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Evolution of Ecosystems under an Anthropogenic Load: From Disorganization to Self-Organization

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Abstract—The paper presents a concept of the sustainability of aquatic ecosystems, their disorganization when impacted by anthropogenic pollution, and evolutionary development after the effect of the toxicants decreased. The general laws of the ecosystem transformations are explained from the viewpoint of the ecological theory and the mechanism of thermodynamic ordering of matter in living systems. The evolutionary development of ecosystems after weakening of induced anthropogenic perturbations is demonstrated to be consistent with the trends of ecosystem successions: from a natural stage through critical one to a stable modification. The latter is characterized by a higher ordering of the matter and a decrease in the entropy. Ecosystems are not able to return to their natural state because they evolved through a critical state to a new stable one, which is characterized by highly ordered state of the matter.

Keywords: aquatic ecosystems, anthropogenic load, critical state, evolutionary development

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INTRODUCTION

The most important thermodynamic characteristic of organisms, ecosystems, and the biosphere as a whole is a state of low entropy, i.e., the ability to reproduce and maintain a highly ordered state of the matter. The energy criterion was used by several researchers (Zavadskii, 1959; Shvarts, 1980; Galimov, 2009; Ervin, 1991; Chesser and Sugg, 1996) to understand the principal tendencies and trends in the evolution of the biosphere. In the course of its evolution, the biosphere has developed its optimal organization in relation to the specifics of the usage of assimilated energy at various organization levels of the living matter (Shvarts, 1976). Evolutionary ordering is ensured by the formation of a low-entropy product and its iterative reproduction (Galimov, 2009).

The evolution is realized through ecological relationships that involve all organisms, and its mechanisms maintain a high degree of ordering of the system and the functioning of ecological systems (Gilyarov, 2003). A *mechanism* is understood herein as a system of cause-and-effect relationships in the chain of processes that occur in an ecosystem. The concept of mechanism is commonly applied to processes occurring at the level of an organism and is relatively rarely used with reference to processes at the levels of populations and communities. Nevertheless, understanding relationships between processes in systems at levels higher than that of an organism is often more important for ecology than the identification of disturbances in individuals belonging to a community (Filenko et al., 2005).

Environmental pollution becomes a factor that rapidly changes living conditions on the planet, and this opens a unique possibility to directly observe the course of evolution (Begon et al., 1986; Moiseenko, 2017). Understanding induced anthropogenic transformations of the structural–functional organization of an ecosystem and energy flows at its anthropogenic contamination, which occur at interaction between all elements, is one of the urgent problems of modern ecology and biogeochemistry.

The principal goal of this study was to provide an understanding of the mechanisms of induced anthropogenic variability of ecosystems under significant anthropogenic impacts and the self-organization (recovery) mechanisms of these systems after the elimination of the contamination. The sustainability of ecosystems, their disorganization processes incurred by toxic contaminants, and the self-organization recovery are discussed from the standpoint of the ecological theory (Odum, 1983; Pianka, 1978; Alimov, 2000) and the thermodynamic ordering mechanism of living systems (Prigogine and Stengers, 2008; Galimov, 2009). We attempted to characterize perturbations in ecosystems and mechanisms of their self-organization within the scope of the universalism concept of the life phenomenon in light of E.M. Galimov's theory (Galimov, 2005, 2009).

Lacustrine ecosystems are convenient to analyze the supra-individual organization level of living matter affected by anthropogenic impact and recovery self-organization. The basis of this study is formed by parameters of the degradation and recovery evolution of aquatic ecosystems after their toxic contamination, with reference to contaminated bays in large lakes (Moiseenko, 2011; Moiseenko et al., 2009; Moiseenko and Sharov, 2019).

STABILITY-SUSTAINING MECHANISMS

First of all, we consider the sustainable (stable) functioning of an aquatic ecosystem. Analysis of the literature (Alimov, 1994, 2000; Odum, 1985; Cains, 1990; Pratt and Cains, 1996; Chesser and Sugg, 1996) displays a diversity of approaches to study and definitions of the stability and sustainability of an ecosystem, i.e., its ability to resist the inflow of contaminants. Stability can be estimated as the capability of the system to resist perturbations (resistant stability) and/or its ability to return to the initial state (elastic stability) after the action of the stress factor is eliminated. Elastic stability is often also referred to as the elasticity of an ecosystem (Alimov, 2000).

