ELSEVIER

Ecological Modelling 121 (1999) 103–113

ECOLOGICAL MODELLING

www.elsevier.com/locate/ecolmodel

The use of two lumped models for the analysis of consequences of external influences on the Lake Baikal ecosystem

Eugene A. Silow *

Scientific Research Institute of Biology, Irkutsk State University, PO Box 24, Irkutsk 664003, Russia

Accepted 11 September 1998

Abstract

The application of two lumped models to the prediction of the anthropogenic changes in the ecosystem of Lake Baikal is described. The first model is the static size conversion model, describing the changes in the ecosystem caused by a conservative pollutant present in sub-lethal concentrations. The second one is the model of the ecosystem disturbances. It is based on the data of field experiments and describes the interaction of the ecosystem components with the nutrients and phenolic compounds in the under-ice and summer–autumn seasons. The static model has demonstrated the higher sensitivity of top trophic levels to external influences and necessity to take these levels into account during monitoring works. The model of the anthropogenic disturbances of the Lake Baikal ecosystem has shown higher sensitivity of under-ice community than summer one. The possible reasons are discussed. Exergy content is shown to decrease under the action of conservative pollutant and increase after addition of nutrients and phenolic compounds, reflecting the general shifts in ecosystem. The calculations of buffer capacities demonstrated that exergy buffer capacity seems to be more realistic one than biomass buffer capacity. © 1999 Elsevier Science B.V. All rights reserved.

Keywords: Anthropogenic changes; Effects of pollutants; Exergy, buffer capacity; Lake Baikal

1. Introduction

Prediction of the state of aquatic ecosystems at present becomes more actual in connection with intensification of economic activities, since pollution of the water reservoirs and water courses is able to cause degradation of their ecosystems whose functioning ensures the quality of water.

The greatest freshwater reservoir of the world, Lake Baikal, is not an exception. Though it is situated in the area with relatively low economic

* Tel.: + 7-395-2243079; fax: + 7-395-2345207.
E-mail address: silow@bio.isu.runnet.ru (E.A. Silow)

PII: S0304-3800(98)00169-0

activity, the industry and agriculture in its region are developing rather fast during the last 50 years. The problem of the lake pollution is quite real now (Kozhova and Silow, 1998).

Particular difficulties arise during forecasting the consequences of the action of toxicants on the ecosystems, as it is practically impossible to judge an ecosystem reaction to introduction of a pollutant based on the reaction of individual components. Quite often the ecosystem reacts to toxicants more painfully than its individual components. On the other hand, cases are recorded of lower toxicity for an ecosystem of a number of substances with high toxicity for organisms. This is connected both with the fact that different trophic levels react differently to a toxicant and that the ecosystem stability is in many respects determined by its complexity.

It follows clearly that forecasting of the ecosystems' behaviour is possible only on the basis of experiments with ecosystems as a whole. The only real way for such experiments today is modelling the ecosystems (Jørgensen, 1992a). There is also a necessity for some holistic parameters or indices reflecting the state of ecosystem as a whole.

Among various functions proposed to describe the ecosystem development direction, one, namely exergy, is shown to have such advantages as good theoretical basis in thermodynamics, close relation to information theory, rather high correlation with other goal functions and relative easiness of computation (Jørgensen, 1992a). Firstly applied in ecological modelling at the end of 1970s (Mejer and Jørgensen, 1979), now exergy is used for the estimation of parameters of ecosystem models and development of the models able to predict species composition changes (Jørgensen, 1992b,c; Jørgensen and Nielsen, 1994).

The present work represents an attempt to apply the concept of exergy to modelling of impact of external chemical influences (namely, conservative and metabolizable toxicants and nutrient compounds) on the ecosystem of Lakc Baikal with the use of two models. One of them is created on the basis of field experiments with physical models of the ecosystem-mesocosms.

2. Size conversion model

The static size conversion model employed was initially proposed for Lake Ontario (Borgman, 1985). Here it is applied it to Lake Baikal with some modifications.

