Distributed Self-regulation Induced by Negative Feedbacks in Ecological and Economic Systems

V.V.Gafiychuk

Institute for Applied Problems of Mechanics and Mathematics,
National Academy of Sciences of Ukraine, 3b Naukova str., Lviv,
290601, Ukraine

I.A.Lubashevsky

Laboratory of Synergetics, the Moscow State University, Vavilova str.
46/92, Moscow, 117333, Russia

Robert E. Ulanowicz

University of Maryland Chesapeake Biological Laboratory, Solomons,
MD 20688-0038 USA
(December 28, 2013)

We consider an ecological system governed by Lotka-Volterra dynamics and an example of an economic system as a mesomarket with perfect competition. We propose a mechanism for cooperative self-regulation that enables the system under consideration to respond properly to changes in the environment. This mechanism is based on (1) active individual behavior of the system elements at each hierarchical level and (2) self-processing of information caused by the hierarchical organization. It is shown how the proposed mechanism suppresses nonlocal interaction of elements belonging to a particular level as mediated by higher levels.

1. INTRODUCTION

A great number of natural systems are organized hierarchically. Their hierarchical organization allows that such a system can be divided into a collection of subsystems (which will be called levels) involving many elements that are similar in their properties. The elements of the various levels differ substantially, however, in their characteristics. The subsystems can be ordered according to their mutual interactions: The behavior of an element at each level is determined by the aggregated state of a certain large group of elements belonging to the nearest lower level, while each element of a lower level is directly governed by a given element of the higher level.

Such hierarchical organization is inherent in many ecological and economic systems. For example, we encounter a huge number of goods in an economic market in contrast to relatively few types of raw materials. Hence, the network of products and trade that transforms natural materials into a wide variety of goods will be a highly branching system. Suppose firms of a given type of activity that are approximately equal in power make up a certain level. The market then involves several such levels, from lower ones consisting of retailing companies up to the highest one that deals with the production of raw materials. In this case, the prices of products of firms dealing in wholesale trade are the direct averages of the prices of goods at the terminal retail points that are supplied by these firms.

Hierarchical organization is encountered frequently in ecological systems as well. Ecological systems often form trophic food chains or pyramids. Levels of such an ecosystem are made up of animals comparable in size and playing much the same role in the prey-predator relationships. Energy usually flows from smaller organisms via consumption to larger predators. The linkages from the small organisms generally vary over smaller scales. The larger animals that dominate these smaller organisms do so over larger scales of space and time. That is, because of their wider ambits, predators control larger regions of space for longer times. From this perspective, the hierarchical levels of most pelagic trophic networks are defined according to particle size (Platt et al. 1981). It becomes possible to regard the populations at each level as being continuously distributed across their particular segment of space. This representation of the trophic hierarchy is depicted in Fig.1.

The characteristic feature of hierarchical systems is the nonlocal interference among elements at the same level as mediated by the higher levels. Higher levels in their turn feed only the averaged state of the preceeding levels. Thus, local variations in the behaviors of elements belonging to lower levels reflect the states of elements at higher level over
larger scales. The larger component then changes the state of elements at the lower level in a region whose domain substantially exceeds the size of the initial perturbation. Such nonlocal interaction is not reliable, because it does not stem from the local laws of element interaction between neighboring levels that control the life of the system.

These characteristics make such hierarchical systems fragile with respect to perturbations in the environment. In order for systems to continue living, there should be some mechanism of self-regulation that would maintain system stability and would suppress (at least, to some extent) nonlocal interactions among elements at the same level.

Below we suggest a possible mechanism for such self-regulation. In particular, in the next section we analyze a set of model ecosystems governed by Lotka-Volterra dynamics. Certainly, the dynamics of real ecosystems are far more sophisticated, however, models with Lotka-Volterra dynamics typify many ecosystem characteristics and highlight nonlocal fragility in a most pronounced way.

A cooperative mechanism for self-regulation whereby the hierarchical system as a whole can react perfectly has been developed by [5], [6]. This mechanism consists in the response of each individual element to the small piece of the information available to it on the state of the whole system. The conservation of medium flowing through the supplying network gives rise to a certain processing of information that results in self-consistent behavior of the elements that leads to perfect self-regulation.

II. ECOSYSTEM MODEL AND THE DISTRIBUTED SELF-REGULATION

We begin by considering a simple mathematical model of a pelagic marine ecosystem involving $2N$ levels in which is found a large number of animal species. At the bottom of this system is phytoplankton (level 1) and at the top (level $2N$) stands the population of large predatory fish. The characteristic features that distinguish each level, for example level $i$, are the body size of the individual organisms and the spatial size $\ell_i$ of the domain that is controlled by each individual fish at this level.

