfer of matter from plant to plant by symbiotic micro-organisms, and autolysis.

Anthropogenic disturbance of the equilibria in the biosphere changes the character of natural biological evolution, both on the molecular and on higher levels. Yet the problem of physical interpretation of the process of evolution still remains a riddle, in spite of the attention of many important physicists^[6-8] that has been attracted to it. "The fundamental phenomenon that demands physical interpretation is natural selection. The problem arises of interpreting it in exact molecular terms, i. e., in the final analysis, in the language of quantum mechanics."^[9]

Here it is important to note that the molecular processes that occur in an individual cell are under natural conditions a part of the cycling of matter in a biogeocenosis. Therefore the selection processes that are dictated by this cycling determine the chemical structure of the biological molecules and their evolution. Therefore biophysicists will generally come to understand the cell and its components only when they understand ecological processes.

In a biogeocenosis, the separate individuals interact both with representatives of their own species and with

individuals of other species. The transport of matter among the elements of the system that is shown in Fig. 1 is carried out by the feeding of some organisms on other organisms. This is the so-called trophic relation, or predator-prey interaction. The first models of this interaction were constructed in the studies of Lotka^[10] and Volterra.^[11]

Let a system exist that consists of two species, one of which eats the other. Let the population growth of the prey in the absence of the predator be limited by nothing. Then the rate of increase in the number of individuals of the prey dN_1/dt will be proportional to the total number N_1 of prey. If we assume the growth coefficient ϵ_1 of the numbers of prey to be constant, then the number of prey will increase exponentially with time.

If we assume that the death rate dN_2/dt of the predators in the absence of prey is proportional to the number N_2 of predators with a certain mortality coefficient ϵ_2 , we get an exponential decline in the numbers of predators with time of $N_2(0) \exp(-\epsilon_2 t)$, where $N_2(0)$ is the number of predators at the initial instant of time.

When the two populations coexist, then the dynamics of their populations sharply changes. In the first approximation, we can consider that the rate of predation of the predators on the prey is proportional to the number of prey-predator encounters with a certain constant coefficient γ_1 , i. e., $\gamma_1 N_1 N_2$. The increase in the numbers of predators is also proportional to the quantity $N_1 N_2$, but with the smaller coefficient γ_2 . Thus we get the system of equations^[11]:

$$\begin{aligned} \frac{dN_1}{dt} &= \epsilon_1 N_1 - \gamma_1 N_1 N_2, \\ \frac{dN_2}{dt} &= -\epsilon_2 N_2 + \gamma_2 N_1 N_2. \end{aligned} \quad (1)$$

Interestingly, the nature of the nonlinearity likens these equations to those of dynamic meteorology.^[12]

The prey-predator system described by Eqs. (1) undergoes periodic oscillations when removed from a state of equilibrium. Here the oscillations in the number of predators lag in phase behind those of the prey.

The phase trajectories of the system (1) have the shape of closed curves that satisfy the equations

$$\gamma_2 N_1 - \epsilon_2 \ln N_1 + \gamma_1 N_2 - \epsilon_1 \ln N_2 = \text{const} = G,$$

They lie concentrically about a stationary point of the center type ($N_1 = \epsilon_2/\gamma_2$, $N_2 = \epsilon_1/\gamma_1$). Near the stationary point, the solutions of the system (1) consist in harmonic oscillations having a period that does not depend on the amplitude, and which equals $2\pi/\sqrt{\epsilon_1 \epsilon_2}$. As we go away from the point (ϵ_2/γ_2 , ϵ_1/γ_1), the period of the oscillations begins to depend on the amplitude, owing to the nonlinearity of the equations, while the shape of the oscillations differs appreciably from sinusoidal.

G. F. Gause was the first to study experimentally a predator-prey system. It has turned out that real systems behave in a considerably more complicated way. For example, the prey can poison the predators with its metabolites, and then the oscillations prove to be

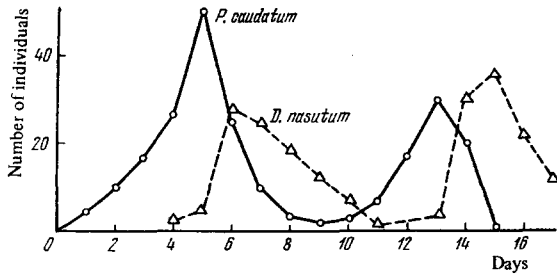


FIG. 2. Cyclic oscillations of the predator-prey type with the example of two types of infusoria.

unstable. However, if one introduces predators at equal intervals into the environment containing the prey in a nutritive substrate, then periodic oscillations are observed in the system. Figure 2 shows the results of G. F. Gause's experiments with two types of infusoria *Paramecium caudatum* (prey) and *Didinium nasutum* (predator). A nutritive broth in an amount that did not limit the system was used as the nutritive medium for the prey. ^[13]

1. VOLTERRA'S MODEL AND OTHER NONLINEAR MODELS OF BIOLOGICAL COMMUNITIES

A. The Lagrangian and Hamiltonian formalism for describing multispecies systems

Above we have treated the simplest system that consists of only two species, whereas natural biocenoses are composed of many hundreds and thousands of species. V. Volterra was able to generalize the equations (1) to the case of n biological species that interact with one another ^[14]:

$$\frac{dN_r}{dt} = \varepsilon_r N_r + \frac{1}{\beta_r} \sum_{s=1}^n \alpha_{sr} N_s N_r; \quad (1.1)$$

Here N_r is the population of the r -th species. The coefficients ε_r determine the behavior of the populations of the organisms in the absence of the other species, and they can be positive or negative. However, not all the ε_r can have the same sign in actually existing systems, since then all the species would either vanish in time (with a negative sign in front of the ε 's), or the populations would grow infinitely (positive signs of the ε 's). The summation on the right-hand side of Eq. (2) reflects the interaction of the r -th species with the rest of the species. Volterra assumed that $\alpha_{sr} = -\alpha_{rs}$. If we should have $\beta_r = 1$, then a decline in the biomass of one species would be compensated exactly by the same increase in the biomass of another species. The positive number $1/\beta_r$ is the Volterra equivalence number. Thus, in the case of pair encounters between the species, the ratio of the number of individuals lost (or gained) per unit time by the s -th species to the number gained (or lost) by the r -th species during the same time is $\beta_s^{-1}/\beta_r^{-1}$. The system of equations (1.1) converts into (1) for the case of two species.

Also V. Volterra paid attention to the analogy of the equations (1.1) to the equations of classical mechanics. ^[15] Yet this analogy is not traced clearly enough

in the form in which they are written, since physically reasonable values of the variables N_r can only be positive. However, in mechanics both the coordinates and the velocities take on both positive and negative values. V. Volterra tried to correct this defect of the equations (1.1) by introducing new phase variables X_r instead of the populations N_r of the species. They are related to the latter by the relationships

$$N_r = \frac{dX_r}{dt}. \quad (1.2)$$

However, the situation becomes complicated in this case by the appearance of nonphysical integrals of motion. E. Kerner found an ingenious way out of this situation by introducing the variables ^[16]

$$v_r = \ln \frac{N_r}{q_r}, \quad (1.3)$$

Here the q_r are the solutions of the stationary equations (1.1). The quantities v_r vary in the physical region from $-\infty$ to $+\infty$.

The equations (1.1) are rewritten in terms of the new variables in the form

$$\beta_r \dot{v}_r = \sum_{s=1}^n \alpha_{sr} q_s (e^{v_s} - 1). \quad (1.4)$$

If we multiply (1.4) by $q_r (e^{v_r} - 1)$, and sum over r from 1 to n , owing to the antisymmetry of the α_{sr} , we get

$$\sum_{s=1}^n \beta_s q_s \dot{v}_s (e^{v_s} - 1) = 0 \quad (1.5)$$

or after integration:

$$G = \sum_{r=1}^n \tau_r (e^{v_r} - v_r) = \text{const}, \quad (1.6)$$

where $\tau_r = \beta_r q_r$.

The quantity G is analogous to the Hamiltonian function in mechanics. Therefore Eqs. (1.4) can be rewritten in a form analogous to Hamilton's equations:

$$\frac{dv_r}{dt} = \sum_{s=1}^n \frac{\alpha_{sr}}{\beta_s \beta_r} \frac{\partial G}{\partial v_s}. \quad (1.7)$$

By analogy with mechanics, it proves possible to introduce also the Lagrangian:

$$\Lambda = \frac{1}{2} \sum_{s,r} \left(\frac{\alpha_{sr}}{\beta_s \beta_r} \right)^{-1} v_r \dot{v}_s - G. \quad (1.8)$$

We should note the limitation of a theory constructed by analogy with mechanics, since here the essential role is played by the antisymmetry of the matrix α_{sr} , which is nonsingular when of even order. This means that there must be an even number of species in the system in a steady state, which contradicts the observations.

B. Limiting factors. The Liebig principle

In the initial stage of population of a new environment, the rate of growth of the population depends only on the population itself at the given instant of time. Here, if N is the number of individuals in the popula-

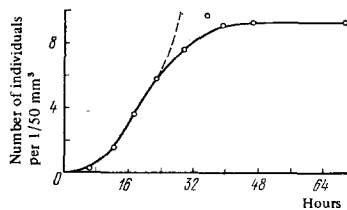


FIG. 3. Growth curve of the biomass of yeast.

tion, t is the time, b is the birth rate, and d is the death rate, the equation of growth of the population has the form

$$\frac{dN}{dt} = (b - d) N. \quad (1.9)$$

If $b > d$, then when the population has lived in the new environment for a certain time, its density reaches a high enough level that the aggravated struggle for existence will depress the growth rate. Verhulst proposed that, if K is the maximum number that the population can reach in the given environment, then the rate of growth of the population will decline according to the law $(b - d)(K - N)$, and one can write the population growth equation in the form

$$\frac{dN}{dt} = (b - d) N (K - N). \quad (1.10)$$

Upon integrating this equation, we get an expression for the sigmoid logistic curve. There are now many experimental data that confirm this relationship.