If we assume the size of the organism as the rough indicator of the trophic level, we can write

$$R_j/P_j = (L_j/L_i)^k \tag{1}$$

reflecting the constancy of relations between the sizes of the organisms belonging to the 'predator' (L_j) and 'prey' (L_i) trophic levels, connected with the efficiency of using the production of the level i consumed as the ration (R_j) for the production of level j (P_j), where k is the size conversion effectiveness. We can calculate

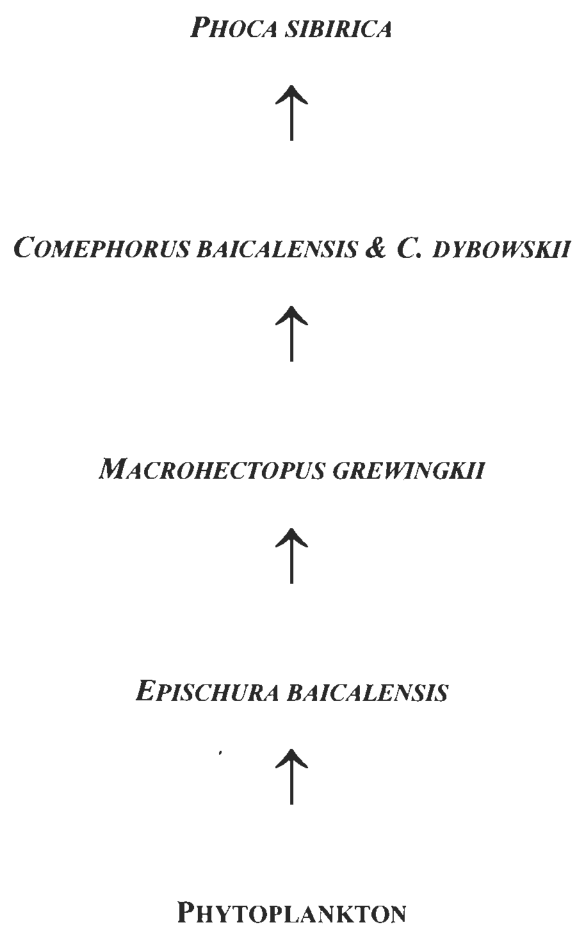

Fig. 1. The main trophic chain of the lake pelagic ecosystem.

Table 1
Structure of ecosystem model—unperturbed and in the presence of a toxicant

Organisms	Log (size) [mm]		Biomass (kJ m^{-2})	
	From	To	Unperturbed	With toxicant
Phytoplankton	−2	−1	20.0 ± 4.2	33.9 ± 6.7
Herbivorous zooplankton	−1	0.5	26.4 ± 5.0	28.0 ± 5.4
Carnivorous zooplankton	0.5	1.4	13.8 ± 2.5	9.2 ± 1.7
Fish	1.4	2.7	17.2 ± 3.3	7.9 ± 1.7
Seal	2.7	3.2	4.2 ± 0.8	2.5 ± 0.4

Table 2
Changes of exergy content due to input of toxicant

Components of ecosystem	Conversion factor	Exergy (10^3 kJ m^{-2})		ΔEx	Ratio $\Delta Ex/Ex_1$
		Unperturbed, Ex_1	With toxicant, Ex_2		
Detritus	1	9.3	9.3	0	0
Phytoplankton	3.4	0.07 ± 0.01	0.12 ± 0.02	0.05	0.71
Herbivorous zooplankton	144	3.9 ± 0.7	3.9 ± 0.7	0	0
Carnivorous zooplankton	287	4.0 ± 0.7	2.6 ± 0.5	−1.4	−0.35
Fish	344	5.9 ± 1.1	2.7 ± 0.6	−3.2	−0.54
Seal	402	1.7 ± 0.3	1.0 ± 0.2	−0.7	−0.41
Total	–	22.1 ± 2.3	16.9 ± 1.5	−5.2	−0.24

$$k = \log(R_j/P_j)/\log(L_j/L_i) \quad (2)$$

If the production is proportional to the sizes of the organisms we can write

$$P_j = cLj^{-k} \quad (3)$$

where c is the constant. It will be applicable also for the relation of the production to biomass (B):

