

Homeostasis and Self-Similarity of Biological System Dynamics

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Presented by Academician V.N. Bol'shakov July 26, 2006

Received October 10, 2006

DOI: 10.1134/S0012496607020196

Homeostasis is the stability of parameters of an open dynamic system that are important (or even necessary) for the existence of the system. This was stated by the physiologist Kennon, who studied animal organisms and introduced term homeostasis [1]. However, since the development of cybernetics in the late 1940s [2], the mechanisms responsible for maintaining homeostasis have been identified with negative feedback loops. Terms were substituted: the regulation of environment (if it is an internal environment) was equated with self-regulation; however, these terms are not the same. Not all parameters of organisms are stable: a relative constancy of the most important physical and chemical parameters of the body, such as acidity, inner pressure, chemical composition, etc., does not mean that there are no consistent changes (growth and development).

The parameters (attributes) of homeostatic systems are formally subdivided into two groups: some parameters are normally constant, whereas others vary. According to the general theory of systems, an object (system) that has mechanisms responsible for maintaining homeostasis may be presented as two indissolubly related, interdependent parts (subsystems), one of which varying and the other remaining constant.

One part of such a system—subsystem X —performs work (using an external source) to maintain constancy of the other (stable) subsystem E . The changes in the parameters reflecting dimensional parameters (the substance and/or energy content) of the system is described as

$$\frac{dX}{dt} = X(A - kR - F),$$

$$\frac{dE}{dt} = FX - RE,$$

where A is the specific rate of the inflow of energy and/or substance to subsystem X , R is the specific rate of irreversible dissipation of energy in the subsystem E , F is the specific energy consumption by the subsystem X used to stabilize the subsystem E , and k is an arbitrary coefficient. The stationary condition for E is $FX = RE$.

Ecological systems belonging to different structural levels, from the organism–environment level to the biosphere (the biota–inanimate matter system) may be represented as homeostatic systems [3]. The term homeostasis was used in the title of the first work on the biotic regulation on Earth [4]: the gas composition of atmosphere, for instance, is not self-regulated; its constancy is maintained by the animate component of the biosphere (Earth's biota) using external (solar) energy.

Homeostatic mechanisms may be represented by either negative (“self-regulation” or “competition of system elements”) or positive (“self-acceleration” or “cooperation of system elements”) feedbacks: both cases comply with the condition $F/X = R/E$ [5, 6].

A biological system cannot be indefinitely small (because vital processes such as synthesis and decay of biological macromolecules are not indefinitely small) or indefinitely large.

Hence, the rate of inevitable energy dissipation by an active living subsystem (respiration) and the rate of energy outflow in the concentrated form (the energy of chemical bonds of rejected substances) must have at least two components: immanent components, which characterize the specificity of living subsystem, and the components that are determined by the effects of homeostatic mechanisms.

Previously, we showed [6] that, in this case, the dynamics of a biological system may be described by the equation

$$\frac{dX}{dt} = (w_X - v_X X)X - C_X, \quad (1)$$

where w_X is the immanent component of specific production, v_X is the specific intensity of the respiratory component, which is determined by the work needed for homeostasis maintenance, and C_X is the intensity of

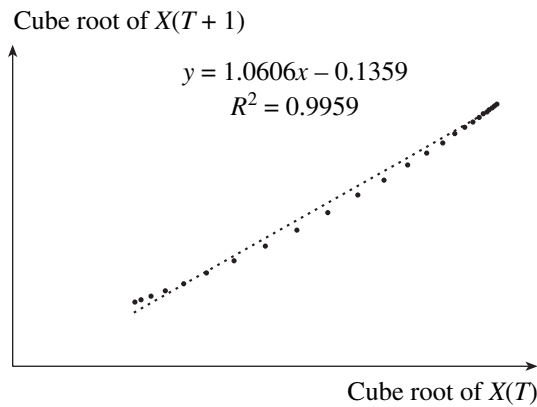


Fig. 1. The fit of values obtained with the use of Bertalanffy's recurrent equation (the dotted line) to the values obtained by numerical simulation using model (3) at $b = 0.5$ (large dots). The corresponding equation of linear regression (the regression coefficient does not differ from 1, and the initial ordinate does not differ from 0) and the determination coefficient are shown.