When studying the origin of life on the level of self-reproducing molecules, E.M. Galimov emphasized that a biological system "tries" to organize itself in a manner that induces irreversible processes in this system that prevent an entropy increase and minimize it: "...the stability of biological systems is caused by their essential linearity, their ability to reproduce themselves, and by the fact that these systems are not simply complicated by comprise sets of subsystems ..." (Galimov, 2009).

Stable functioning (stationarity) is a function of the resistibility of an ecosystem to the effects of any destabilizing factors, such as toxic contamination, eutrophication, and/or changes in hydrological characteristics. In the course of its successive evolution, an ecosystem reaches its mature (climactic) state. It was proposed (Alimov, 2000) to assume the measurable parameters of the stability of communities or ecosystems as the limits within which characteristics of the communities or systems can vary without extending outside the annual average fluctuations established during the evolutionary development of a given system and typical of it. Table 1 lists the key characteristics of the natural state of three lakes in northwestern Russia (period 1 is the natural state), which have varied insignificantly since the relatively stable ecosystems were formed. Of course, ecosystems can sometimes evolve, for example, lakes can get older (up to the development of swamp systems), but this process can proceed for thousands to millions of years. Here we discuss the preindustrial period of time, when the environmental conditions varied relatively little (during one to two preindustrial centuries).

Let us distinguish features characterizing the stability of ecosystems and try to explain them from the standpoint of the universality of functioning mechanisms of living systems in view of E.M. Galimov's theory (Galimov, 2009). The features of stably functioning ecosystems will be explained in terms that describe the nature of the life phenomenon at an organization level of living matter higher than the organization level of an individual organism.

Relationships between forces and flows. The inflow of energy subsidies into an ecosystem (in the form of biogenic and organic compounds) is constant, and the production (P) is counterbalanced (within annual fluctuations) by losses to breathing (R), i.e., $P/R \approx 1$. Biologically available forms of elements and compounds are utilized in the ecosystem, i.e., compounds coming from outside are consumed in biogeochemical cycles, and the excesses are expelled by means of burial or outflows, as is typical of open systems.

The **irreversibility and coupling of linear processes** are maintained by ascending (from producers of consumers of order 1, 2, 3....N_i) and descending energy and material flows because of the operation of decomposers, i.e., an important stationarity requirement is thus satisfied: the linearity of energy transfer within an open system (ecosystems are systems of this type). The consumption of energy resources at each level of the hierarchical organization is coupled with energy losses to breathing, biomass increase, and reproduction in the ensemble of the functional units of the ecosystem (in subsystems). In the overall biological cycling, production is coupled with destruction. The evolution of a sequential chain (network) of stationary systems was viewed (Galimov, 2005) as means of evolutionary ordering in both ontogenesis and phylogenesis.

Low-entropy systems. The structural complicatedness of ecosystems is defined by such a number and diversity of species that can minimize energy losses (dissipation) when energy is transferred from one subsystem to another in the trophic structure. It depends of natural abiotic factors, such as climate, landscape features, etc. More complicated ecosystems are formed when the energy and material flows are intense (as, for example, in tropical ecosystems), and hence, the diversity systematically increases from northern to southern latitudes, with a simultaneous increase in the flows, which are counterbalances by losses to production, breathing, assimilation, and output. The entropy of a mature stable ecosystem is at a minimum.

Functional consistency as a measure of ordering is one of the requirements of stationarity as is defined by the number of species and the specifics of their functioning in the trophic structure of the ecosystem (in both its ascending and descending energy transfer lines), which minimize and dissipate energy. In each and any stationary ecosystem (with its abiotic and biotic characteristics), a high functional consistence is reached in successions from the producers to consum-

Table 1. Principal indicators of water quality and the state of communities in large lakes in northwestern Russia during key periods of their transformations: (1) natural state, (2) intense pollution, (3) decrease in the pollution and the revival of the ecosystem (based on data from Moiseenko and Sharov, 2019)