G. F. Gause was one of the first to show the validity of the logistic law for populations of yeast cells.^[17] Figure 3 shows the growth curve of the yeast *Saccharomyces cerevisiae*. If the medium is renewed at short intervals of time, then the multiplication is exponential (dotted curve). Yet if the yeast cells are left alone, then density factors begin to take effect in a certain time, and the exponential curve goes over into a logistic curve (solid line). The points on the curve correspond to the experimental results.

Monod^[18] has given a description of the slowing growth rate as a function of the concentration of the substrate that limits the growth of bacteria. He used the equation for the specific growth rate $(1/N)dN/dt$ that is known in enzymology:

$$b = \frac{b_{\max} S}{K_s + S}, \quad (1.11)$$

Here S is the concentration of the substrate, and K_s is a constant that is numerically equal to the concentration of substrate at which the growth rate reaches half the maximum. The quantity b_{\max} corresponds to the value of the specific growth rate of the population in the exponential phase. Figure 4 shows the specific growth rate of the population of the yeast *Candida tropicalis* as a function of the substrate paraffin.^[19] The solid curve corresponds to Eq. (1.11).

Volterra's model, which was constructed to describe the population changes in a predator-prey system, proves to hold only at low enough concentrations of the interacting populations. This is because this

model assumes the consumption of prey by predators to be proportional to the population of prey at any prey concentrations, however high. We cannot consider this to be physiologically justified. Ivlev^[20] was the first to pay serious attention to this defect at the theory in studies on feeding of fishes. N. Rashevsky^[21] devised a theory to explain Ivlev's law, which determines the rate of consumption of food particles as a function of their concentration in a steady-state feeding regime. Quite recently, V. S. Ten has derived some refined equations for the dynamics of feeding.^[22]

In 1840, Liebig established the "law of the minimum," according to which the growth of plants is limited by the biogenic element having the least concentration. In soils, these limiting elements are very often nitrogen or potassium. In seawater, the abundance of plankton is determined by the phosphate content. The so-called microelements that are used by living organisms in small quantities, but whose supplies in the environment are small and insufficient, can also be limiting. For example, a low copper content in peaty soils causes fragility of stems of wheat and hinders its ripening.

An ecological factor plays the role of the limiting factor also when it exceeds the maximum permissible level. For example, as is well known, copper compounds in large amounts are toxic for organisms.

If any limiting biogenic element is deficient, and it limits the processes that occur in the biological system throughout the entire period of measurement, then it is convenient to use the values of the biomasses normalized to the corresponding biogenic element instead of the population numbers or their biomasses.

A very simple biogeocenosis in which the decomposition of organic matter occurs by autolysis or excretion must consist of at least one species of alga and one species of animal that feeds on it. If the system is closed with respect to matter, then it obeys the equation

$$M_1 + M_2 + M_0 = \text{const} \equiv M, \quad (1.12)$$

Here M_1 and M_2 are respectively the biomass of the plants and that of the animals normalized to the mass of the biogenic factor that constitutes the ecological minimum. We shall denote the mass of this biogenic factor in the environment as M_0 . Upon taking account of Ivlev's law, the system of predator-prey equations for this simple system can be written in the form^[23]

$$\frac{dM_1}{dt} = -d_1 M_1 - \mu \frac{b_2 \max M_1 M_2}{K_2 + M_1} + \frac{b_1 \max M_1 M_0}{K_1 + M_0}, \quad (1.13)$$

$$\frac{dM_2}{dt} = -d_2 M_2 + \frac{b_2 \max M_1 M_2}{K_2 + M_1}; \quad (1.14)$$

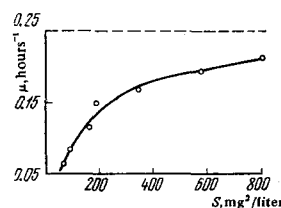


FIG. 4. Relationship of the specific growth rate of yeast to the concentration of the growth-limiting substrate paraffin.

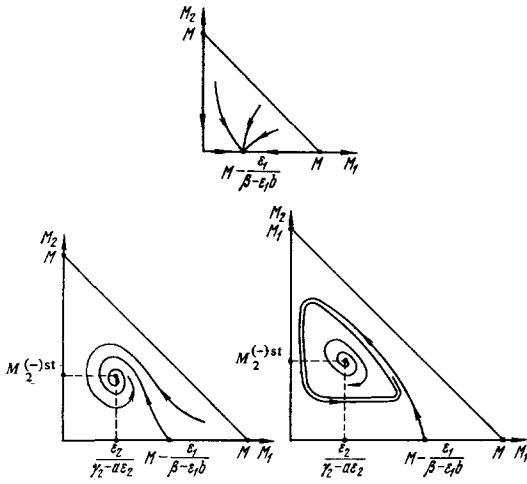


FIG. 5. Nature of the variation in the phase curves in a predator-prey system with increasing concentration of the limiting biogenic element.

Here d_1 and d_2 are respectively the death rates of the plants and of the animals; $b_{1 \max}$ and $b_{2 \max}$ are the specific growth rates of the plants and animals, respectively, in the exponential phase; K_1 and K_2 are constants that are equal to the concentrations M_0 and M_1 at which the growth rate reaches half maximum; and μ is a constant greater than unity. Figure 5 shows on the $M_1 M_2$ plane the variation in the phase curves of Eqs. (1.13) and (1.14) with increasing M . The fact is extremely important that the limit cycle passes ever closer to the coordinate axes with increasing M . The derived equations (1.13) and (1.14) cease to hold at small enough M_1 or M_2 , since the discrete structure of the populations begins to play a role, and the probability of their extinction increases sharply.

We note that Eqs. (1.13) and (1.14) for large K_1 are a special case of the equations studied by Kolmogorov^[24] and Waltman.^[28]

It is interesting here to note the cycle of studies performed by I. A. Poletaev for a predator-prey model in which the limiting factor changes during the process of evolution of the system.^[25,26]

In multispecies systems of the type of (1.1), taking account of a limiting factor also leads to certain new properties. Here we shall study the Verhulst limiting factor, and other cases in the next chapter. When we take account of the Verhulst term, the system of equations (1.1) takes on the form^[27]

$$\frac{dN_j}{dt} = \epsilon_j \frac{K_j - (1/2)(1 + \text{sgn } \epsilon_j) N_j}{K_j} N_j + \frac{1}{\beta_j} \sum_{i=1}^n \alpha_{ij} N_j N_i. \quad (1.15)$$

Equations (1.15) can be written in terms of the variables v_j as follows:

$$\beta_j \dot{v}_j = -\frac{1}{2} \epsilon_j (1 + \text{sgn } \epsilon_j) \frac{q_j}{K_j} (e^{v_j} - 1) \beta_j + \sum_{i=1}^n \alpha_{ij} q_i (e^{v_i} - 1). \quad (1.16)$$

In contrast to (1.5), we get the following expression for dG/dt :

$$\frac{dG}{dt} = -\frac{1}{2} \sum_{j=1}^n \beta_j \epsilon_j (1 + \text{sgn } \epsilon_j) \frac{q_j^2}{K_j} (e^{v_j} - 1)^2 < 0, \quad (1.17)$$

where

$$\frac{1}{2} \epsilon_j (1 + \text{sgn } \epsilon_j) = \begin{cases} 0 & \text{when } \epsilon_j < 0, \\ \epsilon_j & \text{when } \epsilon_j > 0. \end{cases}$$

We can easily see that $dG/dt = 0$ when all the $N_i = q_i$. Thus (1.17) implies stability of the steady states throughout the positive quadrant.

Volterra^[14] elucidated the conditions in which the steady states are stable throughout the positive quadrant in the general case of bilinear and quadratic interactions between the species.

Let the following system of equations hold:

$$\frac{dN_r}{dt} = \left(\epsilon_r - \sum_{s=1}^n p_{rs} N_s \right) N_r, \quad (1.18)$$

where ϵ_r and p_{rs} are constant coefficients. Here we assume that at least one of the $\epsilon_r > 0$, since then not all of the species can disappear in the course of time. Then, if one finds positive coefficients α_i such that the quadratic form

$$\sum_{r=1}^n \sum_{s=1}^n \alpha_r p_{rs} N_r N_s$$

is positive definite, and if all the q_i are positive, the steady state is stable, and the system tends to approach this state from any point of phase space.

C. Taking account of time lag

Thus far the studied models have assumed that the consumed food is immediately spent on creating progeny. Yet these processes are separated in a number of cases by a time interval. That is, the one process lags in time behind the other.

This phenomenon is especially easy to observe in populations of insects. They have a high rate of multiplication, while the time separation between multiplication and the initiation of the density-dependent regulation is determined by the multistep nature of the process of development: egg-larva-pupa-adult (imago).

