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Some Applications of Thermodynamics for Ecological Systems

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1. Introduction

Now ecologists feel necessary to construct the theoretical building of system ecology, to break strong reductionistic tradition of ecology and to include the use of thermodynamics in a new holistic approach to study ecosystems, their structure, functioning and natural history. We tried to present here the current state of thermodynamic view on ecosystems.
The first law of thermodynamics proclaims constancy of the total energy of isolated system for all changes, taking place in this system: energy cannot be created or destroyed. According to the second law of thermodynamics in isolated system entropy is always increasing or remaining constant. All processes in the Universe are oriented to the equilibrium state. Nevertheless, biological systems, and, consequently, ecological systems create order from disorder, they create and support chemical and physical non-equilibrium state – the basis they live on.
In this chapter the general overview of ecosystem as thermodynamic system is given and the concept of Eco-Exergy is introduced. The use of this concept in ecology is demonstrated to be very fruitful. To make it easy for other researchers to use the Eco-Exergy the procedure of exergy evaluation for ecosystems is followed with special attention to dimensions used. The main applications of exergy in modern ecology are reviewed with special focus on practical use of Eco-Exergy, exergy index, and structural exergy for real ecosystem assessment and estimation of their health and disturbance.
Another application of irreversible thermodynamics (Prigogine's inventions) is discussed. The theory of hypercycles, developed for cycles of autocatalytic reactions and widely accepted in biochemistry and molecular biology can also be applied for ecological systems. The model of conjugated hypercycles, applied to ecological systems explains many aspects of their non-linear dynamics and can be used for analysis of oscillating processes in ecological systems.

2. Ecosystem as thermodynamic system

Ecosystem is an open system. It supports structure and functioning due to external energy input. Usually ecosystem consume solar energy in the form of relatively short-wave radiation (visible light), though we know some ecosystems (e.g., at great depth in ocean)

which use chemical energy. Nevertheless general rule is the reception of solar energy by green plants via photosynthesis. They assimilate approximately 0,01 – 3 % of energy of falling radiation and, using this energy, create organic matter (*primary production*) from inorganic compounds (water, carbon dioxide, nitrates, phosphates and a lot of minor substances). The by-product of photosynthesis is oxygen. Organisms, creating primary production are called *producers*. Energy, stored in organic matter is used by producers themselves and is dissipated during the processes of plants respiration, growth and reproduction in the form of heat. The remaining energy, accumulated in plant biomass is used by animals to support their structure and functioning. These processes are balanced at global level, as well as in healthy mature ecosystems. The rate of total organic matter production is called *gross primary production*. The difference between *gross primary production* and the rate of decomposition of this substance by plants themselves is called *net primary production*. Organisms, consuming plants (*consumers*) can utilize not more than 10 % of net primary production consumed, the rest being dissipated in the form of heat. Predators (*secondary consumers*) can use not more than 10 % of primary consumers production. The dead bodies of plants and animals, organic wastes, produced by the last etc. are decomposed and reduced to primary inorganic compounds, available for the new cycle of production/destruction by *decomposers* or *reducers* (bacteria and other microorganisms).
The rate of total increase of ecosystem biomass (yield) is known as *productivity*. In healthy, mature, balanced ecosystem it is equal to zero (or relation of production to respiration, P/R, is equal to one). So, ecosystem consumes high quality energy of solar radiation, uses part of it to support itself and dissipates the rest in the form of heat, increasing the total entropy of whole system Sun – ecosystem – environment. We have seen the ecosystem is functioning according to both the first and the second laws of thermodynamics.

2.1 Ten basic laws of ecology

Previously (Jørgensen & Fath, 2004) eight basic laws of ecology were proposed, but now it was decided to split one of them into three laws (Jørgensen, 2006-2007, 2011). These ten laws or Ecological Laws (EL) are listed below.

1. Mass and energy conservations are valid for ecosystems.
2. All ecosystem processes are irreversible and are accompanied by entropy production and exergy destruction.
3. All ecosystems are open systems embedded in an environment from which they receive energy—matter input and discharge energy—matter output.
4. Ecosystems have many levels of organization and operate hierarchically.
5. The components in an ecosystem form a complex interactive, self-organizing ecological network.
6. The carbon based life on Earth, has a characteristic basic biochemistry which all organisms share.
7. Thermodynamically, carbon-based life has a viability domain determined between about 250-350 K.
8. After the initial capture of energy across a boundary, ecosystem growth and development is possible by 1) an increase of the physical structure (biomass), 2) an increase of the network (more cycling) or 3) an increase of information embodied in the system.
9. Biological processes use captured energy (input) to move further from thermodynamic equilibrium and maintain a state of low-entropy and high exergy relative to its

surrounding and to thermodynamic equilibrium (**The First Ecological Law of Thermodynamics**).

10. If the ecosystem is offered more pathways or combinations of pathways to move away from thermodynamic equilibrium, then the combinations of pathways that move the system most away from thermodynamic equilibrium (=yield the highest Eco-Exergy of the ecosystem) will win (**The Second Ecological Law of Thermodynamics**).

3. Eco-exergy

The exergy of a system is a measure of its deviation from thermodynamic equilibrium with the environment, and represents the maximum capacity of energy to perform useful work as the system proceeds to equilibrium, with irreversibility increasing its entropy at the expense of exergy (Ludovisi, 2009). Taken by itself, the total exergy of an ecosystem is a measure of the change in entropy content from the equilibrium and the actual state (Svirezhev, 2000).

We may distinguish between technological exergy and Eco-Exergy: technological exergy uses the environment as reference state and is useful to find the first class energy (work) that a power plant can produce, Eco-Exergy uses as reference state the same ecosystem with the same temperature and pressure but at thermodynamic - chemical equilibrium (Fig. 1). Below we use the terms exergy and Eco-Exergy as synonymic.

The development and maintenance of the far-from-equilibrium condition of ecosystems is due to the steady storage of free energy into complex organic structures, biosynthesized from simple inorganic compounds. Accordingly, the total exergy of an ecosystem actually reflects the accumulation of biomass into the system, irrespective of the distribution of biogenic matter among ecosystem components. Exergy is a measure of the free energy of a system with contributions from all components including the energy of organisms. The measure for exergy in ecology also includes a factor to weigh the "complexity" of the ecological species. Moving from macroscopic to microscopic information storage, the exergetic contribution due to information grows and becomes even three orders of magnitude higher than the physical one in the more complex living systems. The capacity of packaging information at the molecular level (DNA) that differs from one organism to another can be taken into account using Eco-Exergy function.

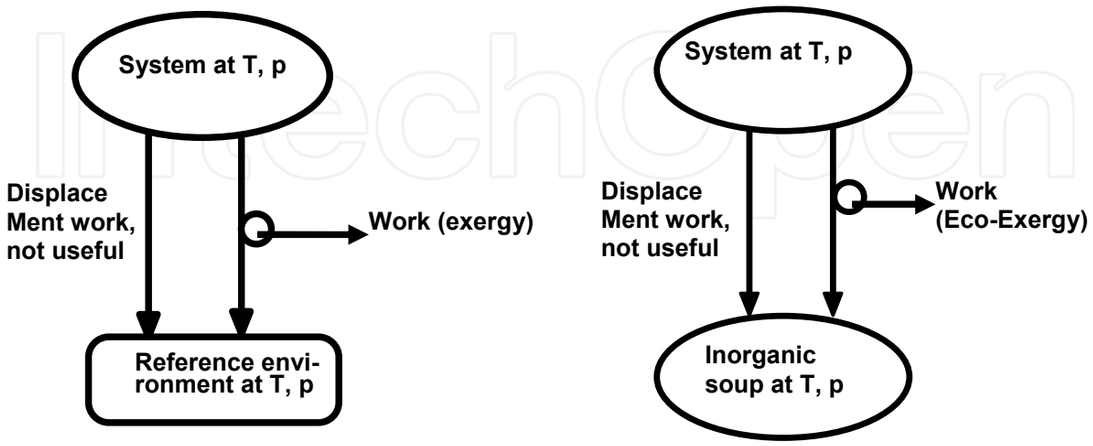


Fig. 1. Exergy is calculated for the system relatively to reference environment, Eco-Exergy relatively to the same system at the same temperature and pressure, but as inorganic solution without life and even organic molecules.