Parameter	Imandra Lake			Onega Lake			Ladoga Lake		
	Evolutionary periods and numerical values of parameters								
	1	2	3	1	2	3	1	2	3
P_{tot}/PO_4, mg/L	6/1	26/21	28/5	8/1	54/30	23/4	10/3	178/100	30/8
N_{tot}/NO_3, mg/L	260/17	436/102	360/80	350/110	750/120	620/77	450/130	920/240	705/220
Si, mg/L	1.0	1.1	0.3	2.0	1.2	0.3	1.0	0.5	0.2
Toxic load ($\Sigma C_i/MPC_i$)*	0.1	3.2	1.5	0.1	0.9	0.3	0.1	1.8	0.8
Phytoplankton									
Chl *a*, μg/m^3	0.3	3.8	5.9	0.7	8.4	8.6	0.7	8.0	9.6
Biomass, g/m^3	0.1	3.6	4.8	0.1	2.4	2.2	0.5	5.5	2.5
Abundance, cells 10^6/L	0.1	3.8	4.6	0.1	3.6	3.4	0.4	12.3	3.7
H (Shannon biodiversity index), bit/spec.	3.2	2.5	4.7	3.7	3.3	5.6	3.4	3.1	5.4
Zooplankton									
Biomass, g/m^3	0.3	1.7	2.2	0.1	2.9	1.4	0.6	2.8	1.9
Abundance, $10^3/m^3$	15.0	271.0	407.0	3.0	110.0	91.0	13.0	143.0	58.0
H (Shannon biodiversity index), bit/spec	2.8	1.9	3.6	2.3	1.7	3.7	–	–	4.1
Macrobenthos									
Biomass, g/m^3	0.6	35.0	24.5	0.6	3.2	15.2	1.6	4.8	12.9
Abundance, $10^3/m^3$	0.5	4.3	8.6	0.2	2.4	8.5	0.8	1.1	3.7
H (Shannon biodiversity index), bit/spec.	3.5	1.6	1.8	2.6	2.0	2.2	–	–	2.4

* Toxic load, $\Sigma C_i/MPC_i$, is calculated as the total of concentrations of toxic compounds (Ni, Cu, Pb, phenol, and lignosulphonate) normalized to the harm-limiting parameter (MPC).

ers and decomposers. Biological diversity is defined by functional correspondence both within the set of the subsystems (microbial, phyto- and zooplankton, benthos, and fish communities) and between them, which decreases the energy losses.

An iterative character of the processes. Ecosystems are not just complicated systems but consist of a great number of subsystems: environment—communities—members (species)—individual organisms. Under stable conditions, the dominance of species is constant and is maintained by species using the K selection strategy in their life cycle (Pianka, 1978), i.e., by long-lived species, which consume more energy to maintain their metabolism, growth, and reproduction. As an iterative process, reproduction is energy consuming. Because of this, longer maturation and rarer reproduction compared to those of *r*-selected species decreases energy dissipation at reproduction (i.e., iterations), because each iteration is associated with inevitable energy dissipation. Iterativity is inherent not only to individuals but also to the whole system in the coherent ensemble of the reproduction structures.

In a stably functioning ecosystem, which is characterized by a great complicatedness and a certain amplitude of natural variability, all species require food resources to provide energy for their metabolic processes. However, species differ in the proportions of food resources spent on growth, production, and maintenance of basic metabolism and in how much material can be stored in their tissues, fat depots, and/or reproduction organs. If the amounts of introduced and removed material are equal, with regard to dissipation minimization, then the state of the system remains stable with time (within annual fluctuations). If the introduction of material is greater than its removal, the system adapts itself by increasing the number of organisms responsible for more complete utilization of the introduced and produced material.

