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Exergy changes in lakes around the world under pressure from global change

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Abstract

Eco-Exergy, an indicator reflecting the state of an ecosystem and the degree of disturbance acting on it is described and a method of calculation is given. The possible changes in lake ecosystems due to Global Change according to the widely accepted "new paradigm" in limnology are listed and discussed. The expected changes of exergy caused by changes in ecosystems are the following: the total pelagic Eco-Exergy content in large lakes must have the tendency to increase, while structural Eco-Exergy of pelagic community of such lakes is to have a demonstrated trend to decrease. While in case of two large lakes (Geneva and Baikal), for which the long-term dynamics of exergy is preliminary analysed, these effects are not observed, the question needs further investigation.

Keywords: Large lakes, pelagic ecosystems, Eco-Exergy, structural Eco-Exergy, Global Change

Introduction

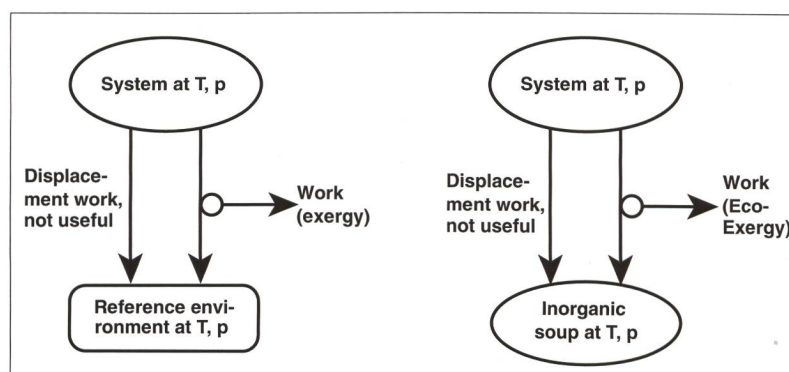
At present, a so called "new paradigm" (Livingstone 2008; Gerten 2008) of limnology, denies the individuality of lake ecosystems and relative constancy of limits, within which parameters of every lake ecosystem fluctuate. This new paradigm proclaims that lake ecosystems respond in concordance, being united by common hydrological cycles and climate, and the unidirectional trend caused by global changes in the environment (climate change and pollution). If this is so, comparable changes in the pelagic community will cause similar trends in such ecosystem state goal functions as exergy and structural exergy (see next paragraph). Taking into account that these goal functions are used for the assessment of the degree of ecosystem perturbation, it is necessary to know which changes of exergy can be caused by general tendencies for lakes according to the "new paradigm", now accepted by many limnologists

(Wilhelm and Adrian 2008; Thackeray et al. 2008; Jöhnk et al. 2008 and many others), if not by everybody among them, believing in Global Change.

Eco-Exergy

The term "exergy" denotes a measure of the quality of energy; as energy is used in any process, it loses quality and decreases in exergy. Basically, the exergy is a measure of the thermodynamic distance of a system from equilibrium with the surrounding environment, and therefore, it is both a quantitative and qualitative measure of the energy (mostly free energy in the context of ecological systems) incorporated into a system. It represents the maximum capacity of energy available to perform useful work as

Fig. 1. Exergy is calculated for the system relatively to the reference environment, Eco-Exergy relatively to the same system at the same temperature and pressure, but as an inorganic solution without life and even organic molecules. (after Jørgensen 2011).



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the system proceeds towards equilibrium, with irreversibly increasing its entropy at the expense of exergy (Ludovisi 2009). Taken by itself, the total exergy of an ecosystem is a measure of the difference in entropy between the equilibrium and the actual state (Svirezhev 2000). The exergy of a system in equilibrium with its environment is zero.

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 synonyms

The equation for exergy calculation was proposed by S.E. Jørgensen in 1977:

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

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} - concentration of the same component in the state of thermodynamic equilibrium with environment. Mol; n - number of components. This equation is transformed into the following working formula (look for details Silow et al. 2011a, b): 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

$$Ex / RT = \sum_{i=1}^N c_i \cdot \beta_i \cdot [\text{g detritus equivalent m}^{-3}] \quad (2)$$

where Ex - exergy, J; R - gas constant, J Mol⁻¹ K⁻¹; T - temperature, K; c_i - biomass concentration, g·m⁻³; and β_i - recalculating coefficient, reflecting quantity of information, stored in organism. This exergy now is often called Eco-Exergy (sometimes - exergy index) to distinguish it from physical or technological exergy (Jørgensen 2011).