Hutchinson^[29] first described a competition for food between adults and larvae. She considers the coefficient $K - N$ to be the regulating factor in the equation for the logistic curve. Since there is a time separation that is equal to the development cycle T between the density increase and the corresponding reaction, we obtain the following expression in place of the logistic curve:

$$\frac{dN(t)}{dt} = (b - d) N(t) (K - N(t - T)). \quad (1.19)$$

The solution of this equation for small enough T oscillates about a level that corresponds to the capacity K of the environment, and the amplitude of the oscillations declines with time (Fig. 6).

Nicholson (see^[30]) has observed cyclic oscillations in

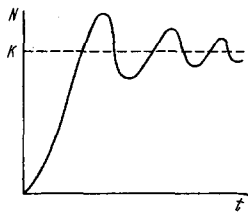


FIG. 6. Population dynamics with account taken of time lag.

population caused by the lag factor in experiments with the green carrion fly *Lucilia cuprina*. In a series of experiments in which the adults received food in unlimited amount, while the food of the larvae was limited, he observed periodic oscillations in the populations. When there came to be too many larvae, they intensely competed with one another, the death rate rose, and the population density fell to a level where the normal growth of larvae was restored. Then the population increased anew (Fig. 7). He also observed an analogous pattern in the case in which the larvae had an excess of food, while the adults received food in unlimited amount.

Volterra studied the lag factor with the example of a predator-prey system.^[14] He showed that if the species do not exist in steady states, and the lag is limited, then the population numbers oscillate for an unlimited number of times about the steady states.

A set of interesting new results has recently been obtained in a whole series of studies on population equations involving lag.^[31-35]

May^[36] has studied the effect of lag on the stability of ecosystems. He concluded from the example of models of communities having two trophic levels that inclusion into a system that is stabilized by a limited-resource mechanism of a time lag exceeding the characteristic time of the system destroys its stability. Yet one can lengthen the characteristic time of the entire system by adding another trophic level, and can render it again stable.

D. Behavior of ecosystems in space

One of the first studies on the behavior of populations in space was the article of Kolmogorov, Petrovskii, and Piskunov,^[37] which treated the displacement of one genotype by another. They assumed in the problem that individuals having a certain trait have an advantage in the struggle for existence over those that lack it. If ρ is the concentration of individuals that possess the useful dominant trait, then the equation describing the variation of this concentration in space will have the form

$$\frac{\partial \rho}{\partial t} = D \Delta \rho + \alpha \rho (1 - \rho)^2 \quad (1.20)$$

(we assume that each individual moves in a random direction in the interval between birth and death). Here D is the diffusion coefficient of the useful gene. We assume that the ratio of the probability of survival of an individual that has the useful trait to the same probability for an individual that lacks it is $1 + \alpha$, where $0 < \alpha \ll 1$.

If at the initial instant of time the individuals having the useful trait exist at $x < x_0$ with a probability density of unity, while those that lack it exist in the region $x > x_0$ with a probability density of unity, we can naturally expect the region of densities having $\rho = 1$ to propagate in time from left to right. An asymptotic density profile will also be established in time. The development of this study has permitted study of an entire series of chemical reactions involving diffusion, in particular combustion reactions.^[38]

Equations can analogously be constructed with account taken of diffusion for different species that interact with one another. Let $\rho_i(\mathbf{x}, t)$ be the density of the i -th species, and $\mathbf{j}_i(\mathbf{x}, t)$ be the flux density of the i -th species. Then, if Volterra's hypothesis holds for the predator-prey system, we can write

$$\begin{aligned} \frac{\partial \rho_1(\mathbf{x}, t)}{\partial t} + \text{div } \mathbf{j}_1(\mathbf{x}, t) &= e_1 \rho_1(\mathbf{x}, t) - \gamma_1 \rho_1(\mathbf{x}, t) \rho_2(\mathbf{x}, t), \\ \frac{\partial \rho_2(\mathbf{x}, t)}{\partial t} + \text{div } \mathbf{j}_2(\mathbf{x}, t) &= e_2 \rho_2(\mathbf{x}, t) + \gamma_2 \rho_1(\mathbf{x}, t) \rho_2(\mathbf{x}, t). \end{aligned} \quad (1.21)$$

As for the fluxes \mathbf{j}_1 and \mathbf{j}_2 , we can write then in the following form by analogy with the case of multicomponent diffusion^[56]:

$$\begin{aligned} \mathbf{j}_1 &= -D_1 \nabla \rho_1 - d_1 \nabla \rho_2, \\ \mathbf{j}_2 &= -D_2 \nabla \rho_2 + d_2 \nabla \rho_1, \end{aligned} \quad (1.22)$$

Here D_1 and D_2 are the self-diffusion coefficients of the prey ρ_1 and the predator ρ_2 , d_1 is the speed of flight of the prey from the predators, and d_2 is the speed of pursuit of the predators after the prey.

Near the steady state $e_2/\gamma_2, e_1/\gamma_1$, the equation for the small perturbations Q_1 and Q_2 ($\rho_1 = (e_2/\gamma_2) + Q_1, \rho_2 = (e_1/\gamma_1) + Q_2$) satisfies the equations

$$\frac{\partial^2 Q}{\partial t^2} - (D_1 + D_2) \Delta \frac{\partial Q}{\partial t} + (D_1 D_2 + d_1 d_2) \Delta \Delta Q - (\lambda_1 d_2 + \lambda_2 d_1) Q = 0. \quad (1.23)$$

If we neglect self-diffusion, so that the motive force for migration is the pursuit and flight of the predators and prey, then the solution of Eq. (1.23) is a superposition of undamped plane waves. Yet when the self-diffusion differs from zero, then the waves decay with the coefficient

$$\beta = \frac{1}{2} (D_1 + D_2) k^2,$$

where k is the wavenumber. That is, oscillations having short wavelengths decay most quickly.

We assumed in (1.22) that the flight and pursuit

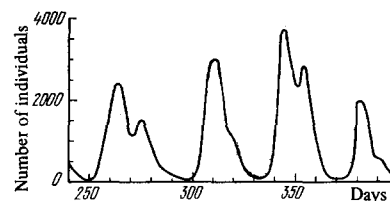


FIG. 7. Oscillations in the population of flies whose density is regulated by the amount of food given to the larvae.

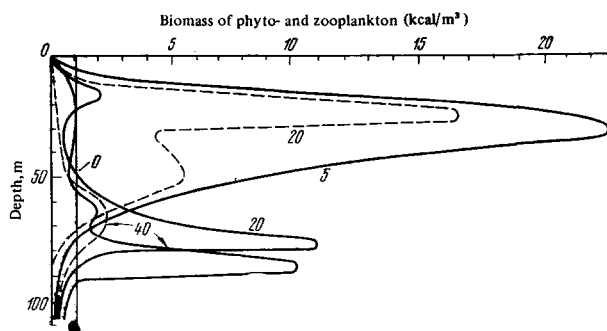


FIG. 8. A calculation of the dynamics of the depth distribution of phyto- and zooplankton in an upwelling zone.

fluxes are equal, apart from a constant factor, to the density gradients of the predators and the prey, respectively. This approach allows spontaneous creation of predators and prey to occur, even in the case in which the corresponding population densities equal zero throughout space at the initial instant. Therefore it proves more natural to write the fluxes in the form^[39]

$$j_1(x, t) = -d_1 \rho_1 \frac{\partial \rho_2}{\partial x} - D_1 \frac{\partial \rho_1}{\partial x},$$

$$j_2(x, t) = d_2 \rho_2 \frac{\partial \rho_1}{\partial x} - D_2 \frac{\partial \rho_2}{\partial x}.$$

Further complication of the studied systems permits one to proceed to mathematical modeling of biogeocenoses. In a series of studies, A. A. Lyapunov has constructed a mathematical model of a biogeocenosis of pelagic species in tropical ocean waters.^[40-42]

In this system, the primary production of phytoplankton is restricted by the illumination, by the concentration of biogenic elements (nitrogen and phosphorus), and by the maximum rate of multiplication of the phytoplankton. The phytoplankton is used as food by the zooplankton. The organic residues that are formed upon death of the phyto- and zooplankton, and also the excrement of the animals, are subject to gravitational settling. Thereby the zone of active photosynthesis in the ocean is continually depleted of biogenic elements. Hence the productivity of the open regions of the ocean is extremely low (less than the productivity of a desert).

The biogenic elements are replenished in the upper 200-meter photosynthetic zone in the regions of the so-called upwellings, or zones of rising deep waters rich in nutritive salts.

On the basis of the modified equations of A. A. Lyapunov with account taken of the law of limiting rations of V. S. Ivlev, the associates of the Institute of Oceanology have devised a numerical model of an ecosystem of pelagic species in a region of rising deep waters in the western part of the equatorial zone of the Pacific Ocean.^[43] The coefficients were obtained by using the method proposed by Lyapunov^[41] from the data of the observations of the 50th cruise of the scientific research ship "Vityaz'."

In this model,^[43] the zooplankton was divided into a number of groups: filterers, small predators (cyclo-pods), intermediate predators (calanoids), and large

predators (chaetognaths and polychaetes). The larger species feed on the smaller.

The biomasses of the species that constitute the biocenosis vary as one follows the current away from the upwelling. These changes are determined both by the depletion of the photosynthetic layer in biogenic factors, and by interspecies interactions. If one were to drift with the current from the upwelling zone, one would observe a maximum biomass of phytoplankton in 5-10 days. The filterers reach a maximum on the 30th day, and the predatory species on the 35-50th day.