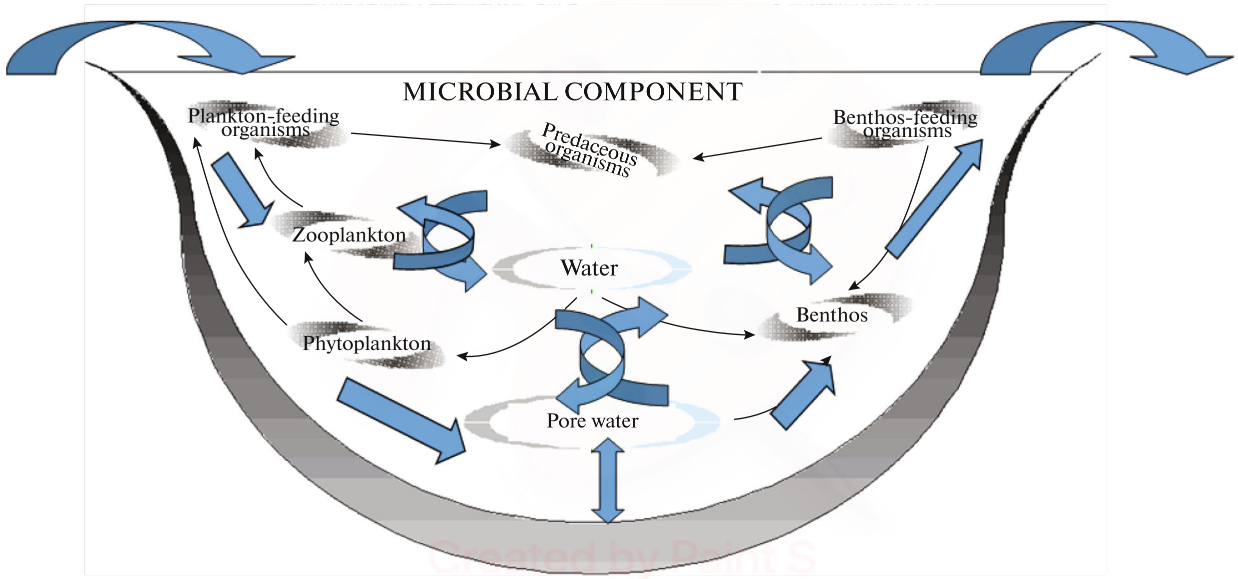

Fig. 1. Indications of stable functioning of an ecosystem: the material inflow into the ecosystem is constant, production varies within annual fluctuations and is counterbalanced by losses to breathing, material flows are balanced, processes in the ensemble of structure units are coupled, species in the trophic structure proceed in functional correspondence, and the iterativity of subsystems is relatively low.

This may look like complication. Finally, in case of material deficit (i.e., when material consumption exceeds its introduction), the system simplifies itself (Odum, 1983; Alimov, 2000). An ecosystem thus occurs in a stationary state until material introduction into the ecosystem is counterbalanced by material losses, with regard to the minimum dissipation (Fig. 1).

TOXICANTS AS A DISORGANIZING FACTOR

When a destructive factor (such as toxic pollution) impacts an ecosystem, it is able to eliminate some of its species, depending on their genotypic tolerance and phenotypic plasticity. Perturbations affect the structure of the ecosystem (the number of species and the population sizes), and hence, functions become disturbed in subsystems in the whole ecosystem (Atchison et al., 1996). While some populations decrease their sizes, other increase them, and energy flows in the system are thus modified. Stationary systems remain highly stable and flexible while both necessary conditions of stationarity (energy inflow and material exchange) are satisfied. Violation of these conditions precludes the origin of low-entropy structures, and the system dies (or reorganizes itself) (Galimov, 2009). Death can occur on a molecular, cellular, or organism levels, and can take place on an ecosystem level only as disorganization processes.

In the concept of *energy subsidies* (Odum, 1983), these subsidies are understood as any energy sources that increase the fraction of energy that can be spent on reproduction. The subsidies can be a moderate influx of organic and biogenic compounds into the ecosystem, but their high and irregular influxes are regarded as a stress factor. Toxic contamination is viewed only as a stress factor, which leads to disorganization of the ecosystem and to energy dissipation. If energy subsidies are greater than the toxic load, the productivity of the system increases and the system simplifies itself, and a further strengthening of the toxic stress factor suppresses the biological productivity and diversity of the ecosystem. As energy flows in any of these directions change, the ecosystem suffers changes, i.e., it occurs in a critical state until reaching a qualitatively new equilibrium state. C.H. Walker with colleagues (Walker et al., 1996) presented generalized data on changes in ecosystems induced by toxic contaminations and distinguished the following stages in the variability of the communities: (1) the number of species decreases, (2) the population size decreases, and (3) the size of the population may increase because of resistant species.

We have identified principal features that characterize the aquatic ecosystems in three lakes during their disorganization as a consequence of complex contamination (Moiseenko and Sharov, 2019). Table 1 (period 2: intense pollution) lists the principal parameters of biogeochemical cycling and structural changes in the communities: the data demonstrate obvious similarities in the modifications of ecosystems in polluted bays of the three lakes.

Along with an increase in the total phosphorus concentrations, an increase was detected in concentrations of biologically available forms that cannot be utilized by the ecosystem at this transformation stage, and they become a reserve for the intensification of production processes and increase in the biomass of the primary producers (phytoplankton). The structure of the phytoplankton biomass changes toward the dominance of blue-green, green, and cryptophyte algae, which are resistant to pollution. Cryptophyte algae are known to be capable of mixotrophic feed. Having small sizes, they maintain rapid biomass circulation in the ecosystem, i.e., ensure more efficient utilization of energy subsidies as opposed to disordered dissipation. The zooplankton is dominated by small rotifers. In the zooplankton and benthos communities, the populations of typical northern species diminish as susceptible to toxicants, and this leads to a reduction of the overall species diversity.