Another indicator of ecosystem state, based on Eco-Exergy, was proposed - structural or specific exergy (structural or specific Eco-Exergy). Structural exergy is the exergy related to total biomass (Silow 1998; Xu et al. 1999). Unlike total exergy it does not depend on biomass and it reflects the ability of an ecosystem to accept and utilize the flow of energy from external sources, serving simultaneously as an indicator of ecosystem development, its complexity and the level of evolutionary development of biological species composed in it.

$$Ex_{str} = \left(\sum_{i=1}^N c_i \cdot \beta_i \right) \cdot \left(\sum_{i=1}^N c_i \right)^{-1} \quad [J] \quad (3)$$

We can measure the following aspects of an ecosystem state with Eco-Exergy: 1) the distance from thermodynamic equilibrium, i.e. a 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, consequently, the ability of ecosystem to regulate interactions between organisms or groups of organisms.

Corresponding β coefficients (recalculating coefficients, reflecting quantity of information, stored in organism and depending on the number of informative genes and number of cell types in the organism) were calculated for many systematic groups and are published regularly (Jørgensen et al. 2005; Jørgensen 2006; Jørgensen and Faith 2011; Jørgensen 2011). These coefficients reflect relative complexity of organisms (simpler organisms have lower β values). New β values are added every year (Table 1).

Changes in Lakes Caused by Global Warming

Let's observe the possible consequences of climate change for lake ecosystems basing on the modern limnology paradigm on structure and functioning of aquatic ecosystems (Hutchinson 1957, 1967; Wetzel 2001; Kalff 2002; Schwoerbel and Brendelberger 2005).

If the surface temperature of the air rises, so the temperature of the surface water increases too. Long-term increases of air temperature will cause an increase in water temperature of the surface layer of a lake. If persistent the temperature of the whole epilimnion will increase. There are three phenomena connected with these processes: (i) strengthening of water column stability, (ii) prolongation of stratification, and (iii) increase of epilimnion volume. These phenomena were observed in Scandinavian lakes (Pettersson et al. 2003; Jackson et al. 2007), Lake Zürich, Switzerland (Livingstone 2003), Lake Constance, Switzerland and Germany (Straile et al. 2003), other European lakes (George et al. 2000; Livingstone Dokulil 2001; Elliott et al. 2005; Blenckner et al. 2007), in Great African Lakes (O'Reilly et al. 2003), in Great Laurentian Lakes (King et al. 1997), and in Experimental Lake Area in Ontario, Canada (Schindler et al. 1996; Schindler 2001; Findlay et al. 2004), lake Washington (Arhonditsis et al. 2004), lakes of Wisconsin, USA (Magnuson et al. 1990), South America (Baiguin and Marinone 1995; Solo 2002), Antarctica (Quayle et al. 2002).

Climatic changes must be reflected by hydrochemical parameters also, as climate influences both processes

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

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

in the waterbody and watershed. So, we can expect a decrease of oxygen content and an increase of the nutrients concentration in the hypolimnion, due to strengthening and lengthening of lake stratification. Actually lowering of oxygen content is already observed in some lakes (Straile et al. 2003; Livingstone 2003; Jankowski et al. 2006; Peeters et al. 2007; Wilhelm and Adrian 2008). An increase in nutrients, in particularly phosphorus also has been observed in the hypolimnion of many lakes, due to internal processes (Pettersson et al. 2003; Wilhelm and Adrian, 2008), and an increase of nutrient loading from the watershed (Yoshioka et al. 2002; Prowse et al. 2006).

These serious changes in hydrology and hydrochemistry of water body must unavoidably be reflected in the biota. We can expect an intensive development of phytoplankton, changes in its composition, an increase of microbial activity, and consequently changes in zooplankton composition and fish population.

In deep oligo- and monomictic lakes the decrease of spring mixing causes lowering of silicates and phosphates concentration prior to phytoplankton development (Goldmann et al. 1989; Straile et al. 2003; Salmaso 2005). The consumption of nutrients by phytoplankton further decreases the concentration of dissolved nutrients. Consequently, earlier phytoplankton development due to warming (Adrian et al.