One also observes a variation in time of the vertical concentration profiles of the biomasses of phyto- and zooplankton (Fig. 8). On the 10th day, the supply of biogenic factors in the upper layer has been almost completely exhausted. Yet at a depth of 10-20 m, where the optimal light intensity for photosynthesis occurs in tropical regions, a maximum mass of phytoplankton is maintained. At the same time, a lower maximum in the phytoplankton begins to be formed, owing to the biogenic factors that enter from the upper layer and the influx of biogenic factors through the thermocline. As the upper layer becomes depleted, vertical transport of biogenic elements from below the thermocline via turbulent exchange begins to play a role. The upper maximum in the phytoplankton completely vanishes.

The dynamics of biological productivity arising from the intensity of turbulent exchange in the photosynthetic layer of the sea has been studied in^[44]. A system was treated that consists of phyto- and zooplankton. The development of the phytoplankton was limited by the illumination and by the nitrogen concentration. The biological coefficients of the model were calculated from data on the dynamics of the biomasses for the pelagic species of the White Sea, as obtained by the Department of Hydrobiology of Moscow State University in April-October, 1971. The solid lines in Fig. 9 show the dynamics of the biomass of the phytoplankton for a coefficient of turbulent exchange of 5 m²/day as calculated from the temperature trend with depth in the White Sea in 1971. The circles show the results of the observations. The dotted line is the calculation from the model in the absence of exchange.

We can easily see that the existence of the coefficient of turbulent exchange synchronizes the maxima throughout the depth. The total bioproductivity declines, owing to turbulent diffusion of the phytoplankton into the lower horizons.

2. KINETICS OF BIOGEOCENOSSES HAVING A FIXED MASS OF A LIMITING BIOGENIC ELEMENT

A. The Volterra-Gause theorem

If species belong to the same trophic level, then competition arises among them, owing to the limitation of the substances that they use, energy, space, and poisoning by metabolites. Competition between species was first studied theoretically by Volterra.^[14] Let M_i be the biomass of the i -th species of the community that we are studying. When the food is unlimited, the coef-

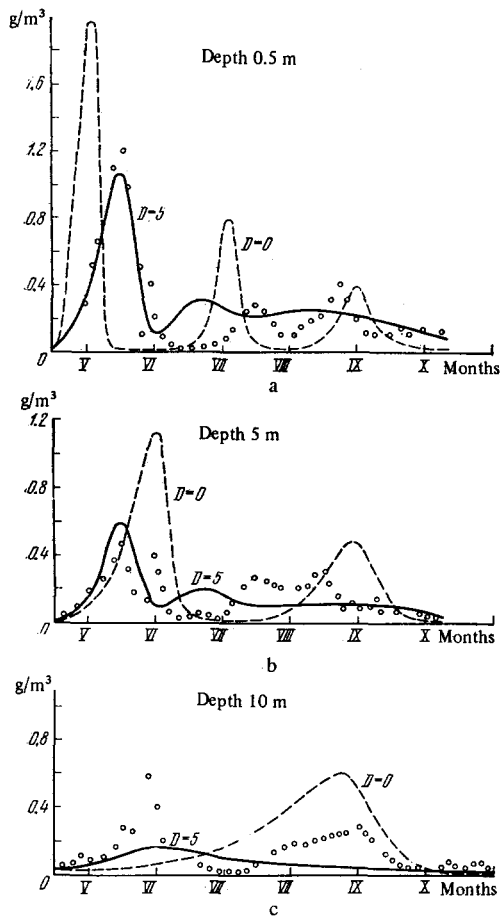


FIG. 9. Dynamics of the biomass of phytoplankton as a function of the depth and of the coefficient of turbulent exchange.

coefficients of natural-increase ϵ_i are positive constants. In the actual case, the coefficients of increase will decline monotonically as the food is consumed:

$$\epsilon_i = \gamma_i F(M_1, M_2, \dots, M_n),$$

where F is a symmetric positive function that increases monotonically with increasing M_i , and which characterizes the exhaustion of the resource, with $\gamma_i > 0$. In the very simple case of a closed cycle, in which the same biogenic factor fixes the limitation all the time, the function F in units of the mass of this biogenic factor has the form $\sum_{i=1}^n M_i$, while $\epsilon_i = M\gamma_i - \bar{\epsilon}_i$, where $\bar{\epsilon}_i$ is the death rate, while M is the total concentration of the limiting biogenic factor in the system.

When all the M_i are zero, then there is no competition, and $F=0$. Thus, the system of differential equations that describes the competition among the species has the form

$$\left. \begin{aligned} \frac{dM_1}{dt} &= M_1 [\epsilon_1 - \gamma_1 F(M_1, M_2, \dots, M_n)], \\ \dots &\dots \\ \frac{dM_n}{dt} &= M_n [\epsilon_n - \gamma_n F(M_1, M_2, \dots, M_n)]. \end{aligned} \right\} (2.1)$$

We can easily verify that the positive solutions of this system of equations always remain bounded. In fact,

if F proves to be larger than any of the ϵ_i/γ_i , then the corresponding dM_i/dt become negative, and owing to the monotonic growth of the function F with increasing M_i , the given M_i cannot increase further.

If we eliminate the function $F(M_1, M_2, \dots, M_n)$ from the r -th and s -th equations of (2.1) and integrate the obtained equation, we get

$$\frac{M_r^{1/\gamma_r}}{M_s^{1/\gamma_s}} = \frac{(M_r^0)^{1/\gamma_r}}{(M_s^0)^{1/\gamma_s}} \exp\left(\frac{\epsilon_r}{\gamma_r} - \frac{\epsilon_s}{\gamma_s}\right)t, \quad (2.2)$$

Here M_r^0 and M_s^0 are the initial values of the biomasses of the r -th and s -th species.

Let $\epsilon_1/\gamma_1 > \epsilon_2/\gamma_2 > \dots > \epsilon_n/\gamma_n$. Then we have:

$$\lim_{t \rightarrow \infty} \frac{M_i^{1/\gamma_i}}{M_1^{1/\gamma_1}} = \infty \quad (i > 1).$$

This implies that all the $M_i (i \geq 2) \rightarrow 0$. Thus we have derived the famous theorem of Volterra: If species inhabit a single ecological niche, then one of them always supplants the others.

Gause^[45] performed the first experimental test of Volterra's theorem. He cultivated two similar species of infusoria: *Paramecium caudatum* and *P. aurelia*, in a closed volume into which he regularly introduced as food the bacterium *Bacillus pyocyaneus*, which does not multiply in a single culture with the infusoria. Figure 10 shows the results of the experiment. When cultivated individually, the population of each of the infusoria gives a typical logistic curve whose asymptote is determined by the amount of food introduced. Yet when both species are cultivated together, they intensively compete with one another, and in two weeks *P. aurelia* has completely supplanted *P. caudatum*. That is, the species survives that consumes the food more intensively, and which has a lower death rate.

An analogous pattern of selection is also observed on lower levels in the catalytic replication of protein molecules. One can understand why enzymes arose in the process of evolution: they accelerate the reactions of biosynthesis by a factor of many thousands.^[46]

To supplement what we have said, we note that the Volterra-Gause theorem is also obeyed in the case in which the nutrition of the competing species is regenerated within the studied system.^[47] Figure 11 shows a diagram of the material cycle in a system that consists of plants (producers), detritus, reducers, mineralizing detritus, and non-living nutritive material that

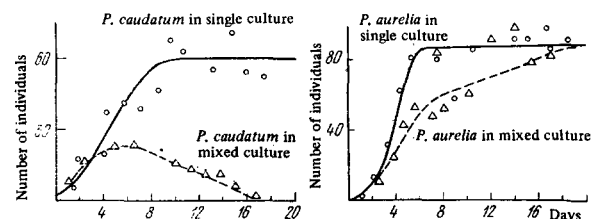


FIG. 10. Competition between two similar species that have a common ecological niche.

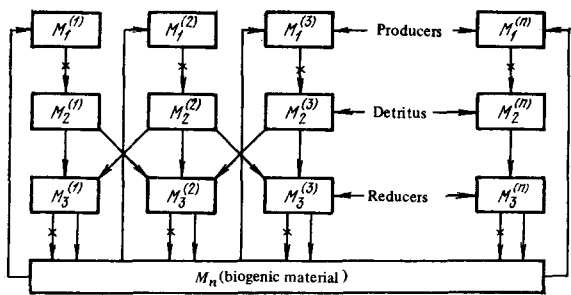


FIG. 11. Diagram of the circulation of matter in an ecosystem: producers, detritus, reducers, and biogenic material.

is used by the plants. The crossed arrows denote the fluxes of matter that arise from processes of death of living organisms. We can naturally assume the rate of these processes to be proportional to the biomasses of the corresponding populations. The plain arrows denote the fluxes of matter caused by active interactions of living organisms with one another and with non-living nature. If we assume that the limiting factor is not altered in the interaction process, then the equations for the dynamics of the biomass of the individual species of plants have the form

$$\frac{dM_1^{(i)}}{dt} = -\varepsilon_1^{(i)} M_1^{(i)} + \gamma_1^{(i)} \frac{M_1^{(i)} M_n}{K_1^{(i)} + M_n}.$$

The given system of equations lacks steady states when more than one $M_1^{(i)}$ differs from zero. Without complication, we can convince ourselves that the only stable state among them proves to be a steady state of the species for which the quantity $K_1^{(i)}/[(\gamma_1^{(i)}/\varepsilon_1^{(i)}) - 1]$ is least.