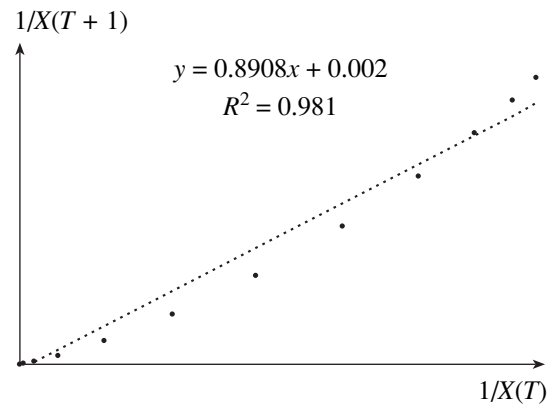


Fig. 2. The fit of values calculated with the use of the Verhulst-Pearl recurrent equation (the dotted line) to the values obtained by numerical simulation using model (3) at $b = 1$ (large dots). The designations are the same as in Fig. 1.

the respiratory component which is determined by the necessity to spend energy on homeostasis maintenance and the rate of substance rejection.

In turn, w_X is the difference between the specific inflow of substance and energy and the corresponding immanent components of outflows, such as respiration and rejection [6].

The parameters of Eq. (1) may depend, in the general case, on the state of system X . In concordance with the self-similarity principle [7] and the well known universality of allometric relationships [8], the simplest and most acceptable form of such a relationship may be $f(X) = kX^{b-1}$, where b is the allometric coefficient (fractal dimension), which is not necessary integral:

$$w = k_1 X^{b-1},$$

$$v = k_2 X^{b-1},$$

$$C = k_3 X^{b-1}.$$

Therefore, Eq. (1) assumes the form

$$\frac{dX}{dt} = k_1 X^b - k_2 X^{b+1} - k_3 X^{b-1} \quad (2)$$

and can be rewritten as

$$\frac{dX}{dt} = r_0 X^b \left(1 - \frac{K_1}{X}\right) \left(1 - \frac{X}{K_2}\right), \quad (3)$$

where r_0 is a coefficient that determines the growth rate, K_1 is the lower (unstable) stationary state of system X , and K_2 is its upper (stable) stationary state. Equation (2) at $b = 1$ describes the dynamics of a population characterized by intrapopulation competition (at a high density, the rate of population growth is decreased) and cooperation (the rate of population growth is small if

the population size is small because of a higher mortality). These equations, which describe "Allee's effect" [9], were studied earlier in detail [10, 11].

Equations (1) and (2) are based on the concept that the "active" subsystem in the homeostatic system not only provides self-development, but also keeps the "passive," "buffer" subsystem in the stationary state. These equations represent living systems of any rank because they have at least one energy inflow and two outflows, i.e., dissipation (respiration) and the outflow to other systems (rejection of substance). Comparison of these equations with Eq. (3) suggests that the parameters of Eq. (3) (r_0 , K_1 , and K_2) may be interpreted in terms of the flows of substance and energy, which are based on the fundamental laws of nature (the first and second laws of thermodynamics). Note that the parameters in Eq. (3) do not depend on the coefficient b , i.e., they are invariant with respect to the fractal dimension. Moreover, they are interrelated: they may be expressed in terms of the parameters of Eq. (2):

$$K_2 = \frac{1}{2k_2} \left(k_1 - \sqrt{(k_1^2) - 4k_2k_3} \right),$$

$$K_2 = \frac{1}{2k_2} \left(k_1 - \sqrt{(k_1^2) - 4k_2k_3} \right),$$

$$r_0 = \frac{1}{2} \left(k_1 - \sqrt{(k_1^2) - 4k_2k_3} \right).$$

The changes in coefficient b determine the relative rate of the approach of a growing system (the initial condition is $X_0 > K_1$) to the definite size K_2 : it is increased with an increase in b . The growth rate of system for $b < 1$ may be well described by canonical Bertalanffy's equation in the recurrent form [12], which is frequently used for quantitative description of organism growth (Fig. 1):