Here, we accept the following definition of exergy (according to Jørgensen, 1992; Svirezhev, 2000; Jørgensen & Svirezhev, 2004): *Exergy is the distance between the present state of the system and the state of it in thermodynamic equilibrium with the environment, measured in the units of energy*. It demonstrates the amount of work performed to create a given system from its primary components (in the case of ecological systems — from primary chemical compounds). *Exergy related to the total biomass (structural, specific or normalized exergy) measures the possibility of the ecosystem to accept and utilize external fluxes of energy.* It reflects the degree of ecosystem development or complexity, and has advantages in comparison with the total exergy such as independence from the total biomass of the ecosystem and possibility to serve as an indicator, demonstrating the level of evolutionary development of organisms in the ecosystem.

3.1 Eco-exergy calculation

According to **Prigogine's theoreme**, an entropy production in every linear system without external influences is decreasing until it reaches minimum at steady state of dynamic equilibrium. Every living system is thermodynamic open system (EL 3) continuously converting potential chemical energy of organic matter into useful energy of creative processes (EL 9) and, in the end of ends, dispose to environment in the form of heat (EL 2). As a result of it, there is no thermodynamic equilibrium in living system. At temperatures, normal for life (see EL 7), living structures are labile and are destructed constantly. To compensate this destruction the permanent internal work in the form of synthesis is fulfilled. These working synthetic processes are processes producing negative entropy (negentropy), they create order with the use of chemical energy of low-entropy energy-rich compounds (consumers and reducers) or low-entropy energy-rich solar radiation (producers). Termination of these processes causes the loss of order, death. Dead body is in thermodynamic equilibrium with maximal entropy.

Exergy is the useful part of energy involved in some process, i.e. the maximal work fulfilled by the system during transit to thermodynamic equilibrium with environment state. This equilibrium means all components to be: 1) inorganic, 2) oxidized to maximum degree, 3) distributed homogenously (there is no gradients in the system). So, if we shall transfer the system into thermodynamic equilibrium with its environment, temperature and pressure will be equal for system and environment, so the only component exergy consists of will be chemical energy. Differences in temperature and pressure between system and environment are small, so we can ignore them in our calculations. The maximal input to exergetic constituent of ecological system will be done due to chemical energy, stored in organic matter and biological structures (Jørgensen et al., 2000; Jørgensen, Fath, 2011; Jørgensen, 2011). Taking into account this concept Eco-Exergy index can be calculated basing on chemical energy: $\Sigma_i(\mu_c - \mu_{c,o})N_i$, where i – the number of exergy containing components c; μ_c – chemical potential of component c; $\mu_{c,o}$ – chemical potential of component c in inorganic state. Eco-Exergy index for the system is calculated by reference of this system to the same system in the form of inorganic soup (i.e. – without life, structure, information, organic matter). The equation for exergy calculation was proposed by S.E. Jørgensen (Mejer & Jørgensen, 1977):

$$Ex = R \cdot T \cdot \sum_{i=0}^{N} [c_i \cdot \ln(c_i / c_{i,eq}) - (c_i - c_{i,eq})], [\mathbf{J}] \quad (1)$$

where Ex – exergy, J; R – gas constant, J Mol^{-1} ·K^{-1}; T – temperature, K; c_i – concentration of component i, Mol; $c_{i,eq}$ – cncentration of the same component in the state of thermodynamic equilibrium with environment. Mol; N – number of components. The problem is to find value of $c_{i,eq}$. From one hand, exergy of compounds can be calculated on the basis of elementary composition. The disadvantage of this approach consists in that, firstly, input of inorganic components into total exergy of ecosystem is too low, secondly, higher and lower organisms have approximately the same stochiometry (EL 6), so their exergy will be equal, that is in contradiction with information constituent of exergy. From another hand, the value $c_{i,eq}$ can be assessed from the probability $P_{i,eq}$ of discovering of component i in thermodynamic equilibrium state:

$$P_{i,eq} = \frac{c_{i,eq}}{\sum_{i=0}^{N} c_{i,eq}} \qquad [\mathbf{1}] \qquad (2)$$

If we could find this probability, we can find the ratio of $c_{i,eq}$ to current concentration.. As inorganic component c_0 prevails in thermodynamic equilibrium state, we can rewrite (2) as:

$$P_{i,eq} \approx c_{i,eq} / c_{0,eq} \qquad [\mathbf{1}] \qquad (3)$$

or

$$c_{i,eq} \approx P_{i,eq} \cdot c_{0,eq} \qquad [\mathbf{Mol}] \qquad (4)$$

Chemical potential of dead organic matter (i =1) can be found from classic thermodynamics as:

$$\mu_1 = \mu_{1,eq} + R \cdot T \cdot \ln(c_1 / c_{1,eq}), \qquad [\mathbf{J \cdot Mol^{-1}}] \qquad (5)$$

where μ - chemical potential. The difference μ_i-$\mu i_{,eq}$ is known for detritus. From (5) we see:

$$c_{1,eq} = c_1 \cdot \exp[-(\mu_1 - \mu_{1,eq}) / (R \cdot T)] \ . \qquad [\mathbf{Mol}] \qquad (6)$$

From (3) at i =1:

$$P_{1,eq} \approx [c_1 / c_{0,eq}] \cdot \exp[-(\mu_1 - \mu_{1,eq}) / (R \cdot T)] \ . \qquad [\mathbf{1}] \qquad (7)$$

For biological components (i =2, 3, 4, …, N) probability $P_{i,eq}$ is composed from probability of detritus production $P_{1,eq}$, and probability $P_{i,a}$ of genetic information collection to determine protein structure. Supposing this events independent:

$$P_{i,eq} = P_{1,eq} \cdot P_{i,a} \quad (\mathrm{i} \geq 2). \qquad [\mathbf{1}] \qquad (8)$$

Equation (1) we can rewrite taking into account (4) as:

$$Ex \approx R \cdot T \cdot \sum_{i=0}^{N} [c_i \cdot \ln(c_i / (P_{i,eq} \cdot c_{0,eq})) - (c_i - P_{i,eq} \cdot c_{0,eq})] \ . \quad [\mathbf{J}] \qquad (10)$$

Then:

$$Ex \approx RT \sum_{i=0}^{N} [c_i (\ln(1/P_{i,eq}) - \ln(c_{0,eq}/c_i)) - (c_i - P_{i,eq}c_{0,eq})] \quad \textbf{[J]} \tag{11}$$

From (3), as $c_i >> c_{i,eq}$, then $1/P_{i,eq} \approx c_{0,eq}/c_{i,eq} >> c_{0,eq}/c_i$. Consequently

$$\left|\ln(1/P_{i,eq})\right| >> \left|\ln(c_{0,eq}/c_i)\right| , \quad \textbf{[1]} \tag{12}$$

after that, we can ignore the second logarithm in the sum:

$$Ex \approx R \cdot T \cdot \sum_{i=0}^{N} [c_i \cdot (\ln(1/P_{i,eq}) - 1) + P_{i,eq} \cdot c_{0,eq})] . \quad \textbf{[J]} \tag{13}$$