B. Stability of ecosystems and diversity of species

Ecological niches can be created in the most varied ways. First of all, they can arise in the spatial separation of the competing species. If one cultures jointly *Paramecium caudatum* and *P. bursaria*, then both species can live together to attain equilibrium,^[17] in spite of having a single source of food for both species, since *P. bursaria* concentrates at the bottom and the sides of the test tube, while *P. caudatum* remains in the free space. In this case, the ecological niches prove to be so different that they permit the organisms to avoid competing. Under natural conditions, spatial separation also permits many species to avoid competing for food. For example, in the forest one distinguishes the arboreal, shrub, and grass layers, which are populated by different species of organisms.

An analogous zonality also exists in aquatic ecosystems. The important vertical zonality is determined by penetration of light into the depth of the water. Moreover, aquatic organisms are distinguished in terms of their habitat as bottom species (benthos) and pelagic species that inhabit the thickness of the water.

It is interesting to note in this regard that several stable ecological niches cannot arise from a complicated chemical composition of the nutritive mixture on which different species of plants can be cultivated, with

an associated alternating limitation by different biogenic factors during the growth process.^[48]

In addition to separation in space, the physiological activity of different organisms can be separated in time. This is brought about by the so-called seasonal biological rhythms, which cause, e.g., the period of multiplication to coincide with a favorable season. Thus, as the theorem of G. F. Gause shows, the possibilities of formation of ecological niches owing to physical factors of the environment are very limited.

However, if each of the species of producers that are nourished by a single substrate has its own feeding consumer that is specialized to it, i.e., the diagram of the material cycle has the form depicted in Fig. 12, then as many producer-consumer pairs exist stably in such a system as the presence of the biogenic elements will allow.^[47] It is not hard to understand why. The consumers regulate the biomass of the producers without allowing any of them to increase so greatly as to supplant the others.

We saw in the second section of the last chapter that the dimensions of the limit cycle in the plane of "producer-consumer" biomasses enlarge with increasing total concentration of biogenic factors in the system, and the system becomes less stable toward discrete perturbations. Yet if the number of producer-consumer pairs increases, then the stability of the system increases correspondingly, since each of the pairs of species selects for itself a fraction of the total mass of biogenic factors, and thus it correspondingly diminishes the mass of biogenic factors that can be used by the other species. Thus, one can advance the hypothesis that species arise in pairs under constant external conditions.

It is of interest to analyze all these conclusions of the theory with the example of biogeocenoses that lie in regions of the Earth where the climatic oscillations are small. For example, one can treat as such a biogeocenosis a tropical rain forest, the flora and fauna of which are infinitely rich in species. One can count 20,000 species of insects in $\approx 15 \text{ km}^2$ in the Panama Canal Zone, whereas there are only several hundred of them in the whole territory of France.^[5] In this

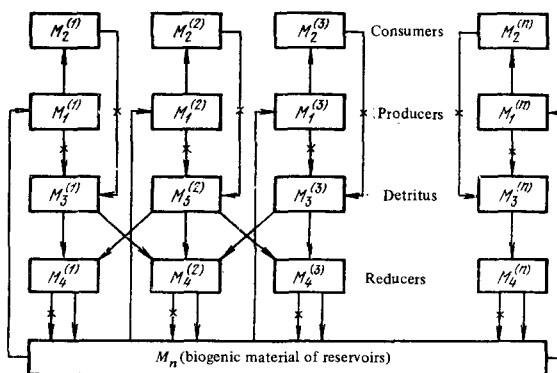


FIG. 12. Diagram of circulation of material in an ecosystem having specialized consumers.

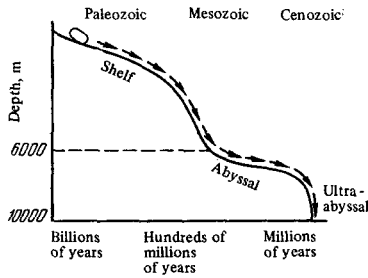


FIG. 13. Relative age of deep-water fauna of the different vertical zones of the ocean bottom.

forest, symbiosis between insects and epiphytes (aerial plants having no roots in the soil) is widespread, and this can give evidence of the generality of their appearance.

Many scientists consider a high rate of evolution and of species formation to be characteristic of a tropical forest. Perhaps this is why precisely these regions have served as the site of origin of new species that entered into the composition of the communities of the moderate and polar zones. Thus, one of the major Soviet botanists, An. A. Fedorov, states that the path of development of the tropical rain forest "has been strictly autochthonous, and has been a phytocenotypical expression, as well as being the background of the grandiose process of formation of the fundamental nucleus of the angiosperms, the homeland of which, of course, lies in the tropics. With respect to the tropical flora, the holarctic and antarctic flora are a secondary phenomenon that has arisen as a result of adaptation to less favorable conditions in the process of singling out and migration from the flora of the tropics."^[49]

In aquatic biogeocenoses, in particular, oceanic, the qualitative diversity of the biota also increases as we go from the polar to the tropical region.^[50] Just as on land, species formation in the ocean mainly occurs in regions where biological factors create favorable conditions for it, i. e., in the tropics in the littoral zone, which is rich in light and biogenic elements, whence the species migrate into regions less favorable for life. Figure 13 shows the growth of the ocean fauna for different vertical zones of the ocean bottom. The formation of the bottom fauna of the ocean shelves should be assigned to the remote Precambrian. The formation of the fundamental abyssal fauna perhaps should be assigned to the Cambrian and the Mesozoic, and the ultra-abysal to the Cenozoic.^[50]

It might seem at first glance that the increased species formation will lead to increased stability of the ecosystem. In fact, the relation is more complicated, as we can see from the following example. If we add to the system shown in Fig. 12 a third level of specialized species, then the biogeocenosis will be unstable, since these species will weaken the regulating action of the species that exist on the second level. Consequently species will be crowded out. That is, the system with the large number of species is less stable in this case.

C. Stability of ecosystems toward colonization by new species

Similar ecosystems develop in all sites having the same physical environment. Equivalent functional niches come to be occupied by the biological groups that exist in the flora and fauna of the given region. Here the ecologically equivalent species may not be taxonomically related. Thus, for example, the cacti, which are widespread in America, are completely lacking in the Old World, yet the milkworts of the African deserts look just like cacti.^[51]

Deliberately or not, man changes the geographical distribution of plants, animals, and micro-organisms. He continually experiments with introductions, though many of them prove to fail; he bears great losses from pests, which often prove to be displaced species. Almost complete replacement of the local species by colonizers has occurred on remote islands and continents. Thus, most of the songbirds found in the Hawaiian Islands have been introduced.^[51]

In order to make a prognosis of the development of the flora and fauna in a given region, one must take account not only of its climatic characteristics and not only of the species that inhabit it, but also of the possible introduction of species from different biogeocenoses, even remote ones. Generally we know rather well the list of species that can migrate into a given concrete biogeocenosis. If, moreover, we know the nature of the trophic relations among the species, then we can construct a diagram of cycling of matter in a certain abstract limiting ecosystem that contains these species.

For the sake of simplicity, let us assume that our limiting ecosystem consists of only three species: one consumer and two producers. The material cycle diagram in this system is shown in Fig. 14c.

We can naturally expect that the number of species that can exist in a certain biogeocenosis depends strongly on the total concentration of biogenic elements, i. e., on

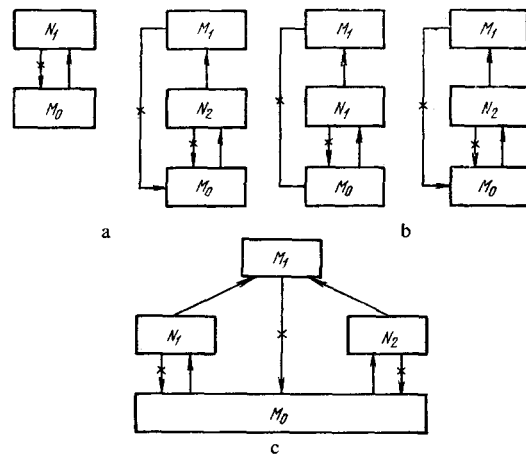


FIG. 14. Examples of trigger and auto-oscillatory states in a biogeocenosis.

$$M = M_0 + M_1 + N_1 + N_2.$$

The system of equations that corresponds to Fig. 14 has the form

$$\left. \begin{aligned} \frac{dN_1}{dt} &= -\varepsilon_1 N_1 - \gamma_1 N_1 M_1 + \beta_1 N_1 (M - N_1 - N_2 - M_1), \\ \frac{dN_2}{dt} &= -\varepsilon_2 N_2 - \gamma_2 N_2 M_1 + \beta_2 N_2 (M - N_1 - N_2 - M_1), \\ \frac{dM_1}{dt} &= -\varepsilon M_1 + \tilde{\gamma}_1 M_1 N_1 + \tilde{\gamma}_2 M_1 N_2. \end{aligned} \right\} \quad (2.3)$$

We assume all the coefficients ε , γ , $\tilde{\gamma}$, and β to be constant.

Let $\varepsilon_2/\beta_2 > \varepsilon_1/\beta_1$. Then we can easily find from the condition of stability of the steady states that not even a single species can exist in the system when $M < \varepsilon_1/\beta_1$.