1999; Peeters et al. 2007) leads to earlier lowering of silicates, nitrates and phosphates (Anneville et al. 2002; Weyhenmeyer et al. 2007; Thackeray et al. 2008).

From the other hand, long and stable summer stratification causes the growth of cyanobacteria (Jöhnk et al. 2008) and, consequently / potentially (depending on the cyanobacterial taxa) nitrogen fixation. High temperatures can stimulate the growth of other algae (Elliott et al. 2005; Huber et al. 2008). So, significant increase of primary production in Arctic lakes is demonstrated for XXth century (Michelutti et al. 2005). The rise of temperature was shown experimentally (Rae and Vincent, 1998) to stimulate first the smallest algae (0.2–2.0 μm), than intermediate sized ones (2.0–20 μm), and then large ones (20–200 μm). The earlier ice-off and reinforced input of nutrients from the watershed favours the mass development of small forms of diatoms (Bradbury et al. 1994; Mackay 2007).

The growth of small-sized rapidly reproducing algae causes on the one hand, better feeding conditions for infusoria, flagellates, rotifers and cladocerans (filter feeding zooplankton), and on the another hand, worse feeding conditions for copepods and other catchers. The transfer of energy to higher trophic levels can be decreased by 40–65% (Moline et al., 2004). Both, direct influences of higher temperatures as well as changes in feeding conditions affect the shifts in zooplankton composition (Patalas 1990; Patalas and Salki, 1992). Warming causes a shift in the cladocerans: copepods ratio, as cladocerans react faster to an increase in food availability and to temperature (Straile et al. 2005). With an increase in temperature, the development of cladocerans influences greatly the whole ecosystem (Mayer 1997; Elser and Urabe 1999; Gillooly and Dodson 2000; Carpenter et al. 2001; Sommer and Sommer 2006). The whole structure of the ecosystem changes due to trophic chains restructuring (Winder and Schindler 2004, Yoshioka et al. 2002).

Expected and Observed Changes of Eco-Exergy in Lakes

Now we can transform the changes in lake ecosystems discussed above into changes of Eco-Exergy we may expect, using Table 1. We can predict the

increase of total Eco-Exergy, as the primary production is predicted to increase with warming, and total biomass will be increasing, in a way similar to eutrophication.

Structural Eco-Exergy, vice versa, must decline if there are changes as listed above. Actually, for phytoplankton the preferential development of cyanobacteria and other small sized fast reproducing forms algae is shown under global warming. They have lower conversion factors, than large-sized slowly growing phytoplankton species. It is the first driver of structural Eco-Exergy decrease. An increase of bacterial biomass is expected. This is a second driver of structural Eco-Exergy decrease. Changes in zooplankton composition can be the third driver of structural Eco-Exergy decrease, as the coefficient for cladocerans is lower than that for copepods. In the case of extreme events with hypolimnion isolation and anoxic conditions, fish kills will be followed by dramatic decrease of structural Eco-Exergy.

Nevertheless, if we take lakes with calculated long-term dynamics of exergy and eco-exergy for their pelagic ecosystems (Silow et al. 2011c), e.g. lake Geneva (1974-2005) and lake Baikal (1950-1999), we see that Eco-Exergy in these lakes does not (yet?) behave in complete accordance with our predictions. The total Eco-Exergy in lake Baikal tends to increase, while in Geneva lake it remains approximately the same. Structural Eco-Exergy in Geneva lake is decreasing, while in lake Baikal it has no trend, neither a decrease nor an increase. Long-term dynamics

of the lake Geneva is more determined by the program of lake restoration, including re-oligotrophication and pollution prevention, which caused a more intensive grazing of fishes on zooplankton and consequent phytoplankton development, resulted in a structural Eco-Exergy decrease. As for lake Baikal, though some trends in its ecosystem can be explained by climate changes, this giant lake remains too conservative and too inert to follow general tendencies rapidly.

Conclusion

So, if the hypothesis proposed in the “new paradigm” in limnology is true, the total pelagic Eco-Exergy content in large lakes must have a tendency to increase, while structural Eco-Exergy of pelagic community of such lakes would tend to decrease. Yet, in the case of two big lakes (Geneva and Baikal), for which the long-term dynamics of exergy are preliminary analysed, these effects are not observed, hence the question needs further investigation.

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