The abundances of eurybiont species in the zooplankton and benthos communities increase because of the high concentrations of biogenic elements and the absence of competition relationships with typical inhabitants of northern water bodies, which are vulnerable to toxic effects. The dominance of eurybiont species is therewith enhanced in all communities. The zooplankton communities are dominated by small rotifers, and the benthic ones are characterized by the development of large masses of organisms of the chironomid–oligochaete complex. The decrease in the abstract masses of individuals typical of the phyto- and zooplanktonic communities indicate that they are dominated by small-sized species (*r*-selected species), which ensure a faster biomass cycling in the ecosystem and the utilization of additionally supplied energy subsidies. The proportions of predatory species in the zooplankton and fish communities decrease (Moiseenko, 2009; Moiseenko and Sharov, 2019).

The aforementioned features indicate that the ecosystems of the three lakes are in critical states in intensely polluted areas, and these features correspond to an unstable stressed states of the ecosystems. On the one hand, the elimination of the most susceptible and vulnerable species decreases the competition, and on the other hand, the surviving species receive more energy subsidies and get advantages for their growth and reproduction. This, in turn, simplifies the biological diversity of the system and disturbs the pathways of energy transfer. In such situations, the development of a new structure of the system becomes unpredictable because of indirect secondary effects of recolonization (Chesser and Sugg, 1996).

Experimental data confirm general relations and trends of diversity in aquatic ecosystems. It has been demonstrated (Filenko et al., 2005) that not only advantages for their development are thereby got by small members of the community, but also the abundance of small individuals increases within the population, which indicates that the mechanism is of universal nature. The reduction in the species diversity, the regression of opportunistic and increase in the small-sized species are viewed by several researchers as a result of structural transformations in the communities under the selective effect of the toxic factor (Pratt and Cains, 1996; Falk et al., 2006; Palmer et al., 2007).

From the standpoint of the energy criterion, the operation of a destructive (disturbing) factor, for example, toxicants, increases the entropy of the biological systems during their disorganization. Chaos is determinate and exhibits certain relations (Prigogine and Stengers, 1984). Below we list the principal features of a critical state of an ecosystem as a high-entropy chaotic system that has determinate relationships.

Disturbance of the balance in the energy and material flows. Anthropogenically induced flows of biogenic elements result in excess biologically available nitrogen and phosphorus species, i.e., the flow of the energy subsidies exceeds their utilization in the ecosystem: the P_{tot}/PO_4 ratio decreases at a drastic increase in the phytoplankton biomass (Table 1, period 2: intense pollution). The relatively high abundances of some resistant species shall be maintained by abundant energy resources, which are released because their transfer pathways are disturbed in the original historically formed ecosystem.

Disturbance of (or breaks in) the linearity of energy transfer and energy dissipation. The decrease in the abundance of typical stenoecic northern species, which are vulnerable to toxicants, is associated with an increase in the abundances of some eurybiont species (the dominance drastically strengthens). The abundance of the latter species significantly increases thanks to high concentrations of biogenic elements in the absence of competition with other habitants at toxic contamination. Examples are the abundances of rotifers in the phytoplankton communities, chironomids in the zoobenthos, green and blue–green algae in the phytoplankton, etc. Toxic contamination betters surviving conditions for resistant eurybiont species because of the release of food resources, whereas other species are therewith suppressed by the toxic agent. Disturbances in energy transfer in the trophic structure leads to the disordered dissipation of the energy when it is transferred from one to another subsystem.

Acceleration of the iterativity of the system. The decrease in the abstract individual mass of organisms in the phyto- and zooplankton communities provides evidence of the dominance of small-sized species (*r*-selected species), which makes iterations more frequent in both the subsystems and the ecosystem as a whole. Among species with similar tolerance, advantages in the competition are received by small-sized species, which are characterized by high-frequency reproduction and alternation of generations. This phenomenon is typical of numerous taxonomic groups and, as was mentioned above, has been verified experimentally (Filenko et al., 2005).

Disturbances in the linearity of the processes result in that small errors (glitches in the functioning of eco-

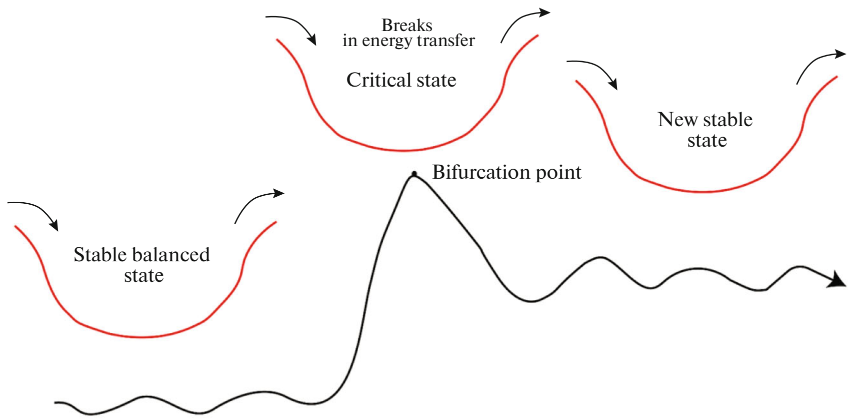

Fig. 2. Evolution of an ecosystem through a critical state to its new stable state.