$$P_j/B_j = aL_i^{-n} \quad (4)$$

where a and n are the coefficients. It is possible to express the biomass from Eq. (3) and Eq. (4) as

$$Bi = ca - 1L_i n^{-k} \quad (5)$$

Taking into account the size spectrum of the organisms belonging to one trophic level ranging between the limits x and y, and using the function

$$f(L) = mL^h \quad (6)$$

we can calculate the biomass of the trophic level as

$$B_{xy} = \int_{L_x}^{L_y} f(L)\,dL = m(L_y^{h+1} - L_x^{h+1})/h + 1 \quad (7)$$

where h and m are the constants. From Eq. (5) and Eq. (7) we can see $h + 1 = n - k$. Then, we can introduce

$$b = m(n-k)^{-1} \quad (8)$$

and write

$$B_{xy} = b\ (L_y^{n-k} - L_x^{n-k}) \quad (9)$$

Now, basing on the rations, productions and sizes in such 'predator–prey' pairs as 'phytoplankton–Epischura', 'Epischura–Macrohectopus', 'Macrohectopus–Comephorus', and 'Comephorus–seal' (Fig. 1), known from the literature (Afanasyeva, 1977; Starikov, 1977a; Popovskaya, 1978; Votintsev, 1978; Kozhov, 1998) we can estimate

$k = 0.61 + 0.3$
$n = 0.56 + 0.12$

$b = -34.96 + 7.79.$

Taking into account that *Epischura baicalensis* and *Comephorus* species are the main components

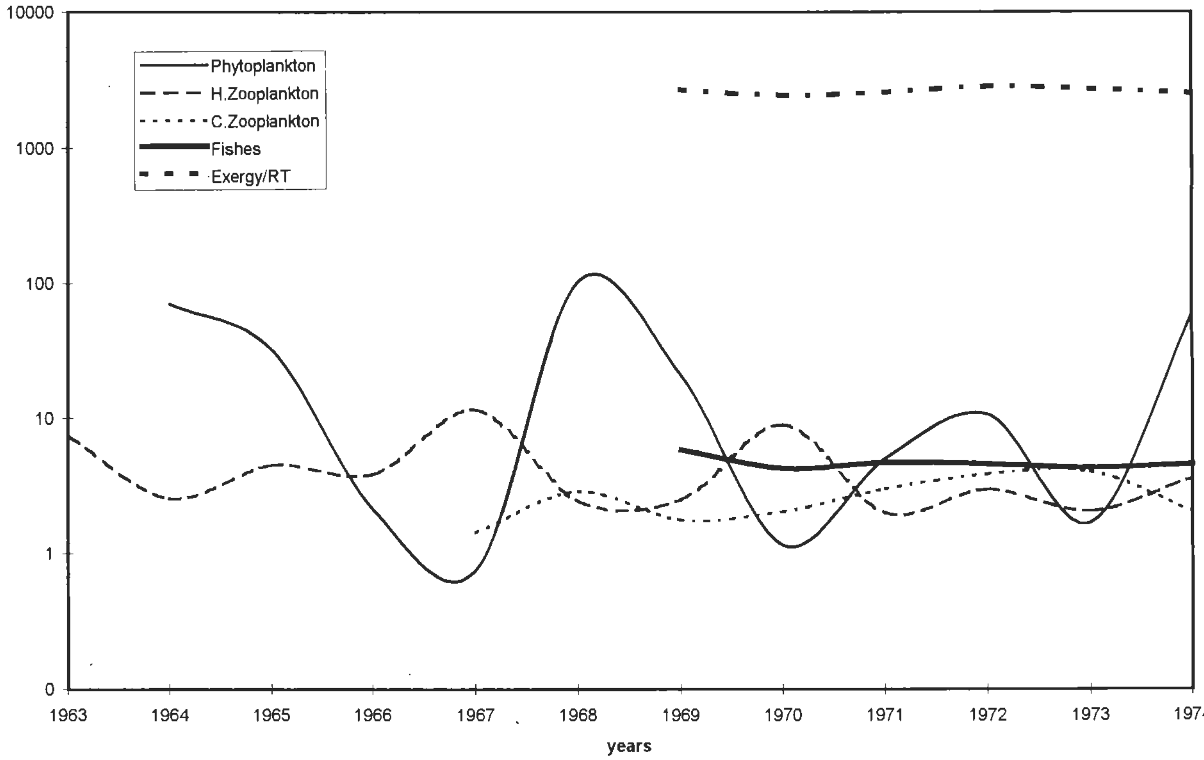

Fig. 2. The dynamics of components (g m^{-2}) and exergy content (g detritus m^{-2}) of lake pelagic ecosystem.