Also $1 << \ln(1/P_{i,eq})$ and $P_{i,eq} \cdot c_{0,eq} \approx 0$, then:

$$Ex \approx -R \cdot T \cdot \sum_{i=1}^{N} c_i \cdot \ln P_{i,eq} . \quad \textbf{[J]} \tag{14}$$

where summation starts from 1, as $P_{0,eq} \approx 1$. Taking to (14) $P_{i,eq}$ from (8) and $P_{1,eq}$ from (7), we have the following expresseion to calculate exergy:

$$\frac{Ex}{R \cdot T} \approx -\sum_{i=1}^{N} c_i \ln\left(\frac{c_1}{c_{0,eq}}\right) + \left(\frac{\mu_1 - \mu_{1,eq}}{R \cdot T}\right) \sum_{i=1}^{N} c_i - \sum_{i=2}^{N} (c_i \ln(P_{i,a})) \quad \{\textbf{Mol}] \tag{15}$$

In (15) the first sum is insufficient in comparison with the rest two, so:

$$\frac{Ex}{R \cdot T} \approx \left(\frac{\mu_1 - \mu_{1,eq}}{R \cdot T}\right) \cdot \sum_{i=1}^{N} c_i - \sum_{i=2}^{N} (c_i \cdot \ln(P_{i,a})) . \quad \textbf{[Mol]} \tag{16}$$

Exergy in (16) sufficiently depends on organism complexity, as it is connected with information stored in genetic code. This equation can be used to calculate exergy of ecosystem components. If we take detritus (i =1), we know that free energy released from it equals approximately 18,7 kJ·g^{-1}. Taking T=300 K, R=8,31 J·Mol^{-1}·K^{-1} , and average Mol mass of detritus about 105 g·Mol^{-1}, we obtain the following for detritus exergy in m^3 of water:

$$Ex_1 = 18,7 \cdot c_1 \quad \textbf{[kJ m}^{-3}\textbf{]}, \quad \text{or} \quad \frac{Ex_1}{R \cdot T} = 7,34 \cdot 10^5 \cdot c_1 \quad \textbf{[g m}^{-3}\textbf{]} \tag{17}$$

So, we can rewrite (16) as

$$\frac{Ex}{R \cdot T} \approx 7,34 \cdot 10^5 \cdot c_i - \sum_{i=2}^{N} (c_i \cdot \ln(P_{i,a})) . \quad \textbf{[g m}^{-3}\textbf{]} \tag{18}$$

Now we are to find $P_{i,a}$ – the probability of creation of specific genetic information, characteristic for the organism given. Originally (Jørgensen, 1992, 2002; Jørgensen et al.,

2000) $P_{i,a}$ was determined basing on number of informative (structural) genes (each gene codes the sequence of 700 aminoacids in average) for various taxonomic groups:

$$P_{i,a} = 20^{-700g} \quad (i \geq 2), \qquad [1] \tag{19}$$

where g – число генов. Then exergy of typical single cell alga (850 genes approximately) can be calculated as:

$$\frac{Ex_{a\lg a}}{R \cdot T} \approx 7{,}34 \cdot 10^5 c_i - c_i \ln 20^{-700 \times 850} \approx 25{,}2 \cdot 10^5 c_i \quad [\mathbf{g^*m^{-3}}] \tag{20}$$

If we relate values of different components of ecosystem exergy to one of detritus ($7{,}34 \cdot 10^5$), we shall get relative recalculation coefficient β_i. Corresponding coefficients were calculated for many systematic groups and published (Jørgensen, 1992; Bendoricchio & Jørgensen, 1997; Jørgensen et al., 2000). These coefficients reflect relative complexity of organisms (simpler organisms have lower β values). Later, with the use of new genetic data and some indirect methods of β values assessment, ratio of non-informative genes to total genes number and others, new list of β was composed and published (Jørgensen et al., 2005; Jørgensen, 2007). New β values are added every year (table 1).

Therefore, total exergy of ecosystem, based on chemical energy of organic matter (biomass) and information, stored in living organisms (recalculating coefficient β), can be calculated as:

$$Ex / RT = \sum_{i=1}^{N} c_i \cdot \beta_i . \quad [\mathbf{g\ detritus\ equivalent\ m^{-3}}] \tag{21}$$

This exergy now is often called Eco-Exergy (sometimes - exergy index) to distinguish it from physical or technological exergy (Marques et al, 2003; Jørgensen, 2006, 2007).

Another indicator of ecosystem state, based on Eco-Exergy, was proposed – structural or specific exergy (structural or specific Eco-Exergy). Structural exergy (Ex_{str}) is the exergy related to total biomass (Silow, 1998, 1999, 2006; Xu et al., 1999, 2001, 2004, 2005; Marques et al., 2003; Jørgensen, 2006a). Unlike total exergy it does not depends on biomass and it reflects the ability of ecosystem to accept and utilize the flow of energy from external sources, serving simultaneously as indicator of ecosystem development, its complexity and level of evolutionaty development of biological species composed in it.

$$Ex_{str} = (\sum_{i=1}^{N} c_i \cdot \beta_i) \cdot (\sum_{i=1}^{N} c_i)^{-1} . \qquad [1] \tag{22}$$

We can measure the following aspects of an ecosystem state with the Eco-Exergy: 1) the distance from thermodynamic equilibrium, i.e. general measure of total complexity of ecosystem; 2) structure (biomass and network size) and functions (available information) of ecosystem; 3) ability of ecosystem to survive (expressed via biomass and information of system).

Structural exergy reflects: 1) efficiency of energy use by organisms; 2) relative information content of ecosystem and, 3) consequently, the ability of ecosystem to regulate interactions between organisms or groups of organisms.

Group	Exergy conversion factor, β	Group	Exergy conversion factor, β
Minimal cell	5,8	Brachiopoda	109
Bacteria	8,5–12	Seedless vascular plants	158
Archaea	13,8	Rotifera	163
Yeasts	18	Insecta	167–446
Alga	15–298	Chironomida	300
Cyanobacteria	15	Moss	174
Dynophyta	18	Crustaceans	230–300
Green microalgae	20	Cladocera	232
Diatoms	66	Copepoda	240
Macrophyta (alga)	67–298	Amphipoda	290
Rhodophyta	92	Mollusca	297–450
Protozoa	31-97	Bivalves	297
Amoeba	38	Gastropoda	312–450
Gastrotricha	97	Gymnosperm	314
Fungi	61	Macrophytes (Phanerogam)	356–520
Nemertina	76	Flowering plants	393–543
Worms	91–133	Fish	499–800
Cnidaria	91	Amphibia	688
Plathelminthes	120	Reptilia	833
Oligochaeta	130	Aves	980
Nematoda	133	Mammalia	2127
Sponges	98	Homo sapiens	2173

Table 1. Exergy/Biomass Conversion factors for different groups of organisms, after Silow & Mokry, 2010

3.2 Eco-exergy and structural exergy applications in ecology and environmental science

3.2.1 Eco-exergy in theoretical ecology and in aquatic ecology

We have seen above exergy approach was demonstrated to be very fruitful during the analysis of the application of thermodynamic principles and laws to the main fundamental concepts of ecology at the end of the XX century. The analysis of three thermodynamic laws expressions in ecological rules together with exergy analysis led to formulation of the 10 Ecological Laws, in particular the Fourth (Ecological) Law of Thermodynamics, EL9 (Patten et al., 1997; Jørgensen et al., 1999; Straškraba et al., 1999; Jørgensen, 2006b).

Non-equilibrium thermodynamics models based on the concept of exergy provided a common basis for representing many aspects of ecosystem development and response to environmental impacts as a single measure (Pykh et al., 2000). The use of exergy made possible the investigation of the flows of an ecosystem in terms of exergy and to arrange the system as a hierarchically ordered sequence of systems, thermodynamically embedded in each other (Nielsen, 2000). Experiments with mathematical models supported the

hypothesis that an ecosystem can coordinate the most complex behaviour in the case of high level of exergy of the systems at the edge of oscillation before entering into the chaotic situation (Mandal et al., 2007). The thermodynamic notion of exergy was shown to give better insight both to the patterns of nonlinear ecosystem behaviour and to comparison of the patterns in ecological modelling (Svirezhev & Steinbom, 2001).