The existence of the following inequality is necessary and sufficient for existence of a stable steady state in a system having one species:

$$\frac{\varepsilon_1}{\beta_1} < M < \frac{\varepsilon_1}{\beta_1} + \frac{\varepsilon}{\gamma_1}.$$

The further progress in filling the biogeocenosis with species with increasing M is highly determined by what the relationship is between the quantities γ_2/β_2 and γ_1/β_1 . When $\gamma_2/\beta_2 > \gamma_1/\beta_1$, then a necessary and sufficient condition for existence of a steady state consisting of two species (M_1 and N_1) has the form

$$M > \frac{\varepsilon_1}{\beta_1} + \frac{\varepsilon}{\gamma_1}. \quad (2.4)$$

Yet if $\gamma_1/\beta_1 > \gamma_2/\beta_2$, then two stable steady states can exist with the very same value of M (the trigger variant). With a relationship of the limiting mass and of the coefficients that has the form

$$\frac{\varepsilon_1}{\beta_1} < \frac{\varepsilon_2}{\beta_2} + \frac{\varepsilon}{\gamma_2} + \left(1 + \frac{\gamma_2}{\beta_2}\right) \frac{(\varepsilon_2/\beta_2) - (\varepsilon_1/\beta_1)}{(\gamma_1/\beta_1) - (\gamma_2/\beta_2)} < M,$$

$$M < \frac{\varepsilon_1}{\beta_1} + \frac{\varepsilon}{\gamma_1},$$

a variant is realized that has two stable steady states as shown in Fig. 14a. Yet when inequalities of the following form are satisfied:

$$\frac{\varepsilon_1}{\beta_1} + \frac{\varepsilon}{\gamma_1} < \frac{\varepsilon_2}{\beta_2} + \frac{\varepsilon}{\gamma_2} + \left(1 + \frac{\gamma_2}{\beta_2}\right) \frac{(\varepsilon_2/\beta_2) - (\varepsilon_1/\beta_1)}{(\gamma_1/\beta_1) - (\gamma_2/\beta_2)} < M,$$

$$M < \frac{\varepsilon_1}{\beta_1} + \frac{\varepsilon}{\gamma_1} + \left(1 + \frac{\gamma_1}{\beta_1}\right) \frac{(\varepsilon_2/\beta_2) - (\varepsilon_1/\beta_1)}{(\gamma_1/\beta_1) - (\gamma_2/\beta_2)},$$

then the variant is realized that is shown in Fig. 14b. For this to happen, it suffices to have $\tilde{\gamma}_1 < \tilde{\gamma}_2$.

The studied variants imply that, if one introduces a species N_2 for which $\gamma_2/\beta_2 > \gamma_1/\beta_1$, then its introduction into the system (M_0 , N_1 , M_1) will fail. Yet, conversely, if one introduces the species N_1 into the system (M_0 , N_2 , M_1), then this introduction will always be successful. Consequently the aboriginal species N_2 will be completely supplanted. However, if the condition $\gamma_1/\beta_1 > \gamma_2/\beta_2$ is satisfied, i.e., the system can exist in trigger states, then the result of introduction depends highly on the initial state of the studied biogeocenosis and the number of individuals of the colonizing species.

When the mass M becomes larger than the quantity

$$\frac{\varepsilon_1}{\beta_1} + \frac{\varepsilon}{\gamma_1} + \left(1 + \frac{\gamma_1}{\beta_1}\right) \frac{(\varepsilon_2/\beta_2) - (\varepsilon_1/\beta_1)}{(\gamma_1/\beta_1) - (\gamma_2/\beta_2)}$$

and the condition $\gamma_1/\beta_1 > \gamma_2/\beta_2$ is satisfied here, then biogeocenoses with two species prove to be unstable, and the only possible variant turns out to be a self-oscillatory one with three species (Fig. 14c).

We can naturally expect that more complex triggers can also arise in more complicated systems having crossed relations between producers and consumers. The trigger behavior of biogeocenoses imposes restrictions on anthropogenic action, since when strong enough influences are exerted, the system no longer returns to its former state.

3. THE STATISTICAL MECHANICS OF ECOSYSTEMS

A. The theory of Kerner, non-ergodicity of Volterra systems

The problem of the possible application of the methods of statistical physics and thermodynamics to biological systems has been intensively discussed in the physical literature, since biological systems are not equilibrium systems.^[52-54] Generally biogeocenoses contain a large number of species—many hundreds and even thousands. Therefore Lotka^[10] has also proposed using the apparatus of statistical physics for describing ecosystems, E. H. Kerner^[55,56] has devised a statistical theory that uses the apparatus of W. Gibbs for biological associations that are described by the equations of V. Volterra (Eqs. (1.4)).

In the phase space v_r , the state of each of the biological associations constitutes a point, while the state of an ensemble is an ensemble of points. If we take a sufficiently large number of biological associations, then, following Gibbs, we can introduce in the phase plane a fluid of density $\rho(v_1, v_2, \dots, v_n)$ that describes the behavior of the ensemble. Since the number of points in the ensemble does not vary (the fluid is nowhere created nor destroyed), we can write an equation of continuity:

$$\frac{\partial \rho}{\partial t} + \sum_{r=1}^n v_r \frac{\partial \rho}{\partial v_r} + \sum_{r=1}^n \rho \frac{\partial v_r}{\partial v_r} = 0. \quad (3.1)$$

The last summation in (3.1) vanishes owing to the antisymmetry of the α_{ij} . Therefore the theorem of Liouville is automatically satisfied.

By analogy with statistical mechanics, E. Kerner introduced a microcanonical and a canonical ensemble. We have the following distribution function for the microcanonical ensemble:

$$\rho = \rho_0 \delta(G - G_0).$$

The average over the microcanonical ensemble of the function

$$\frac{\partial G}{\partial v_r} = \tau_r \left(\frac{N_r}{q_r} - 1 \right)$$

is zero. This implies that the average over the ensemble of N_r is q_r .

We have the following expression for the time-averages:

$$\lim_{T \rightarrow \infty} \frac{1}{T} \int_0^T \frac{d \ln N_r}{dt} dz \rightarrow 0.$$

Therefore

$$\varepsilon_r + \frac{1}{\beta_r} \sum_{s=1}^n \alpha_{sr} \frac{1}{T} \int_0^T N_s dt \rightarrow 0.$$

which implies that

$$\lim_{T \rightarrow \infty} \frac{1}{T} \int_0^T N_s dt = q_s.$$

That is, the averages over the ensemble and over time of the quantity N_k are equal to one another. However, as we shall show below, ergodicity still does not hold, since the averages over the ensemble and those over time are not equal for the higher moments.

One can derive all the fundamental thermodynamic relationships by starting with Gibbs' phase integral. E. Kerner found an analog of the Dulong-Petit law, or a general rule of "thermodynamic" mixing of biological associations having different "temperatures." E. Kerner also constructed curves for the variation of the analogs of entropy and free energy with increasing "temperature." Goodwin^[57] used an idea analogous to that of E. Kerner for constructing a statistical mechanics of biochemical systems.

Other statistical characteristics have also been proposed for describing biological communities. It was assumed here in introducing these characteristics that communities that are more complicated in structure are also more stable (as we have seen above, this is generally not true). For example, Margalef^[58, 59] has proposed using a quantity called the diversity for describing communities:

$$D = -N \sum_{i=1}^n p_i \ln p_i. \quad (3.2)$$

Here $p_i = N_i/N$, $N = \sum_{i=1}^n N_i$, N_i is the population of the i -th species in the community, and n is the number of species. We can easily see that the diversity differs from the informational entropy only in the factor N .

MacArthur^[60, 61] has proposed a measure analogous to (3.2), where p_i was taken to mean the probability of transport of energy along a given pathway. Svirezhev^[62] has made a critical review of these theories.

Just as in statistical mechanics, the problem of substantiating E. Kerner's theory rests on proving the properties of mixing and ergodicity of the solutions of V. Volterra's equations.

Krylov^[63] has shown that, if the dynamic trajectories in phase space are unstable at every point, and specifically, two trajectories passing through close-lying points strongly diverge from one another, then the system is a mixing one. Then an initial element of the phase volume will elongate into a very long and thin fila-

ment that will wrap itself ever more over the entire hypersurface $G = \text{const}$. In this case we can apply statistical mechanics. Unfortunately, Eqs. (1.4) are not of this type.^[64] One can easily derive from (1.4) an equation for the distance Δv_r between phase points on two different trajectories v_r and v_r' that started from close-lying points at the initial instant of time:

$$\beta_r \frac{d}{dt} \Delta v_r = \sum_{s=1}^n \alpha_{sr} q_s (e^{v_s} - e^{v_s'}).$$

If we multiply the left- and right-hand sides of this equation by $q_r (e^{v_r} - e^{v_r'})$ and sum over r for small Δv_r , we get

$$\sum_{r=1}^n \beta_r q_r \frac{\Delta v_r^2}{2} = \text{const.}$$

On the other hand, near the steady states for the trajectories themselves, we shall have $G = \sum_{r=1}^n \beta_r q_r [1 + (v_r^2/2)] = \text{const}$. If the initial values of $|\Delta v_r|$ are small in comparison with v_r , then, as we see, the trajectories will never diverge far enough. That is, there is no mixing.