systems) are increased by iterations, so that the results of the evolutionary development become virtually unpredictable after a number of iterations (distortions). Manifestations of nonlinearity and accumulation of iteration errors leads to the degradation of the system (Galimov, 2009), as seen in the contaminated bays of the lakes discussed herein.

A critical state of ecosystems can be regarded as a bifurcation point, at which the system is restructured (Fig. 2).

Features of critical states of ecosystems (when energy dissipation increases) also show evidence of fighting against the chaos and an increase in the entropy: the sizes of organisms in the communities decrease, they start to more efficiently utilize energy (food) resources, the abundance of dominant stable species increases, biomass cycling in the ecosystem becomes faster, production is exported, etc. These mechanisms ensure the utilization of the excess energy resources that are introduced as subsidies or are released when the linearity of material transfer in the ecosystem is disturbed. The entropy can be decreased not only by complicating the structure but also by accelerating the cycling of the biomass, which is maintained by short-cycle and smaller sized species (or individuals of a single species).

EVOLUTION OF ECOSYSTEMS AFTER THEIR POLLUTION

Most publications devoted to processes of natural recovery are focused on the aftereffects of a single factor or on the recovery of some species, regardless of the whole complex of interactions in ecosystems and communities (Erwin, 1991; Atchison et al., 1996; Palmer et al., 2005; Falk et al., 2006). The nature of changes in the communities can be interpreted based on features of populations consisting of individuals (Begon et al., 1986). Pollution disturbs and modifies many relationships and links in the ecosystems (Walker et al., 1996), and their recovery (or rather the formation of ecosystems with new features) shall proceed with the origin of many direct, indirect, and reverse interaction means. The evolution of a system after its toxic stress cannot still be fully predicted scientifically (Cairns, 2005).

Consider the evolution of ecosystems during a new stage, when the effect of the disorganizing factor (flow of toxic compounds in our situation) has been eliminated. The origin of a stable ecosystem (return to a stable state) is controlled by laws of entropy minimization typical of living systems of any organization level.

Key features that characterize the ordering of material and the self-organization of ecosystems during a stable (mature) stage after a critical state (bifurcation points) are comparable to those of processes in lacustrine ecosystems in northwestern Russia (Fig. 3; Table 1, period 3: pollution decrease).

Rebalancing the material and energy flows. Accumulated biogenic elements are involved in biogenic cycling in the ecosystem, as follows from the decrease in the concentrations of mineral species of phosphorus and nitrogen, i.e., bioavailable forms of biogenic elements are utilized more efficiently. For example, the P_{tot}/PO_4 in Imandra Lake was 8.7 in 2003 (upon the pollution was reduced), whereas this ratio was 2.6 in 1978–1983 (during the pollution period) (Moiseenko et al., 2009). The decrease in the concentrations of bioavailable species of biogenic elements is a consequence of their utilization by diatoms, which became dominant during the recolonization period, but their abundance was higher than the natural one. Because of this, the biomass of the algae practically did not decrease (or decreased only insignificantly) over the past decades, which indicates that the bioproductivity of the lakes was higher than the natural one. Although the phosphorus inflow into the ecosystems of Ladoga and Onega lakes (in their polluted bays) decreased, the maximum and average biomasses and the chlorophyll content practically did not change during the recovery period (Moiseenko and Sharov, 2019). The concentra-