3.2.2 Eco-exergy and aquatic ecology

There are very few researches devoted to analysis of plankton communities with the aid of exergy. The implications of body sizes of phytoplankton and zooplankton for total system dynamics by optimizing exergy as a goal function for system performance indicator with mathematical models have been analyzed (Ray et al., 2001). A structurally dynamic model based on phosphorus nutrient limitation has been developed for Lake Mogan located nearby Ankara, Turkey. Exergy was applied as a goal function to consider the dynamic adaptation and the seasonality of plankton species (e.g., size shifts) (Zhang et al, 2003a, b).

The ecosystem of the North Sea integrity was approved to be reflected in exergy capture, storage capacity, cycling, matter losses, and heterogeneity (the diatom/non-diatom ratio of planktonic algae was used) with ecosystem model. Its feasibility was assessed as an ecosystem model of the North Sea, for the Elbe plume, after prior satisfactory calibration. The modeling effort suggested that drastic nutrient load reduction from the Elbe alone would have a limited effect on the larger German Bight: even a 60% reduction scenario would only lead to moderate changes in all five indicators (Windhorst et al., 2005).

More representative and multiple are applications of exergy to benthos communities. Exergy was used in optimization models of phytobenthos (Nielsen, 1997). Exergy concept allowed the finding of the best adapted water plants species in a given environmental condition and to explain in a satisfactory way the observed distributions of them in the Lagoon of Venice, Italy (Coffaro et al., 1997).

Exergy storage was estimated for benthic communities of sandy and muddy bottoms of the North Adriatic Sea subjected to experimental disturbance, induced by means of a controlled trawl fishing haul. The results showed a decrease of local exergy content in the disturbed area, with the minimum, both in sandy and muddy bottom, one month after the experimental disturbance. The exergy of the benthic community increased to the reference level, i.e., the surrounding control area, in accordance with the proposed hypothesis on the dynamics of exergy storage during a systems' development (Libralato et al., 2006).

The changes of exergy and specific exergy were studied with data of benthic macrofauna in the Mondego estuary (Western Portugal). Estimates for the exergy indices provided useful indications for the evaluation of environmental impact due to the eutrophication process (Fonseka et al., 2002).

Export of exergy was estimated for benthic communities on the South-Western Atlantic Coast of France. This export was mainly composed of the migration of grazing fish during the warm season, and of cultivated bivalves during the cold season (Leguerrier et al., 2007).

In the following study a self-organizing map for patterning exergy of benthic macroinvertebrate communities of 650 sampling sites in the Netherlands, including 855 species was implemented. Using these datasets, authors have calculated exergy of five trophic functional groups for each sampling site on the basis of the biomass data. Exergy of

different trophic groups responded differently to different water types reflecting characteristics of target ecosystems (Park et al., 2006).
Eco-Exergy and Specific Eco-Exergy were used to characterize the state of the community during the recovery process after damage to the benthic communities caused by ecological engineering Yangtze River, China (Zhang et al., 2009). Changes of the macro-benthic community structure (Venice lagoon, Italy) over almost 70 years were pictured, showing a sharp decrease in its diversity and system efficiency, estimated with the use of exergy (Pranovi et al., 2008).

3.2.3 Eco-exergy as an ecosystem health indicator

The idea to use exergy as an indicator of ecosystem health was proposed by S.E. Jørgensen (1992, 1999, 2002, 2006a,b), but the first applications of exergy as an ecosystem health indicator were fulfilled with mathematical models. Mathematical modelling with the use of exergy was shown to be applicable to explain ecosystem reactions (Jørgensen & Padisak, 1996), and to facilitate the estimation of parameters of models. The first pioneer papers describing the application of exergy indicators for natural aquatic ecosystems were published in 1997 (Xu et al., 1997; Marques et al., 1997). In 1998 the first application of exergy analysis to the results of field and laboratory experiments with real aquatic ecosystem was published (Silow, 1998). This work was continued by few more publications (Xu et al., 1999a, 1999b; Silow & Oh, 2004). The possibility to use such parameters as structural exergy and exergy for estimation of ecosystem state and its changes under various external influences was demonstrated for real natural and experimental ecosystems. These parameters were shown to reflect the state of ecosystem and they can indicate the degree of ecosystem adaptation, decreasing when important for ecosystem functioning components were depressed or eliminated. S.E. Jørgensen (2006a) proposed to use Eco-Exergy, specific Eco-Exergy and ecological buffer capacities as Ecological indicators for ecosystem development and health assessment.
Exergy is now often used for eutrophication assessment (Xu et al., 1999, 2001, 2011a; Fonseca et al., 2002; Marques et al., 2003; Ye et al., 2007), for ecological engineering purposes (Nunneri et al., 2008), for ecosystem health assessment (Vassallo et al., 2006; Libralato et al., 2006; Xu et al., 2011b). Exergy and specific exergy indices as Ecological indicators of the trophic state of lake ecosystems were tested on a set of lakes (Ludovisi & Poletti, 2003). The ecosystem maturity was estimated for Lake Trasimeno (Ludovisi et al., 2005).

3.3 Case study; eco-exergy analysis of lake Baikal state

The first works were fulfilled with the use of mathematic models. Different sensitivity of under-ice and open water plankton communities to contaminant additions was demonstrated. This can be related to different structural exergy content in plankton community. Exergy buffer capacity seems to be a more realistic measure for pliability of ecosystem reaction to external factors than biomass buffer capacity (Silow, 1998, 1999). In field researches the structural exergy of benthic communities at control (pristine) site, and in the region of Baikalsk Pulp and Paper Combine wastewaters discharge region at the same depths and kind of sediments was shown to differ strongly (structural exergy in polluted area was much lower than in pristine one), while biomass and total exergy behaved in not such an expressive way (Silow & Oh, 2004; Silow. 2006). The next step was the analysis of

exergy and structural exergy of plankton community response to different chemical stressors analyzed in mesocosms experiments. Results obtained with mesocosms and microcosms demonstrate structural exergy decrease in experiments proportionally to a value of the added toxicant concentration, while other parameters (biomasses of components, total biomass of community, total exergy) fluctuated (Silow & Oh, 2004; Silow. 2006). Here we present the results of exergy calculations for natural plankton community of the lake Baikal.

Yearly average values of structural exergy during 1951–1999 fluctuated around their long-term average within the limits "long-term average ± mean square deviation" (154,9±26,0) without any trends. More interesting is the picture for total eco-exergy for the same period. It demonstrates well expressed linear trend of increase with $r^2 = 0.31$ (Fig. 2).

We have also analysed the long-term dynamics of exergetic parameters for four limnological seasons at Baikal: inverted stratification (limnological Winter, under-ice season, February – April), spring overturn (limnological Spring, ice melting, May – June), direct stratification (limnological Summer, July – October), fall overturn (limnological Autumn, November – January)[1]. Analysis of eco-exergy and structural exergy behaviour during different seasons cleared that the positive trend of eco-exergy is observed during limnological Summer (Fig. 3, 4).

Dynamics of pelagic plankton biomass in Baikal for 1951-1999 is given in Fig. 2. There is neither expressed directional change of total biomass, nor changes of biomasses of different components (only slight positive trend of zooplankton biomass). Long-term oscillations of individual components are easily observed. Taking into account all discussed above and remembering the relative constancy of the total biomass of pelagic plankton, we can try to explain the tendency of its exergy to increase according to three listed above strategies (EL8 – increase of biomass, increase of network, increase of information). According to the first strategy it is the primary production increase, based on the mass development of small sized alga in summer period. Actually it is observed in the lake (Izmesyeva & Silow, 2010). According to the second strategy it might be some recently observed structural changes in the plankton community (Hampton et al., 2008; Moore et al., 2009; Silow, 2010), and the third startegy is realized through the growth of share of larger zooplankton, like Cladocerans (Pislegina & Silow, 2010). Total biomass of plankton community and its individual components remains constant, while the total exergy of the community tends to increase. This increase can be explained with the principles of S.E. Jørgensen (section 2.1) – the principles of exergy maximization (EL9 and EL10) via the growth of solar exergy consuming capacity, sophistication of ecosystem networking and increase of ecosystem information storage (EL8).