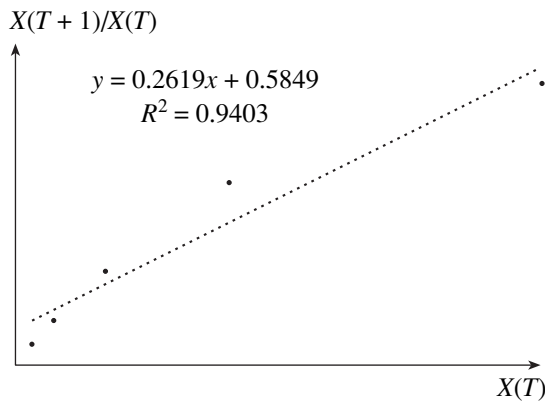


Fig. 3. The fit of values calculated with the use of the recurrent equation (the dotted line) of hyperbolic growth to the values obtained by numerical simulation using model (3) for monotonously increasing part of model curve for $b = 1.5$ (large dots). The designations are the same as in Fig. 1.

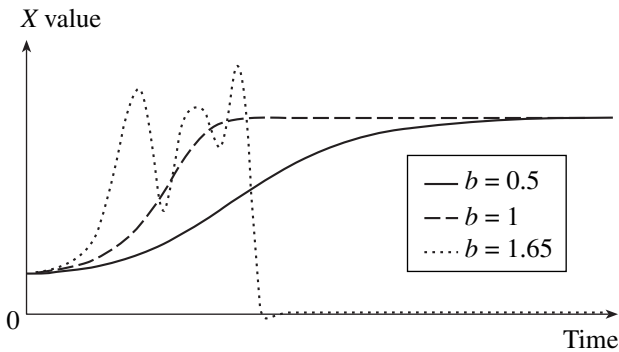


Fig. 4. The dynamics predicted by model (3) for different b values.

$$\frac{dX}{dt} = \eta X^{2/3} - \kappa X.$$

If the regression is constructed on the basis of the classic logistic Verhulst–Pearl equation for population growth in its recurrent form [12], the X growth for $b = 1$ can be described statistically (Fig. 2):

$$\frac{dX}{dt} = rX \left(1 - \frac{X}{K} \right).$$

The growth of subsystem X for $b > 1$, at least in the initial period, may be statistically described by an equation of hyperbolic growth in the recurrent form (Fig. 3),

$$\frac{dX}{dt} = r_1 X (1 + KX),$$

which infers the substitution of differential equations by difference equations, which is inevitable in numerical modeling.

It may be concluded that the fractal dimension—coefficient b in Eq. (3)—characterizes not only the structural level of organization of biological systems, but also the growth rate associated with this level. It seems that the biological systems (at least at the initial

stages) grow relatively (taking into account the scale invariance) faster than the subsystems of these systems.

The use of difference rather than differential equations for the description of the dynamics of biological objects is valid because of biological rhythms (cycles), which determine the characteristic times of the integration of dynamic processes at higher levels [14]. The description of X dynamics by difference equations shows that, when the system grows very fast (b is large, as in the last case) and approaches K_2 , growth is replaced by oscillations, which diverge stronger with an increase in the specific growth rate (determined, cet. par., by b), as it was shown by May [13]. A “too rapidly growing” system is inevitably degenerate at a certain moment (when X is less than the critical value of K_1) (Fig. 4). The faster the growth (and the higher the degree of system organization), the higher the possibility that the growth will be replaced by a rapid decay.

ACKNOWLEDGMENTS

This work was supported by the Presidium of the Russian Academy of Sciences (project no. 3.8 of Program P16), Ministry of Science of the Russian Federation (project no. 2006-RI-112.0/001/337), and Russian Foundation for Basic Research (project no. 05-04-48939).

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