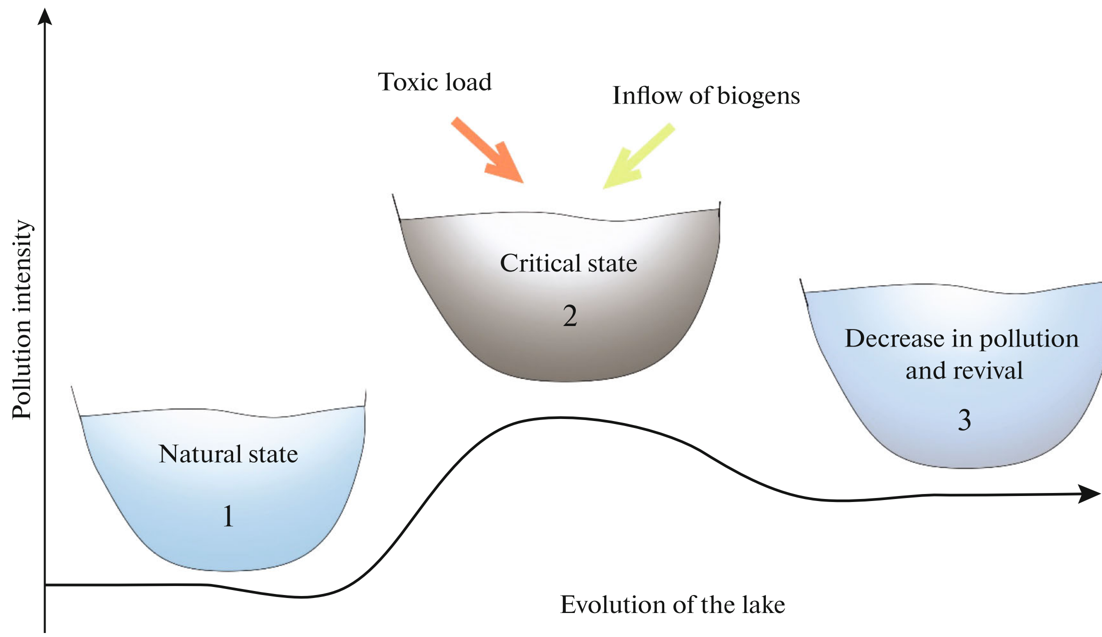

Fig. 3. Features of ecosystems during various stages of their anthropogenic evolution: (1) natural state: biogeochemical cycles are stable within their seasonal fluctuations; (2) critical state: production and destruction processes are misbalanced under the effect of energy subsidies and stress factors; (3) new evolutionary stage: a stable state different from the natural one (Moiseenko and Sharov, 2019).

tions of bioavailable phosphorus forms decreased relative to the total phosphorus concentration, but this decrease was not as significant as in Imandra Lake.

Better linearity of energy transfer as a condition for decreasing energy dissipation. When toxic pollution diminished, as for example, in Imandra Lake, the biotopes were recolonized by northern species and those from more southern waters, and this is confirmed by a still another change in the dominant complexes. The biodiversity index therewith increased, i.e., the system became more complicated. However, the species structure of the communities was different from the natural one, in spite of the fact that some parts of the lake were recolonized by organisms of northern waters. The structural complexity of the ecosystem is therewith reconstructed, but some species typical of the natural state do not reappear (or occur as rare individuals), and the dominance in the communities changes. For example, species occurring as rare individuals in the natural state become abundant, and introduced species appear.

The iterativity of the system decreases, and hence, its susceptibility to "errors" increases. In the evolved ecosystem, the role of the upper trophic levels and predatory species increases. The species diversity index of the planktonic communities increases. The abundances of large individuals and predatory organisms (*K*-selected species) in the zooplankton and benthos, as well as fish, increase, which indicates that the iterativity of the subsystems has decreased and that energy is inevitably dissipated as the system tends toward its ordering.

The aforementioned modification parameters of ecosystems after their toxic stress and associated biogenic pollution are consistent with the character of evolution in the North American Great Lakes. For example, phosphorus concentration in Ontario Lake gradually decreased starting from 1968 through 1985, and the concentration of the element had decreased twice by 1985 and was 6 mg/L in the year 2000. However, the production of phytoplankton and chlorophyll *a* has not changed because of the intense proliferation of cryptomonades (a very small primary producer species). The high biomasses of the cryptomonades maintain the biomass of the primary producers (Grey et al., 1994; *Great Lakes Ecosystem: Report,* 2001). The role of predatory species was found out to has lately increased in the zooplankton communities, and the fish productivity has grown. These facts indicate that the responses of the ecosystem cannot be explained solely by the sluggish water exchange, although water purification obviously contributes to the improvement of the states of the lakes.