The calculated values of structural exergy for different seasons in the lake Baikal plankton for the second half of XX century, on the basis of long-term monitoring data, fluctuate within their natural limits (long-term average ± mean square deviation) and do not demonstrate any positive or negative trends (Fig. 2, Fig. 4). It points to the lack of expressed unfavourable changes in the lake Baikal pelagic.

[1] Lake Baikal is dimictic lake, characterized by two periods of stratification – inverted, when upper layer (0-50 m) of water has the temperature 0–1 °C, layer 50-250 m – 1-4 °C, direct, when temperature of upper layer decreases from 12 °C at surface to 5-6 °C at 50 m, layer 50-250 m – 4-5 °C, and two overturns with temperature at 0-250 m is about 4 °C. Below 250 m temperature is constant about 3,3 °C.

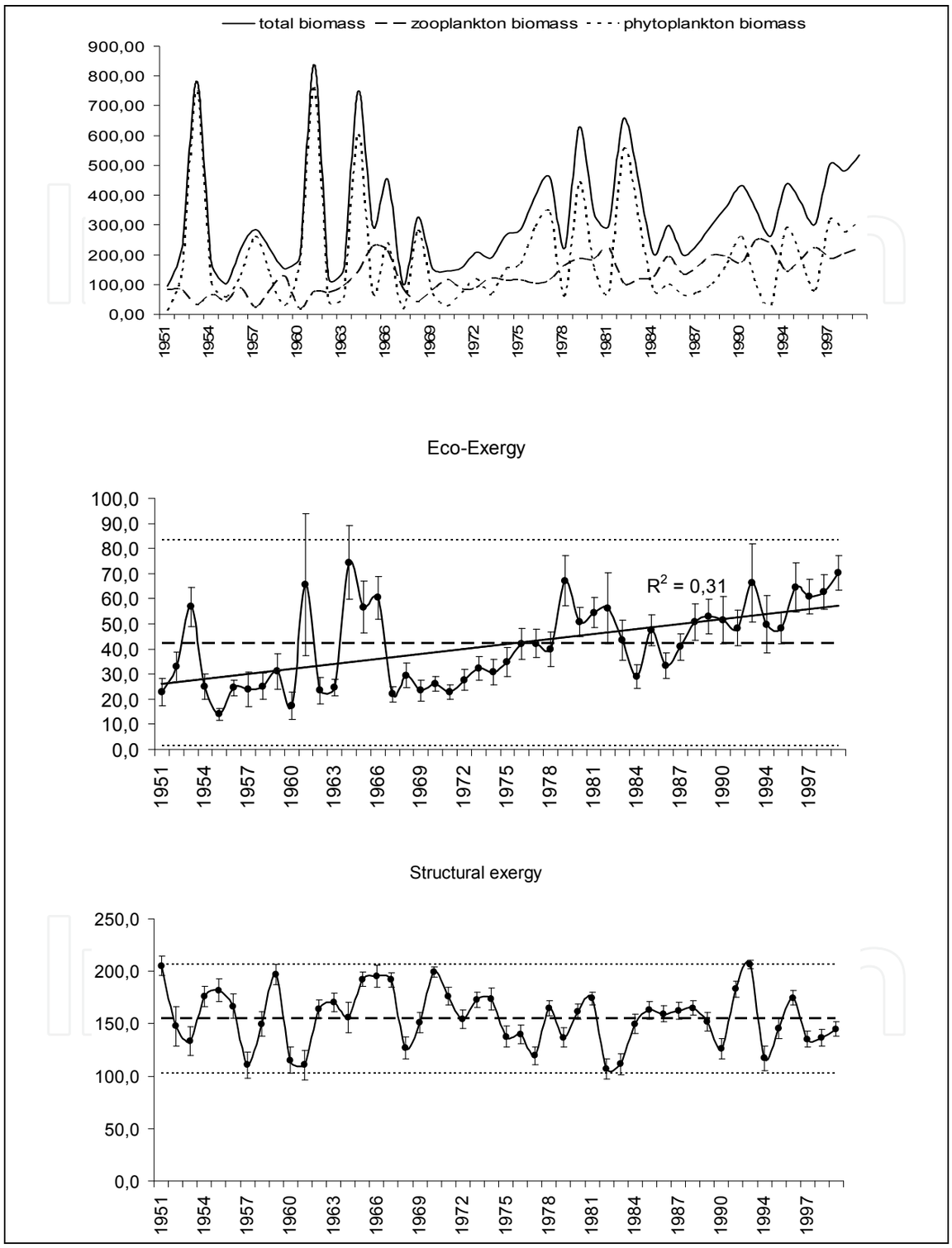


Fig. 2. Long-term dynamics of year-average biomasses of components (mg ·m^{-3}), exergy (g detritus eq ·m^{-3}) and structural exergy of lake Baikal plankton. Dotted line – long-term average.