As has been shown in^[27], the system of equations (1.1) also proves to be non-ergodic near the steady state. In fact, let the solution of Eq. (1.1) have the form

$$N_i = q_i [1 + \delta_i(t)],$$

where the δ_i are small. Then, upon introducing the new variables $x_i = \delta_i \sqrt{q_i \beta_i}$ and neglecting second-order small terms, we get

$$\dot{x}_i = \sum_{j=1}^n C_{ij} x_j, \quad (3.3)$$

where

$$C_{ij} = \sqrt{\frac{q_i}{\beta_i}} a_{ij} \sqrt{\frac{q_j}{\beta_j}} = -C_{ji}.$$

Let A_{kl} be the k -th element of the l -th eigenvector of the matrix C_{ij} :

$$\sum_{k=1}^n C_{ik} A_{kl} = \lambda_l A_{il}.$$

Owing to the antisymmetry of the matrix C_{ik} , we have $\lambda_j^* = -\lambda_j$. Let $A_{ji}^* = A_{ij}^*$. We shall choose the condition of normalization of the matrix A in the form

$$\sum_{i=1}^n A_{ik}^* A_{ij} = \delta_{ij}.$$

That is, A^* is the Hermitian conjugate matrix of A . We can write the general solution of Eq. (3.3) in the form

$$x_i(t) = \sum_{l=1}^n \alpha_l A_{il} e^{\lambda_l t}, \quad \text{where } \alpha_m = \sum_{i=1}^n x_i(0) A_{im}^*.$$

Since the average of N_r over the canonical ensemble is q_r , and owing to the additivity of the function

$$G_v = \sum_{i=1}^v \tau_i (e^{v_i} - v_i)$$

we can easily convince ourselves that the average over the ensemble of $x_i x_j$ is zero. At the same time, the time-average is

$$\begin{aligned} \lim_{T \rightarrow \infty} \frac{1}{T} \int_0^T x_i x_j dt &= \lim_{T \rightarrow \infty} \frac{1}{T} \int_0^T x_i x_j^* dt \\ &= \sum_{mqkl} A_{il} A_{kl}^* A_{jm}^* A_{qm} \lim_{T \rightarrow \infty} \frac{1}{T} \int_0^T e^{(\lambda_i + \lambda_m^*)t} dx_h(0) x_q(0) \\ &= \sum_{klq} A_{il} A_{kl}^* A_{jl}^* A_{qk} x_h(0) x_q(0) = \sum_l A_{il} A_{jl}^* \left| \sum_k A_{kl} x_h(0) \right|^2 \neq 0. \end{aligned}$$

Thus the ergodic theorem is not satisfied. The given example is instructive, since systems of equations that are analogous to Volterra's systems, e. g., those describing the behavior of coupled chains of harmonic and anharmonic oscillators, are widely used in physics.

B. Choice of macroparameters and equations for the trophic levels

In spite of the fact that direct transfer of the methods of statistical physics to study biocenoses faces difficulties, one can construct a certain theory of the macroquantities that describe the behavior of the system as a whole, e. g., construct equations for the trophic levels, by using the equations for the species.

This is important for evaluating the use of the equations for the species to describe the dynamics of the trophic levels. Such a use of predator-prey equations is widespread in constructing portrait models of ecosystems.

Let the system of equations that describes the dynamics of the biomasses of the individual species of organisms have the form^[65]

$$\begin{aligned} \frac{dM_{\text{prey}}^i}{dt} &= \varepsilon_{\text{prey}}^i M_{\text{prey}}^i - \sum_{j=1}^n \gamma_{\text{prey}}^{ij} M_{\text{prey}}^i M_{\text{predator}}^j, \\ \frac{dM_{\text{predator}}^i}{dt} &= -\varepsilon_{\text{predator}}^i M_{\text{predator}}^i \\ &\quad + \sum_{j=1}^n \gamma_{\text{predator}}^{ij} M_{\text{predator}}^i M_{\text{prey}}^j. \end{aligned} \quad (3.4)$$

Here M_{prey}^i is the biomass of the i -th species of prey, while M_{predator}^i is the biomass of the i -th species of predators, $\varepsilon_{\text{prey}}^i$ and $\varepsilon_{\text{predator}}^i$ are respectively the birth rate of the prey and the death rate of the predators, the $\gamma_{\text{prey}}^{ij}$ are the coefficients of consumption of prey by the predators, and the $\gamma_{\text{predator}}^{ij}$ are the transport coefficients of the biomasses of the prey into the biomasses of the predators. All the coefficients are assumed to be constants greater than zero. Let us assume that

$$\begin{aligned} \varepsilon_{\text{prey}}^i &= \varepsilon_{\text{prey}} + \Delta \varepsilon_{\text{prey}}^i, \quad \varepsilon_{\text{predator}}^i = \varepsilon_{\text{predator}} + \Delta \varepsilon_{\text{predator}}^i; \\ \gamma_{\text{prey}}^{ij} &= \gamma_{\text{prey}} + \Delta \gamma_{\text{prey}}^{ij}, \quad \gamma_{\text{predator}}^{ij} = \gamma_{\text{predator}} + \Delta \gamma_{\text{predator}}^{ij}. \end{aligned} \quad (3.5)$$

Here $\varepsilon_{\text{prey}}$ and $\varepsilon_{\text{predator}}$ are the averages of the quantities $\varepsilon_{\text{prey}}^i$ and $\varepsilon_{\text{predator}}^i$, while γ_{prey} and γ_{predator} are the averages of the quantities $\gamma_{\text{prey}}^{ij}$ and $\gamma_{\text{predator}}^{ij}$. Moreover, $\Delta \varepsilon_{\text{prey}}^i$, $\Delta \varepsilon_{\text{predator}}^i$, $\Delta \gamma_{\text{prey}}^{ij}$, and $\Delta \gamma_{\text{predator}}^{ij}$ are much smaller than $\varepsilon_{\text{prey}}$, $\varepsilon_{\text{predator}}$, γ_{prey} and γ_{predator} , respectively.

Let us differentiate (3.4) with respect to time, and replace on the right-hand sides of the obtained equations the derivatives dM_{prey}^i/dt and $dM_{\text{predator}}^i/dt$ by their expressions from (3.4). Next, let us sum each of the obtained equations with respect to i . Consequently, after dropping small quantities of the second order in $\Delta \varepsilon$ and γ , we have

$$\begin{aligned} L_{\text{prey}} &= - \sum_{i=1}^n \Delta \varepsilon_{\text{prey}}^i M_{\text{prey}}^i \bar{M}_{\text{prey}}, \\ L_{\text{predator}} &= \sum_{i=1}^n \Delta \varepsilon_{\text{predator}}^i M_{\text{predator}}^i \bar{M}_{\text{predator}}. \end{aligned} \quad (3.6)$$

Here $M_{\text{prey}} = \sum_{i=1}^n M_{\text{prey}}^i$ and $M_{\text{predator}} = \sum_{i=1}^n M_{\text{predator}}^i$ are the biomasses of the trophic levels, and

$$\begin{aligned} \bar{M}_{\text{prey}} &= -\varepsilon_{\text{predator}} + \gamma_{\text{predator}} M_{\text{prey}}, \quad \bar{M}_{\text{predator}} \\ &= \varepsilon_{\text{prey}} - \gamma_{\text{prey}} M_{\text{predator}}, \end{aligned}$$

$$L_{\text{prey}} = \dot{M}_{\text{prey}} = \left[\frac{d}{dt} (M_{\text{prey}} \bar{M}_{\text{predator}}) + (\dot{M}_{\text{prey}} - M_{\text{prey}} \dot{\bar{M}}_{\text{predator}}) (\bar{M}_{\text{predator}} + \bar{M}_{\text{prey}}) \right],$$

$$L_{\text{predator}} = M_{\text{predator}} - \left[\frac{d}{dt} (M_{\text{predator}} \bar{M}_{\text{prey}}) + (\dot{M}_{\text{predator}} M_{\text{predator}} \bar{M}_{\text{prey}}) (\bar{M}_{\text{predator}} + \bar{M}_{\text{prey}}) \right].$$

(We have also replaced in Eqs. (3.6) the terms like $\sum_{i,n=1}^n \Delta \gamma_{\text{prey}}^{ij} M_{\text{prey}}^i M_{\text{predator}}^j$ and $\sum_{i,j=1}^n \Delta \gamma_{\text{predator}}^{ij} M_{\text{predator}}^i M_{\text{prey}}^j$ by the expressions that we get from (3.4) by summing the latter over i).

Upon differentiating (3.6) with respect to time, and replacing the expressions $\sum_{i=1}^n \Delta \varepsilon_{\text{prey}}^i M_{\text{prey}}^i$ and $\sum_{i=1}^n \Delta \varepsilon_{\text{predator}}^i M_{\text{predator}}^i$ on the right-hand sides of the obtained expressions by their values from (3.6), we get equations for the biomasses of the trophic levels:

$$\begin{aligned} \dot{L}_{\text{prey}} &+ (\dot{\bar{M}}_{\text{prey}} / \bar{M}_{\text{prey}}) L_{\text{prey}} + \dot{\bar{M}}_{\text{predator}} L_{\text{prey}}, \\ \dot{L}_{\text{predator}} &= (\dot{\bar{M}}_{\text{predator}} / \bar{M}_{\text{predator}}) L_{\text{predator}} + \dot{\bar{M}}_{\text{prey}} L_{\text{predator}}. \end{aligned} \quad (3.7)$$

We see that the given system of equations is not a Volterra system of equations of the predator-prey type. As we shall show below, it has qualitatively new properties.