In our opinion, the concept of "delayed response" (Grey et al., 1994) to a decrease in the phosphorus and toxic load inadequately reflects the situation with the transformations of the lacustrine ecosystems. The ecological theory and thermodynamic laws of biological systems indicate that a leading stabilization factor of the modified ecosystems is their new features, which decrease the energy dissipation: biogenic ele-

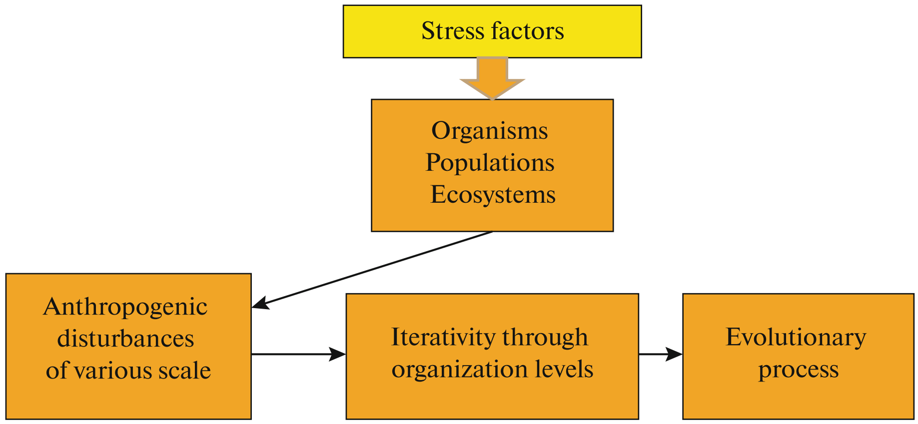

Fig. 4. Evolutionary process in an ecosystem under the effect of stress factors of anthropogenic pollution.

ments from anthropogenic sources involved in the biogeochemical cycling continue to function in the system and maintain the productivity of the phytoplankton and energy transfer through the trophic structure. In response to new perturbations, which are related to a decrease in the inflow of energy subsidies and a diminish in the toxic stress, the "responsive transformations" of the ecosystem develop along another trajectory rather than to return to the earlier successive conditions. "The distortion of the linearity of the processes results in that small errors increase in the course of successive iterations, and consequently, the result becomes practically unpredictable after a certain number of the iterations" (Galimov, 2009). Such errors are, for example, failures in the reproduction of populations and/or in the functioning of the ecosystems affected by pollution, and hence, the direction and rate of the evolution process in the modern biosphere are uncertain (at the current level of understanding). The term *recovery of ecosystems* cannot be regarded in this situation as a synonym of a return to the natural state, but this term should rather be interpreted as the *evolution of the ecosystem toward its new stable modification* (Fig. 4).

Irreversibility occurs at all levels, is monodirectional in time, and plays a constructive role in forming the new structure. Near bifurcations, the main role is played by random factors, whereas deterministic aspects are leading within bifurcation ranges (Prigogine and Stengers, 1984). These fundamentals explain anthropogenically induced processes that occur in aquatic ecosystems when toxic loads on them increase or decrease and confirm that an ecosystem with new characteristics is thereby formed. Obviously, ecosystems evolve (through fighting the "chaos") into new stable modifications and cannot return to their natural states (Fig. 4).

CONCLUSIONS

In the course of their successive evolution, ecosystems reach a mature (climactic) state, which possesses the following features of stability: the energy (entropy) dissipation is low, the processes are coupled, the material and energy flows are balanced, living species occur in a functional correspondence to the trophic structure, and the iterativity of the subsystems is relatively low.

Toxicant affect ecosystems as disorganizing factors, which modify the structures and functions of the ecosystems, and this leads to energy dissipation (entropy increase). A decrease in the size of individual organisms in the ecosystems and an increase in the abundances of species stable under critical conditions make it possible to more efficiently utilize energy in the ecosystems, with this energy received as energy subsidies or released as a consequence of disturbances in energy transfer in the trophic structure of the ecosystems. A critical state of the ecosystem during its toxic pollution shows features of fighting the chaos and a decrease in the energy dissipation by means of the preferable development of small-sized species and individuals, whose more frequent iterations accelerate biomass cycling and energy utilization when the system is transformed into its new stable functioning.

The development of a new modification of the aquatic ecosystems after a decrease in its toxic pollution is consistent with trends and relations in the successions of the ecosystems: from the natural through critical stages toward more stable modifications, whose structure is different from the natural one. In view of this, the term *ecosystem recovery* cannot be (in this situation) identified with the return of the ecosystems to its natural state but shall rather be interpreted as the evolution of the ecosystem toward its new stable state.

Is it possible to restore the natural states of some ecosystems, and how much is this justified? The passage of an ecosystem through a critical state (bifurcation point or a succession of such points) results in irreversible transformations and the origin of new modified ecosystems. The problem of whether it is desirable to try to reproduce natural characteristics of ecosystems is actively debated in the scientific community. We believe that the principal goal in improving the states of natural systems is the maintenance of the key parameters of the structure and functions of the ecosystems, i.e., a high water quality and high bioproductivity.

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