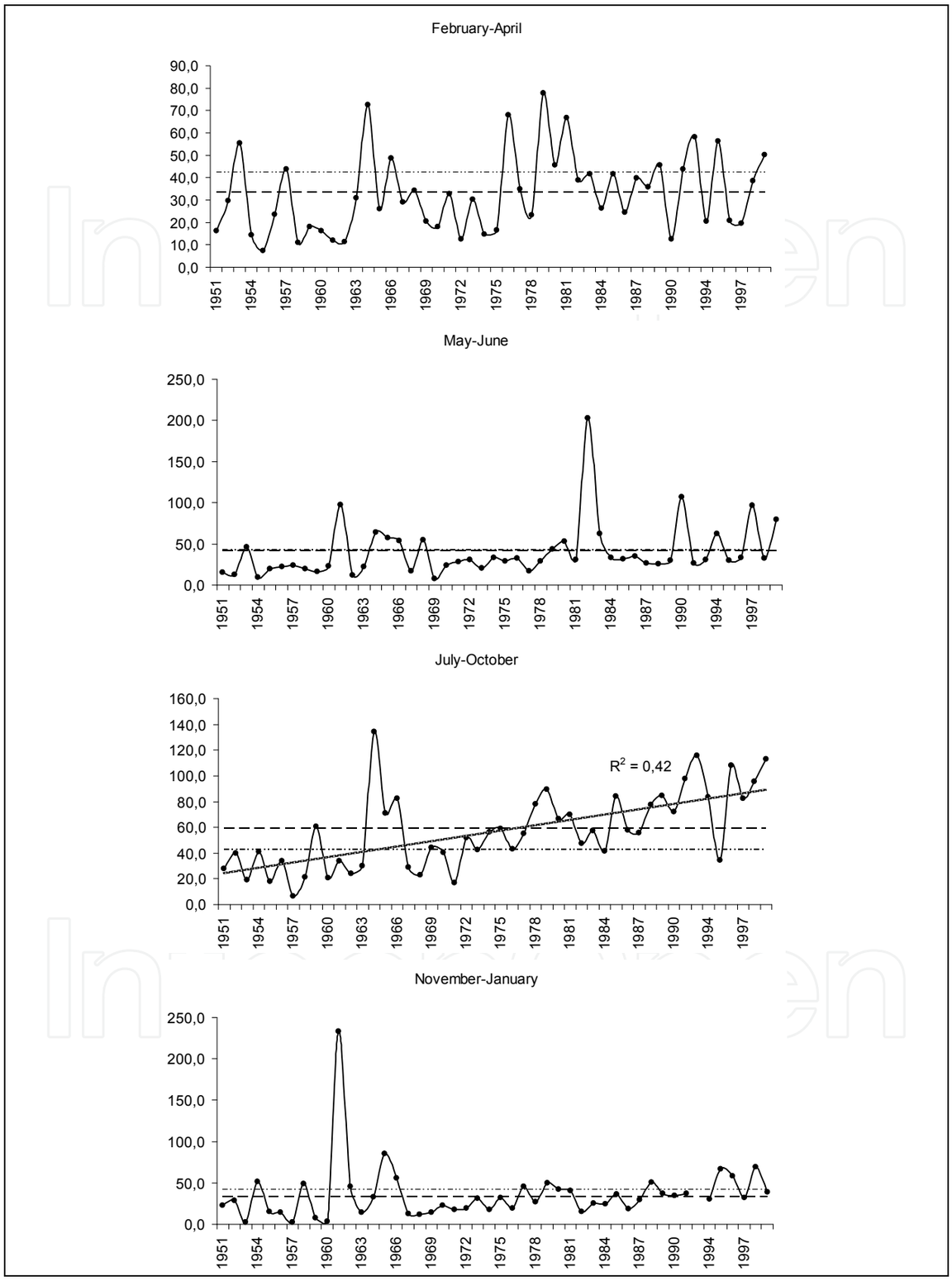


Fig. 3. Long-term dynamics of total exergy (g detritus eq $\cdot m^{-3}$) of lake Baikal plankton for different seasons.

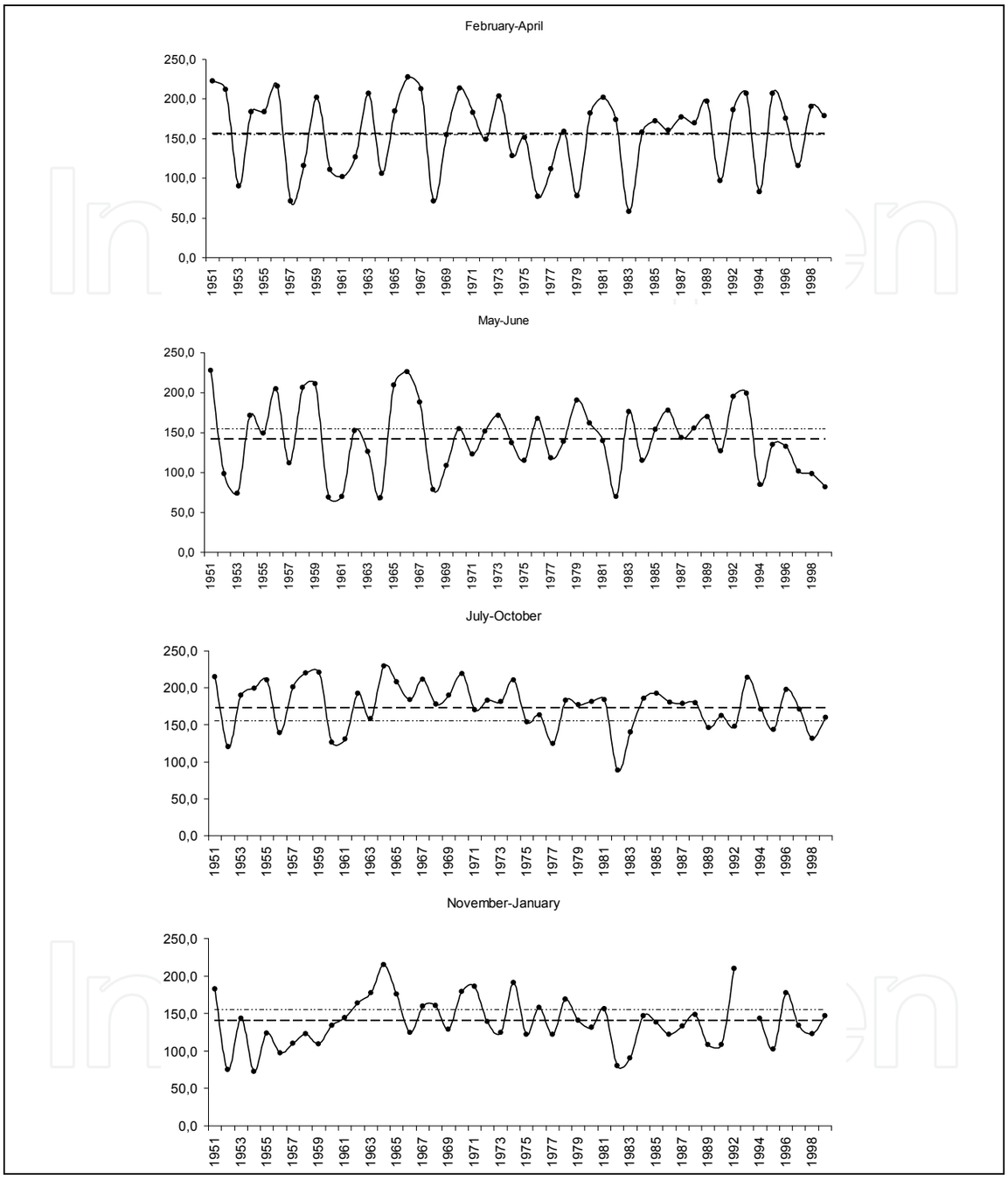


Fig. 4. Long-term dynamics of structural exergy of lake Baikal plankton for different seasons.

As we know from above (sections 3.1, 3.2.4) structural exergy reflects ecosystem health and ability of it to withstand to external influences, e.g. human impact. It is seen from Fig. 4 average long-term under-ice structural exergy (157,2) is practically equal to long-term year-average (154,9), summer structural exergy (175,9) is sufficiently higher than year-average ,

while overturn seasons exergy is lower – 142,5 and 139,4 for spring and fall overturns. It means summer community is much more resistant to external disturbances than under-ice one, and during overturns Baikal is especially sensitive to pollution and other kinds of human impact. It is in good concordance with previously obtained results of our experiments with mathematical models (Silow et al., 1995, 2001; Silow, 1999) and mesocosms (Silow et al., 1991; Silow & Oh, 2004).

4. Hypercycles

One of the characteristic features of ecosystems behaviour are cyclic changes of component biomasses and numbers. They are observed both in natural objects and in artificial ecosystems. Application of Lotka - Volterra and energy flow models to systems containing more than two components demonstrates reducing of oscillation amplitude and stabilization of components parameters at fixed levels (Limburg, 1985; Ruan, 2001; Mougi Nishimura, 2007). Some researchers make their systems to oscillate via chaotic (Stone & He, 2007) or stochastic (Abta et al., 2008) behaviour of its components.
Another fact hardly simulated with the use of existing approaches is "paradox of plankton" - coexisting of two or more species in the same ecological niche (Hutchinson, 1961). To explain it researchers are forced to find any, though very small differences in ecological characteristics of these species, such as optimal temperatures or oxygen contents, growth rates, nutrient thresholds for growth, mortality (Ebenhöh, 1988), time and duration of mass development (Nikolaev, 1986), albeit the last can be not the cause but effect of coexistence.