of the herbivorous zooplankton and fish trophic levels (90 and 95% of biomasses, respectively) we can calculate the size–biomass structure of the Lake Baikal ecosystem (Table 1). If we will assume the presence of conservative toxicant in sub-lethal concentration, increasing metabolic demands of organisms, i.e. causing the necessity for the 'predator' to eat 1.5 times more food to support the same rate of the production, n remains constant, k becomes equal to 0.77. To calculate b we must take into account that the total biomass of the ecosystem is constant due to limitation by nutrients. Then we obtain $b = -8.06$. Now we can calculate the size structure of the ecosystem in perturbed state (Table 1). The share of small organisms increased markedly, the largest deviations taking place in the top trophic levels, biomass of the algae has increased. It is in good accordance with the known main characteristic features of trends expected in stressed ecosystems (Odum, 1985).

Now it is possible to calculate the change of exergy of the Lake Baikal ecosystem model due to intoxication. The concentration of detritus in the Lake Baikal is 0.5 mg l^{-1}, and using the equations and conversion factors given by Jørgensen (1992a,b, 1994) we can estimate the exergy changes for total system and its components due to toxicant input (Table 2). It is seen that the total exergy of the system decreased, while the exergy of some biotic components (herbivorous zooplankton) remained at the same level or even increased (phytoplankton). There is visible connection between the trophic level and the change in exergy. Higher levels are negatively affected by the input of toxicants. The total loss of exergy equals one fourth of initial content.

Of course, this model is only a rough approximation of the real ecosystem and operates with hypothetical toxicant. Nevertheless, it demonstrates higher sensitivity of top trophic levels to external influences and necessity to take into ac-

Table 3
The matrices of mutual interferences of the ecosystem model components for principal seasons

Season		Nutrients	Phenols	Phytoplankton	Zooplankton
February to April	Nutrients	−0.11209530	−0.00500225	0.40364040	0.04619371
	Phenols	0.01639400	−0.01640310	−0.00241056	−0.15218000
	Phytoplankton	−0.47260670	−0.04123500	−0.13640300	−0.43919300
	Zooplankton	0.43371280	0.01852740	0.12029700	−0.21648100
July to September	Nutrients	−0.11105550	−0.01800812	−0.18375000	0.00000000
	Phenols	0.05901800	−0.46008400	0.01371950	−0.03520000
	Phytoplankton	0.49260000	0.02679900	−0.16374300	−0.26742000
	Zooplankton	0.00000000	−0.00508349	0.15017800	−0.14718000

count these levels during monitoring observations. It is also seen from the results that such parameter as exergy can serve as holistic indicator of ecosystem state trends.

3. Ecosystem component deviations model

Fig. 2 represents the dynamics of the components of the Lake Baikal ecosystem (Beckman and Afanasyeva, 1977; Shimaraev and Afanasyeva, 1977; Starikov, 1977b; Popovskaya, 1978). It is clearly seen that the inter-annual fluctuations of phytoplankton and zooplankton biomasses are very significant and affect the exergy content of the ecosystem, causing its fluctuations in a rather wide range. If we reduce our task only to estimation of possible anthropogenic impacts consequences we can avoid natural ecosystem dynamics modelling.

In the first approximation, an equation may be given for the lumped lake model as follows:

$$dR/dt = Q(R^* - R) + U \tag{10}$$

where R is the vector of ecosystem components state; R^* is the vector of ecosystem components unperturbed state; U is the vector of external control; and Q is the matrix of mutual interactions of components.