The flow of biomass in this trophic system is assumed to be governed by the Lotka-Volterra model, which describes hierarchical level $i$ in terms of the spatial distribution of the biomass $c_i(\mathbf{r}, t)$ and treats the interaction between different levels as feeding relations, where the larger species play the role of predators and the smaller, those of prey. According to what was discussed in the Introduction, we assume that the characteristic lengths $\{\ell_i\}$ of the control by individuals meet the following inequalities

$$\ell_1 \ll \ell_2 \ll \ldots \ll \ell_{2N} \tag{2.1}$$

This assumption may be justified on allometric grounds, i.e. most physiological processes scale as an algebraic power of body size. Here we are extending the allometric notion to include the ambiits of the organisms in question (Zotin 1985, Cousins 1985).

The dimensionless distribution $c_i(\mathbf{r}, t)$ is governed by the equation

$$\tau_i \frac{\partial c_i}{\partial t} = (c_i c_{i-1} - c_i c_{i+1} + \alpha \delta_{i1} - \beta_i c_i) - \ell_i \nabla J_i, \tag{2.2}$$

where $\tau_i$, $\beta_i$ are given constants, and the term $\alpha \delta_{i1}$ ($\delta_{i1}$ is the Kroneker symbol) describes the input of biomass through the first level (phytoplankton). Equation (2.2) is an example of the standard form of the Lotka-Volterra dynamics as applied to a linear trophic chain (with the exception of the last term on the right-hand side.) The final term describes the dynamics of nonuniformites in the spatial distribution of species $i$, where $J_i$ is the movement of its members through space. Usually, the relationship between the $J_i$ and nonuniformites in their distributions, $c_i(\mathbf{r}, t)$, is written in the form (Svirezhev,1987)

$$J_i = -\ell_i \nabla c_i. \tag{2.3}$$

Expression (2.3) actually corresponds to the passive behavior of animals undergoing random motion in space and independent both of other members of the same species and of their predators and prey. In this paper we account for the active behavior of animals at every hierarchical level. This means that each animal attempts, (1) to avoid any region where the concentration of members of the same species is large, in order to decrease the competition for feed resources, (2) to prefer to visit domains containing high concentrations of prey and, (3) to avoid regions with many predators. Such active behavior will be described by the following expression:

$$J_i = \ell_i \left[-(1 + \omega_{i,i} c_i) \nabla c_i - \omega_{i,i+1} c_i \nabla c_{i+1} + \omega_{i,i-1} c_i \nabla \langle c_{i-1} \rangle_{\ell_{i-1}} \right] \tag{2.4}$$

where $\omega_{i,i}$, $\omega_{i,i+1}$, and $\omega_{i,i-1}$ are positive constants and $\langle c_{i-1} \rangle_{\ell_{i-1}}$ is the concentration of prey averaged over the domain of their individual lifespans. Let us specify the value of $\langle c_i \rangle_{\ell_i}$ by the expression
\[
\langle c_i \rangle_{\ell_i}(r) = \int dr' A \exp \left\{ \frac{(r - r')^2}{2\pi \ell_i^2} \right\} c_i(r)
\] 
(2.5)

where \( A \) is a normalization constant. The nonlinear terms in expression (2.4) are those responsible for the self-regulation. It should be noted that a similar expression for \( J_i \) has been used by V.V. Alexeev (1976) and P.S. Landa (1983) to describe the active behavior of zooplankton.

Let us analyze in particular how a perturbation occurring initially at a lower level propagates through the trophic system to its highest levels and the opposite case, i.e., a perturbation moving from top to bottom. In the first case it is useful to introduce the quantities

\[
c_i^0 - c_{i+1}^0 + \alpha \delta_{i1} - \beta i c_i^0 = 0.
\]

Linearizing equation (2.2) and expression (2.4) with respect to steady-state perturbation \( \delta c_i \propto \exp(i kr) \), we get for \( i \geq 2 \)

\[-k^2 \ell_i^2 ((1 + \omega_{i,i} c_i^0) \delta c_i + \omega_{i,i+1} c_i^0 \delta c_{i+1} - F(k \ell_{i-1}) \omega_{i,i-1} c_i^0 \delta c_{i-1}) + c_i^0 \delta c_{i-1} - c_i^0 \delta c_{i+1} = 0 \]
(2.6)

where \( F(k \ell_i) = \exp \{-\frac{1}{2} k^2 \ell_i^2 \} \) is the Fourier transform of the kernel of integral operator (2.5).