4.1 Description of models

Nicolis & Prigozhin (1977) basing on the following suggections:

$$\begin{gathered} A + X \xrightarrow{k} 2X \\ X \xrightarrow{d} A \\ A + X = N = const \end{gathered} \tag{23}$$

where A - food, X - component biomass, N - general organic matter content in closed system, k, d - growth and death rate coefficients, obtained

$$\frac{dX}{dt} = kX(N - X) - dX \ . \tag{24}$$

This equation is identical to those used for description of autocatalytic processes, where component X serves as catalyst for self-creation from substance A. Such autocatalytic and self-reproduction units can be regarded in cycles called hypercycles (Eigen & Schuster, 1979).
Ecosystem also can be described as hypercycle, where every next trophic level obtains material from previous level to reproduce itself as autocatalyst. Example of such structure is given in Fig. 5. Phytoplankton obtains nutrients from bacteria to create organic matter with the use of external energy (solar irradiation). Zooplankton feeding on phytoplankton obtains organic matter for growth. Bacteriae in turn get food supply from zooplankton corpses and faeces. Of course, this scheme is idealized as bacteriae obtain food from

phytoplankton extracellular products and dead phytoplankton cells, zooplankton can consume not only phytoplankton but also bacteriae etc. Nevertheless this scheme represents the most important ways of energy and matter transfer in closed ecosystem including producers, consumers and reducers. Dynamics of components is determined by following system of equations

$$\begin{aligned} dx_1/dt &= f(x_1, \mu_1, \phi(x_3)) - g(x_1, \varphi(x_2)), \\ dx_2/dt &= f(x_2, \mu_2, \phi(x_1)) - m(x_2), \\ dx_3/dt &= f(x_3, \mu_3, \phi(x_2)) - m(x_3), \end{aligned} \quad . \tag{25}$$

where x_i - biomasses, f - growth functions, m - death functions, g - grazing function, ϕ - effectiveness of energy and matter conversion (for phytoplankton - relation between bacteriae concentration and nutrients availability) between components, φ - effectiveness of grazing, μ - maximum growth rate. Indices i mean: 1 - phytoplankton, 2 - zooplankton, 3 - bacteriae. Function parameters were calculated at the ecosystem stability condition $dx_i/dt=0$.
Also we have investigated a system including two species of phytoplankton (x_{11}, x_{12}) competing for nutrient supply and two species of zooplankton (x_{21}, x_{22}), and bacteriae (Fig. 6). Starting biomasses for these newly introduced species at stability state were $x_{12}=0{,}33\ x_{11}$, $x_{22}=0{,}1\ x_{21}$. System was described by the following equations:

$$\begin{aligned} dx_{11}/dt &= f(x_{11}, \mu_{11}, \phi(x_3), \xi(x_{11}, x_{12})) - g(x_{11}, \varphi(x_{21})), \\ dx_{12}/dt &= f(x_{12}, \mu_{12}, \phi(x_3), \xi(x_{12}, x_{11})) - g(x_{12}, \varphi(x_{22})), \\ dx_{21}/dt &= f(x_{21}, \mu_{21}, \phi(x_{11})) - m(x_{21}), \\ dx_{22}/dt &= f(x_{22}, \mu_{22}, \phi(x_{12})) - m(x_{22}), \\ dx_3/dt &= f(x_3, \mu_3, \phi(x_{21}, x_{22})) - m(x_3), \end{aligned} \quad . \tag{26}$$

where ξ - competition for nutrients function.

4.2 Behaviour of models

Dynamics of model (25) after external influence shows its returning to the stability point. Such behaviour is characteristic for stable non-linear systems (Gnauck, 1979).
There are no oscillations in this system, it always returns to stable state after initial biomasses changes. To make the system oscillate it is necessary to imitate input of nutrients or toxicants into it (Fig. 7). We can remind similar situation obtained by group of R. Pal et al. (2009). Their phytoplankton – zooplankton – nutrients model (with much more sophisticated mathematics, than ours) demonstrated oscillations under toxification. In other works oscillations of ecosystem components were caused by externally driven forces (oscillating environment) (Eladydi & Sacker, 2006; Koszalka et al., 2007). Hypercycles with not more than three components are shown to remain stable with equilibrium concentrations of components regardless with initial concentrations (Köppers, 1985).
Model (26) demonstrates oscillation behaviour around stability point but never reaches it (Fig. 8). It is in good accordance, e.g. with the biomass fluctuations and species population

fluctuations, cased by increase of community size and complexity (Fowler, 2009). It may be connected with the competition for resources (in our case – for nutrients, released by bacteria), as in many works similar results were obtained. For example, in system of two plant populations, competing for one nutrient (Damgaard, 2004), two predators, competing for one prey (Saleem et al., 2003; Yu et al., 2011), three microbial populations, competing for resources (Li, 2001).

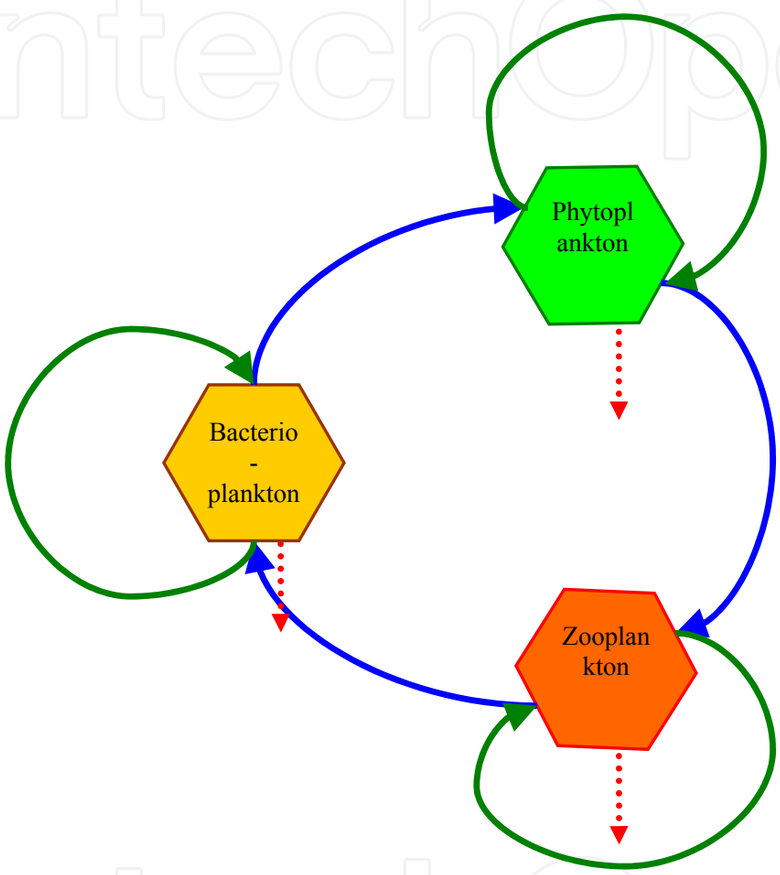


Fig. 5. Idealized scheme of ecosystem as hypercycle. Blue arrows – flows of energy and matter between ecosystem components, green – self-reproduction of components, yellow arrow – income of low entropy (high exergy) energy from external source (Sun), dotted arrows – dissipation of energy in the form of high entropy (low exergy) heat energy.

5. Conclusion

It is now becoming clear that the movement away from thermodynamic equilibrium, and the subsequent increase in organization during ecosystem growth and development, is a result of system components and configurations that maximize the flux of useful energy and the amount of stored exergy. Both empirical data, as well as theoretical models, support these conclusions. Exergy is widely used in ecology to analyze theoretical problems and to solve applied tasks. The most perspective use of exergy parameters in recent ecology is the use of them as ecosystem health indicators.

Exergy, and, especially structural exergy, is shown to be a good health indicator for ecosystems in many model, experimental, field and complex case studies.
The application of exergy calculations to long-term dynamics of the lake Baikal plankton demonstrates the steady state of plankton community structural exergy and well observed increase of its total exergy.
Presented model of two competing hypercycles shows: 1) simultaneous coexistence of two ecologically equivalent phytoplankton species obtaining nutrients from the one source; 2) auto-oscillations of all the components included in model in constant environmental conditions, similar to those observed in real ecosystems.