In the general case, in order to derive the equations for the macroscopic quantities (i. e., for the biomasses of the trophic levels) from the equations for the microscopic quantities (i. e., from the equations for the species), we must systematically replace the one set of time functions $M_{\text{prey}}^i(t)$ and $M_{\text{predator}}^i(t)$ by other time functions, respectively by

$$M_{\text{prey}}, \dot{M}_{\text{prey}}, \ddot{M}_{\text{prey}}, \dots, d^{n-1} M_{\text{prey}} / dt^{n-1},$$

and

$$M_{\text{predator}}, \dot{M}_{\text{predator}}, \ddot{M}_{\text{predator}}, \dots, d^{n-1} M_{\text{predator}} / dt^{n-1}.$$

Let us study the solutions of Eqs. (3.7) near the steady states

$$M_{\text{predator}} = (\varepsilon_{\text{prey}} / \gamma_{\text{prey}}) + \nu, \quad M_{\text{prey}} = (\varepsilon_{\text{predator}} / \gamma_{\text{predator}}) + \mu, \quad (3.8)$$

where μ and ν are small increments.

Since $\dot{M}_{\text{predator}}/\bar{M}_{\text{predator}}$ and $\dot{M}_{\text{prey}}/\bar{M}_{\text{prey}}$ are of the zero order of smallness with respect to μ and ν , while L_{predator} and L_{prey} are of the first order of smallness, we can neglect the second terms on the right-hand side of (3.8) near equilibrium. (It proves effective to apply the Krylov-Bogolyubov method^[66] far from equilibrium.) Then we can easily integrate (3.7), and we have

$$L_{\text{prey}} = A\bar{M}_{\text{prey}}, \quad L_{\text{predator}} = B\bar{M}_{\text{predator}}, \quad (3.9)$$

where A and B are constants of integration. Comparison of (3.9) and (3.6) shows that

$$A = \sum_{i=1}^n \Delta \varepsilon_{\text{prey}}^i M_{\text{prey}}^i,$$

$$B = \sum_{i=1}^n \Delta \varepsilon_{\text{predator}}^i M_{\text{predator}}^i,$$

which can be determined by starting with the initial conditions.

Upon using (3.8) and (3.9), we get the equations for μ and ν :

$$\begin{aligned} \ddot{\mu} + \varepsilon_{\text{predator}}(\gamma_{\text{prey}}/\gamma_{\text{predator}})\dot{\nu} &= A\gamma_{\text{predator}}\mu, \\ \ddot{\nu} - \varepsilon_{\text{prey}}(\gamma_{\text{predator}}/\gamma_{\text{prey}})\dot{\mu} &= -B\gamma_{\text{prey}}\nu. \end{aligned} \quad (3.10)$$

The characteristic roots of this system, with account taken of the smallness of $B\gamma_{\text{prey}}$ and $A\gamma_{\text{predator}}$ as compared with $\varepsilon_{\text{prey}}\varepsilon_{\text{predator}}$, can be written in the form

$$k_{1,2} \approx \pm \sqrt{\varepsilon_{\text{predator}}\varepsilon_{\text{prey}}}, \quad k_{3,4} \approx \pm \sqrt{(1/2)AB\gamma_{\text{predator}}\gamma_{\text{prey}}}. \quad (3.11)$$

Thus, the dynamics of the biomass of the trophic levels can be described as a sum of two oscillations, a fast one and a slow one.

Figure 15 gives the results of computer calculations of the dynamics of the biomasses of individual species and of the entire lower trophic level for the case of a two-level model system having three species on each of the levels. We can distinctly see the fast and slow oscillations. The lack of mixing is manifested in the fact that the phase differences of the fast and slow oscillations hardly vary, but only oscillate weakly about certain mean values. In the case where the ecological

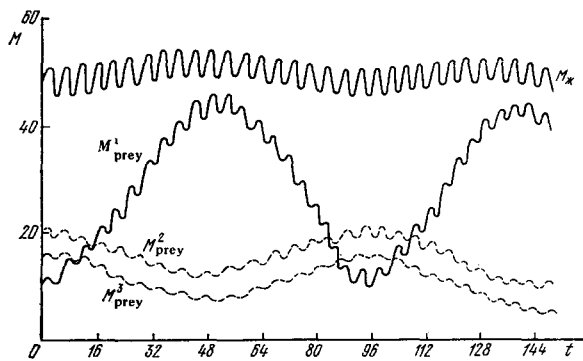


FIG. 15. Variation in the number of prey for a two-level trophic system for the case of weakly diverging coefficients (three species per level). Values of the coefficients: $\varepsilon_{\text{prey}}^1 = 3 \pm 0.3$, $\varepsilon_{\text{predator}}^1 = 1 \pm 0.1$; $\gamma_{\text{predator}}^{12} = 0.11 \pm 0.02$, $\gamma_{\text{predator}}^{13} = 0.02 \pm 0.004$. Steady-state values: $M_{\text{prey}}^1 = 10$, $M_{\text{prey}}^2 = 20.8$, $M_{\text{prey}}^3 = 16$, $M_{\text{prey}} = \sum_{i=1}^3 M_{\text{prey}}^i$.

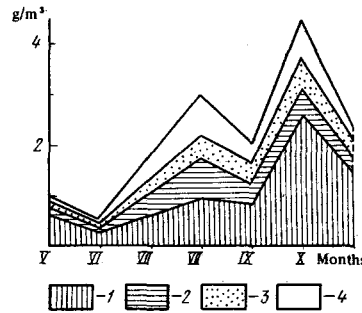


FIG. 16. Variation of the biomass of the phytoplankton in the surface layer of the water of the Ivan'kovskoe reservoir during the vegetative season of 1969. 1—diatoms, 2—green, 3—pyrophyta, 4—others.

coefficients are close together, as is quite evident from the diagram, the fast oscillations for the species that belong to a single trophic level coincide in phase. In this regard, the pattern of seasonal variations of the biomasses of different planktonic algae of the Ivan'kovskoe reservoir (Fig. 16) is of interest.^[71] The oscillations shown in the diagram correspond to the fast oscillations visible in Fig. 15. We can easily see that the maxima of the biomasses for the different species of unicellular algae prove to be synchronized, which confirms the hypothesis of close-lying ecological coefficients.

C. Fokker-Planck equations for describing populations

A serious defect of the deterministic models is that they ignore the natural biological variability under the influence of random factors of the environment. One can overcome this defect by replacing the constant parameters of the deterministic equations that we have studied by random time-dependent functions.

On the other hand, the population interactions within the system can be accompanied by changes in the dynamics of the biomasses of the species entering into the ecosystem owing to random migrations and immigrations. In taking these factors into account, studies of the behavior of the trajectories in phase space or investigations of the stability of the steady states or of the limit cycles when acted on by an individual infinitely small perturbation prove to be totally insufficient. The stability of the system can be estimated far more adequately by using the parameter termed the lifetime of the ecosystem, i.e., the mean time during which the species composition of the system does not vary in spite of random perturbations.

Here ecosystems of the Volterra type, i.e., those describable by Eqs. (1.1), are unstable because of their non-gross nature. We can see this easily with the example of a predator-prey system (Eqs. (1)). On the phase plane N_1N_2 , the solutions of Eqs. (1) have the form of concentrically-lying closed trajectories. If, e.g., the prey can migrate randomly into the ecosystem or emigrate from it, then this process will be represented on the phase plane N_1N_2 as a random shift from a trajectory defined by a certain value of the pa-

parameter G to a trajectory having another (close-lying) value of G . Whether we find the system at a given instant of time on any particular trajectory G_1, \dots, G_R will be determined probabilistically.

Since the trajectory where we find the system is determined only by chance, the probability of finding the system is distributed over an ever larger number of trajectories in the course of time. Thus the probability of finding the system on a trajectory having a large value of G increases. However, these trajectories pass near the coordinate axes. When the phase point proves to lie at a distance less than unity from a coordinate axis, the system becomes degenerate, since a species cannot exist in a number smaller than one individual. It was shown in^[68] that the lifetime of a system of the predator-prey type declines hyperbolically with increasing dispersion of the perturbing factor.

For the gross systems, e.g., for those whose phase portraits are shown in Fig. 5, the lifetime will be determined by the rate of diffusion of the phase point from a stable singular point or a stable limit cycle as a function of random perturbations and of the size of the perturbing factor.

If the random perturbations are small, it is convenient to use the apparatus of the Fokker-Planck equations for studying the probability of finding the ecosystem in any particular state. A Fokker-Planck equation that was constructed on the basis of the deterministic equation of Verhulst has been studied in detail in^[27]. It is interesting to note that it coincides in form with the Bloch equation that is widely known in solid-state physics.

CONCLUSION

The biophysics of ecosystems has posed for physics an entire set of new problems. First of all, there is the study of selection rules in living systems. These selection rules act from the molecular level up to the level of ecosystems, and they involve the nature of the material cycle. Therefore an understanding of the biophysical properties of organisms and their characteristics can be gained only on the basis of a deep understanding of these selection rules. The impact of man on the environment alters the nature of the cycle of the chemical elements in the biosphere, and therefore previously stable systems cease to be so under the new conditions. Apparently the trigger properties of living systems play an especially important role here.

The importance of applying the methods of non-equilibrium statistical mechanics for understanding the theory of evolution of biological systems has been discussed repeatedly in the physical literature.^[52] The study of ecosystems also opens up a large class of objects that occupy an intermediate position between those studied by pure dynamics and by statistical physics. These systems do not obey the ergodic theorem, and they do not possess mixing properties. Yet one can introduce macroparameters to describe them and apply the method of equations of the Fokker-Planck type.

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