Let us analyze in particular how a perturbation occurring initially at a lower level propagates through the trophic system. In other words, the passive ecosystem is fragile. When the animals exhibit active behavior, however, all the values \( f_i \) depend substantially on the parameter \( \omega_{i,i} \). As follows from (2.9), for \( i < i^* \) the values \( f_i \) and \( f_{i+1} \) are related by the expression

\[
f_i = \frac{c_i^0}{c_{i+1}^0} f_{i+1}
\]
(2.9)

In order to analyze the behavior of the quantities \( f_i \) as the level \( i \) changes, we fix the wave number \( k \) such that \( k \ell_i < 1, \) whereas \( k \ell_{i+1} \gg 1 \) for a particular level \( i^* \) (for example, \( k = (\ell_i \ell_{i+1})^{-1/2} \)). As follows from (2.9), for \( i < i^* \) the values \( f_i \) and \( f_{i+1} \) are related by the expression

\[
f_i = \frac{c_i^0}{c_{i+1}^0} f_{i+1}
\]
and for \( i > i^* + 1, \) the value \( f_i \ll 1. \) The magnitude of the quantity \( f_{i+1} \) depends substantially on the parameter \( \omega_{i+1,i^*} \). Indeed, if \( \omega_{i+1,i^*} = 0, \omega_{i^*+1,i^*} = 0, \) the value \( f_{i+1} \ll 1, \) whereas for \( \omega_{i^*+1,i^*} \sim 1, \) we get \( f_{i+1} \sim 1, \) too. Therefore in the first case, which corresponds to the passive behavior of animals, the quantities \( f_{i^*}, f_{i^*+2}, f_{i^*+4}, \ldots \) are large. This last condition means that the relative variations of the concentrations \( \delta c_2/c_2, \delta c_4/c_4, \ldots \), can be large in comparison with the perturbation \( \delta c_1/c_1 \) occurring at the bottom of the trophic system. In other words, the passive ecosystem is fragile. When the animals exhibit active behavior, however, all the values \( f_i \) for \( i < i^* \) are of order unity, so that a small perturbation at the bottom of the ecosystem cannot lead to substantial perturbations at other levels. This is the essence of the proposed mechanism for self-regulation.

It should be noted that perturbations of lower levels lead to responses with consistently the same signs going up the food chain toward top carnivores (big animals). This agrees with the results obtained by Herendeen, 1996. Indeed, stock changes in the ecosystems under consideration can be represented as \( (\{+\}, s, s, \ldots, s) \), signifying that changes in
stocks of the producer (the bracketed term) lead to stock changes at successively higher levels that have the same sign as that of the perturbed lower compartment (Here "s" means the perturbation has the same sign.) Let us now consider the characteristics of the propagation of perturbations from the top to the bottom. In this case it makes sense to consider only perturbations characterized by a spatial scale comparable with the size $\ell_{2N}$ of the domain controlled by the largest predators, that is, we may assume that $k\ell_i \ll 1$ for practically all the levels. Under such conditions we may set $\delta c_1 = 0$, and it is useful to introduce the quantities $\{f_i\}$ specified by the expression

$$f_i = \frac{\delta c_i/c_i^0}{\delta c_{i+1}/c_{i+1}^0},$$

which allows us to rewrite equation (2.8) as follows

$$k^2\ell_i^2 (1 + \omega_{i,i} c_i^0) + c_{i+1}^0 f_i^{-1} = c_{i-1}^0 f_{i-1}.$$  \hspace{1cm} (2.10)

In a similar way we get

$$f_1 = 0,$$

$$f_2 = -\frac{c_{i+1}^0}{k^2\ell_i^2 (1 + \omega_{i,i} c_i^0)} \bigg|_{j=2},$$  \hspace{1cm} (2.11)

and for $i > 2$,

$$f_i = \frac{c_{i+1}^0}{c_{i-1}^0 f_{i-1} - k^2\ell_i^2 (1 + \omega_{i,i} c_i^0)}.$$  \hspace{1cm} (2.12)

Whence it follows that the changes in stocks can be represented as $(-o,s,o, [+])$, where an increase in the stocks of the top carnivores alternates the sign of the perturbations going down the chain. ("0" means that the perturbation has the opposite sign). In addition, the values $f_i$ alternate between small and large as we pass through the levels. In other words, ecosystems configured as trophic chains cannot effectively regulate themselves with respect to perturbations in populations of the large predators. This difficulty does not pertain, however, to our postulated mechanism of self-regulation, which suppresses nonlocal interaction of lower level elements as mediated by the higher levels. In general, our results accord with the consensus among ecologists that bottom-up control tends to be stabilizing, whereas top-down influences are usually destabilizing.