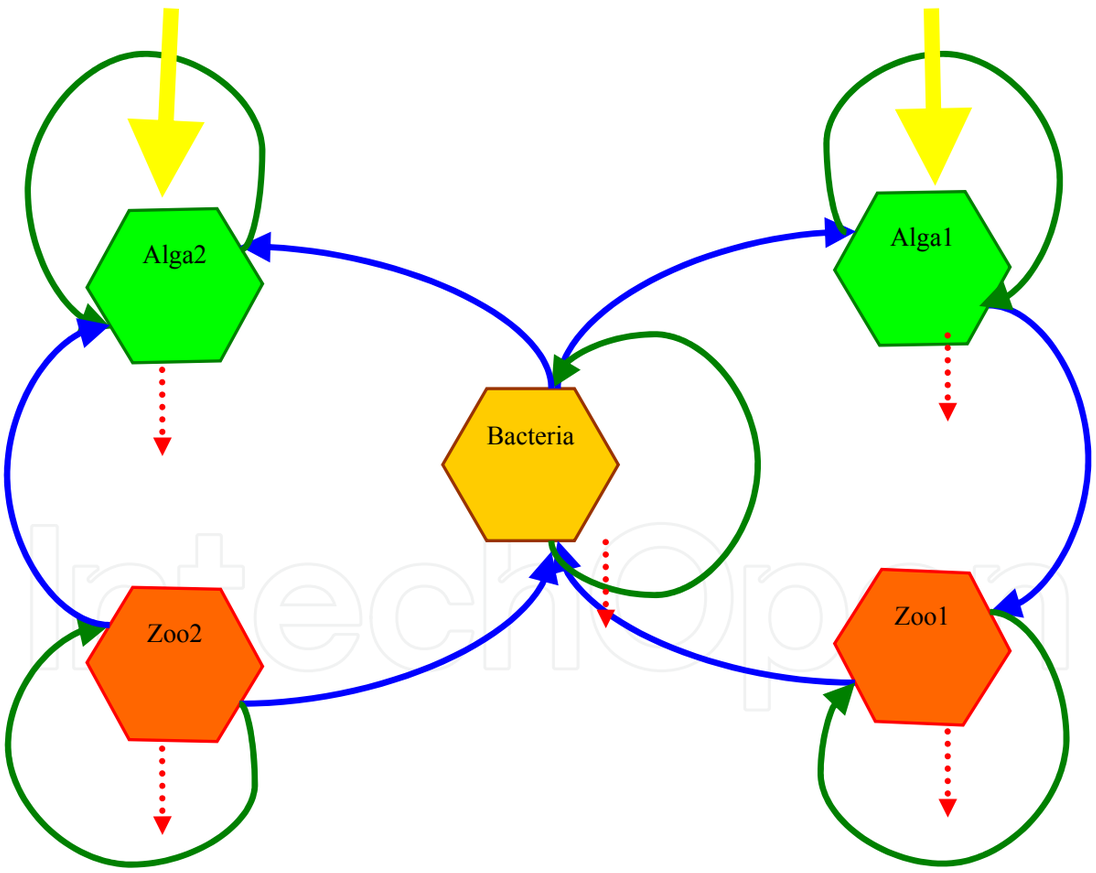


Fig. 6. Idealized scheme of an ecosystem as system of coupled hypercycles.

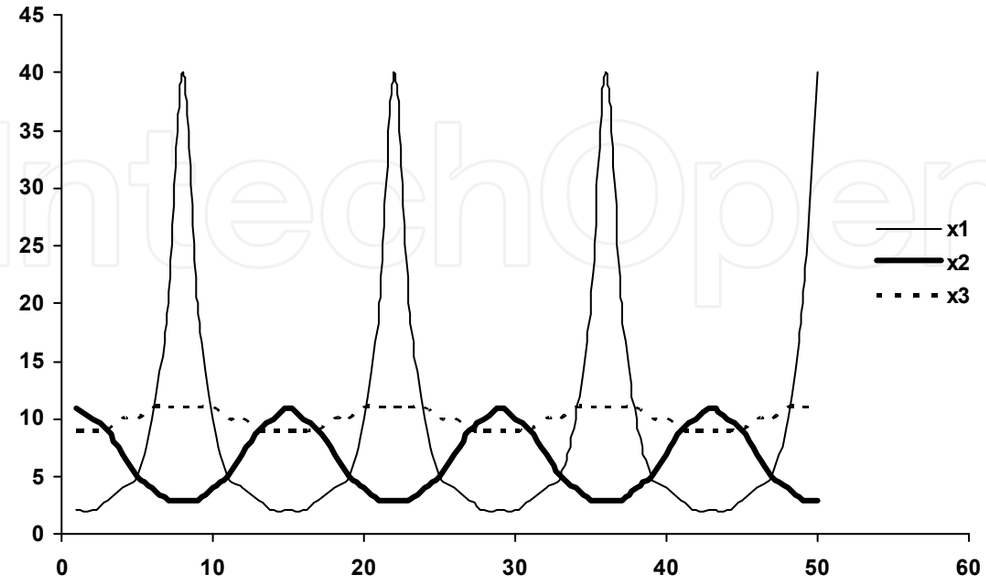


Fig. 7. Dynamics of system (25) at income of pesticide, causing death of 10 % of phyto-plankton, together with nutrients (10% of ecosystem strorage). Y-axis – biomass (kJ m^{-2}), X-axis – years.

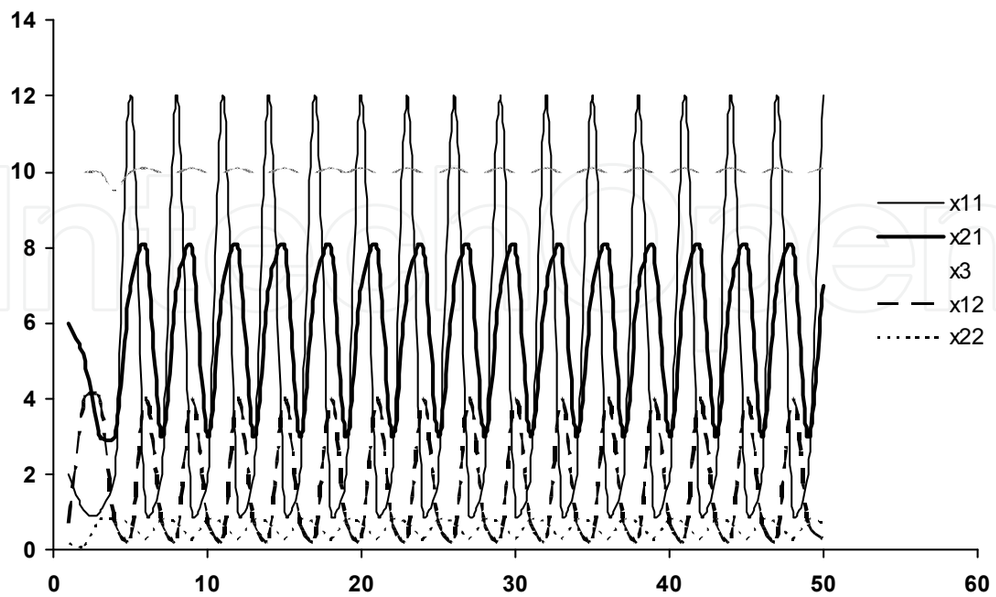


Fig. 8. Dynamics of system (26) without external perturbations.

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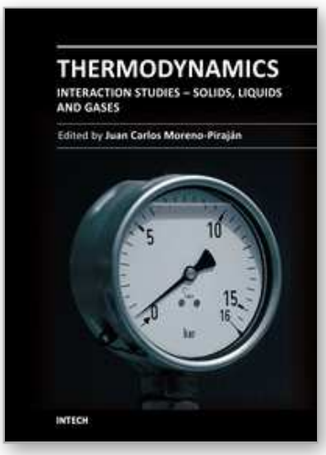
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