### III. SELF-REGULATION IN A MARKET WITH PERFECT COMPETITION

In this section we create a simple, distributed model of a market in which the price of each type of goods does not depend on the demand for goods of other types. In other words, in such a market there is no nonlocal interaction of the flows of different types, which is due to the mechanism of self-regulation to be considered. In this context it is reasonable to confine ourselves to a mesomarket of goods made primarily from the same raw material. Hence, this market will involve a single network that joins the ultimate consumers with all types of producers, including the firms producing the raw material, those producing particular types of goods, and the wholesale sellers. That is, this market supplies consumers in different districts with practically the same set of goods.

The latter assumption allows us to treat the given market as a collection of levels made up of firms with similar activities. Furthermore, we can specify the density of each level of identical firms (for example level $i$) by $\rho_i(r)$ and the material flow through one firm by $x_i(r)$. The levels are ordered according to the power of the firms and the higher the level, the fewer the total number of firms at that level. Each firm buys the product of firms at the level just above it and sells its own product to firms in the next lower level. The highest level consists of the firm that extracts the raw material, and the lowest one is made up of retail sellers. Therefore, each level $i$ also contains micromarkets of products made by those firms and, thus, should be characterized by a spatial distribution of prices, $p_i(r)$.

The conservation of materials at each level allows us to write

$$x_i(r)\rho_i(r) = \int dr' G_{r,r'}^{i,i-1} x_{i-1}(r')\rho_{i-1}(r').$$  \hspace{1cm} (3.1)

Here $G_{r,r'}^{i,i-1}$ is the function specifying the trade interaction between firms at levels $i$ and $i-1$ and is localized in the domain controlled by the individual firms at level $i$. In particular,

$$\int dr' G_{r,r'}^{i,i-1} = 1.$$  

It should be noted that expression (3.1) reflects the fact that the higher the level, the larger the domain of control of firms below it. At the lowest level (level 1, the retail sellers) the flow of goods obeys the equality

$$x_1(r)\rho_1(r) = S(p_1(r) \mid r),$$  

where $S(p_1(r) \mid r)$ is a given function of the consumer demands.

The activity of each firm results in the profit

$$\pi_i(r) = [p_i(r) - p_{i+1}(r)] x_i(r) - t_i(r \mid x_i(r)),$$  

where the function $t_i(r \mid x_i)$ quantifies the total cost of the production activity of firms at level $i$ that are localized in the region $r$. For the highest level ($N$), $p_{N+1}(r) = 0$. The cost $t_i(r \mid x)$ is a convex function of its argument, $x$, i.e. the curve $t_i(r \mid x)$ is slopes upward, and

$$\frac{\partial t_i}{\partial x} > 0, \quad \frac{\partial^2 t_i}{\partial x^2} > 0.$$  

The function also takes into account the fixed cost, that is

$$t_i(r \mid 0) > 0.$$  

The interaction of trade between different levels will be specified by an equilibrium in the supply-demand relations such that each firm maximizes its own profit,

$$\frac{\partial \pi_i}{\partial x_i} = 0,$$  

and the market is assumed to be characterized by perfect competition,

$$\pi_i = 0.$$  

The last equality implies that there is no barrier to any firm entering or leaving the market.

Equations (3.6) and (3.7) constitute the essence of the proposed model for self-regulation of such an hierarchically organized market. We now show that, under the given assumptions, the price of any one type of goods does not depend on the demand for other goods.

As follows from expressions (3.3), (3.4), and (3.5), there is a unique solution of the system of equations (3.6) and (3.7): $x^*_i(r)$, $\Delta p_i(r) = [p_i(r) - p_{i+1}(r)]$ meeting the conditions

$$\frac{\partial \ln \left[ t_i(r \mid x) \right]}{\partial \ln x} \bigg|_{x=x^*_i(r)} = 1,$$  

$$\Delta p_i(r) = \frac{\partial t_i(r \mid x)}{\partial x} \bigg|_{x=x^*_i(r)}.$$  

The value $x^*_i(r)$ and the corresponding value $\Delta p_i(r)$ depend solely on the properties of the function $t_i(r \mid x_i)$, which reflects the efficiency of production. Therefore, because firms at the highest level extract the raw material rather than buy it ($p_{N+1}(r) = 0$), all prices at each level in such a perfect market are specified by the efficiencies of their technological processes and not on their demands. The demand by ultimate consumers for goods at the lowest level determines the total flow of products through the levels. It follows in this case from (3.1), (3.2) that the demand alone determines the density of firms at each level. Therefore, variations in the consumer demand for one type of goods have no effect on the price and flow of goods of another type.
We realize that the models for ecological and economic systems that we have considered are quite simplistic and cannot be applied directly to real systems. Rather, our goal here has been to elaborate the mechanism of self-regulation, which, we believe, is inherent in every natural system. Such a mechanism is required by all natural living systems because of their complex organization and the necessity that at each level they adapt to changes in the environment. Indeed, the very complex organization of ecological or economic systems implies that none of their elements can possess all the necessary information on how the system must adapt to changes in the environment. Indeed, if each element were to interact with every other one, it either would take an infinite time for the system to adapt or the system as a whole would be unstable. One of the ways available for such a system to avoid this problem is to organize itself in hierarchical fashion. Unfortunately, such organization might also cause the system to acquire undesirable nonlocal interactions that are mediated through by higher levels. To suppress such interaction there must be some cooperative mechanism for system self-regulation. In our opinion, this self-regulation is implemented by the active behavior of elements at each level. Each element acts according to only its own goal, responding to only the small amount of information it receives. However, the law of material conservation acting across the hierarchical organization leads to the self-processing of information. Thus, the small amount of information available to each element informs it in an aggregated and implicit way about the state of the system as a whole. Through such a cooperative way the individual behavior of different elements is made consistent across levels and enables the system to respond properly to changes in the environment.

As concerns ecosystems, we hypothesize that this mechanism for self-regulation arises from the preference by animals to move in the direction of increasing prey density and to avoid regions with an increasing number of predators. The latter response dampens variations in the species population which otherwise could become critical, because the higher the population of one prey, the greater the extent its predators will specialize in hunting them to the exclusion of others.

In economic systems, each firm attempts to maximize its own profit, so if the total profit increases in the neighbouring region (either of space or type of goods), firms will tend to relocate (or retool) into this region. Such active behavior gives rise to variations in the density of firms. We have related this active behavior to the condition that the total profit be zero, due to the presence of perfect competition.

[1] Alexeev, V.V. 1976. Biophysics of living organisms communities. Usp.Fiz. Nauk. v.120, 34, p.647. (English transl.: Sov. Phys.-Uspekhi).
[2] Cousins, S.H. The trophic continuum in marine ecosystems: Structure and equations for predictive model. In: R.E.Ulanowicz and T.Platt (Editors), Ecosystem Theory for Biological Oceanography. Canadian Bulletin of Fisheries and Aquatic Sciences. Fisheries and Oceans Canada, Ottawa: 76-93.
[3] Herendeen, R.A. A Unified Quantitative Approach to Trophic Cascade and Bottom-up: Top-Down Hypotheses. 1995. J.Theor. Biol. v.176, p.13-26.
[4] Landa, P.S. Autooscilation in distributed system. Moscow, Nauka (In Russian).
[5] Lubashevskii, I.A., Gafiychuk, V.V. A simple model of self-regulation in large natural hierarchical systems // J.Env.Syst. - 23(3), p.281-289 (1995).
[6] Lubashevsky I.A., Gafiychuk V.V. Cooperative mechanism of self-regulation in hierarchical living systems. e- print of Los Alamos National Laboratory. http://xxx.lanl.gov/abs/adap-org/9808003 (1998): submitted to SIAM J.Appl.Math.
[7] Gafiychuk V.V. Lubashevskii I.A., On hierarchical Structures Arising Spontaneously in Markets with Perfect Competition. J.Env.Systems. - v.25, No.2. - p.159-166. (1996-1997).
[8] Platt, T., Mann, K.H. and Ulanowicz, R.E. 1981. Mathematical models in biological oceanography. UNESCO press, Paris. 157 p.
[9] Scherer, F.M., Ross, D. Industrial Market Structure and Economic Performance. - Houghton Mifflin Company. Boston (1990).
[10] Svirzhev,Yu. M. Nonlinear waves, dissipative structures and catastrophes in ecology. Moscow, Nauka (1987).
[11] Zotin, A.I. 1985. Thermodynamics and growth of organisms in ecosystems. In: R.E.Ulanowicz and T.Platt (Editors), Ecosystem Theory for Biological Oceanography. Canadian Bulletin of Fisheries and Aquatic Sciences. Fisheries and Oceans Canada, Ottawa: 27-37.
FIG. 1. Trophic level representation, where: 0 – phytoplankton, 1 – small organisms, 2 – organisms belonging to different classes, 3 – large predators.