Since modelling of the ecosystem natural dynamics (R^*) is extremely complicated, it is possible to replace this model by a model expressed in deviations relative to R^*:

$$dZ_i/dT = \sum_{k=1}^{n} Q_{Ik}Z_i + U_i \tag{11}$$

where $Z_i(t)$ is the vector of deviations of component i; Q_{ik} is the coefficient of mutual interactions of the components i and k; and n is the number of components.

The concentrations of nutrients, phenolic compounds, phytoplankton and zooplankton were selected as the basic indices of an ecosystem condition. The first two reflect the anthropogenic influence in the forms of eutrophication and toxification, while concentrations of phyto- and zooplankton represent the state of the ecosystem. Microbiological and hydrochemical parameters are present here in a vague form because the coefficients of mutual influences have been determined in field experiments with mesocosms of 2 m^3 volume on a natural background. To estimate the parameters several series of experiments have been fulfilled with addition of the extra amounts of nutrients, phenolic compounds, natural phyto- and zooplankton to experimental bags and comparing the responses of these components with their dynamics in control bags and in the lake. So, mesocosm ecosystem served as 'black boxes' where inputs were varied and outputs were measured. Experiments were carried out during two biologically principal seasons at Lake Baikal (March to April and July to September) from 1986 to 1990 (Silow and Stom, 1989a,b; Silow et al., 1989, 1990). The method of model parameter evaluation has been described earlier (Silow et al., 1995). The matrices of interactions are given in the Table 3. Component concentrations are ex-

Table 4
The maximum deviations of the components of the ecosystem model (μg l^{-1}) in response to starting phenols addition (100 μg l^{-1})

Components	Spring community		Summer community	
	From	To	From	To
Nutrients	−1.52	0.46	−1.80	0.25
Phytoplankton	−4.12	1.21	−1.19	2.68
Zooplankton	−1.11	1.85	−0.51	0.48
Return to initial state in (days)	–	34	–	23

Table 5
The maximum deviations of the components of the ecosystem model (μg l^{-1}) in response to starting nutrients addition (50 μg l^{-1})

Components	Spring community		Summer community	
	From	To	From	To
Phenols	0.00	1.39	0.00	2.95
Phytoplankton	−23.63	8.61	−6.69	24.63
Zooplankton	−9.95	21.69	−1.55	3.68
Return to initial state in (days)	–	36	–	24

pressed in μg l^{-1}, the time step of the model equals 1 day.

In calculation experiments the starting additions of nutrients and phenolic compounds, as well as their permanent inputs were simulated for 90 days. Nutrients were taken as the mixture of phosphate and nitrate with the N:P ratio 5:1. The spring community was more sensitive to the external perturbations, has demonstrated the wider range of deviations and returned to initial state later than summer one (Tables 4 and 5). The permanent addition of phenolic compounds caused the decrease of nutrients concentration, in summer it caused the increase of phytoplankton and decrease of zooplankton biomasses, in spring it acts in contrary way. The equilibrium concentration of phenolic compounds in spring was higher than that of summer (Table 6). Nutrients addition caused a decrease in spring phytoplankton biomass and an increase in summer phytoplankton and zooplankton biomasses. Addition of nutrients to summer community also caused the appearance of phenolic compounds (Table 7).

Table 6
The deviations of the components of the ecosystem model (μg l^{-1}) and exergy content (kJ l^{-1}) in response to phenols addition (100 μg l^{-1} day^{-1})

Components	Spring community	Summer community
Nutrients	−1.56	−1.29
Phenols	98.27	68.45
Phytoplankton	−3.16	1.07
Zooplankton	0.63	−0.16
Exergy	229	−48.22
Reaches new equilibrium state in (days)	45	34

Table 7
The deviations of the components of the ecosystem model (μg l^{-1}) and exergy content (kJ l^{-1}) in response to nutrients addition (50 μg l^{-1} day^{-1})

Components	Spring community	Summer community
Nutrients	38.07	42.10
Phenols	0.00	1.81
Phytoplankton	−20.30	17.34
Zooplankton	11.57	2.26
Exergy	5973	2153
Reaches new equilibrium state in (days)	43	29

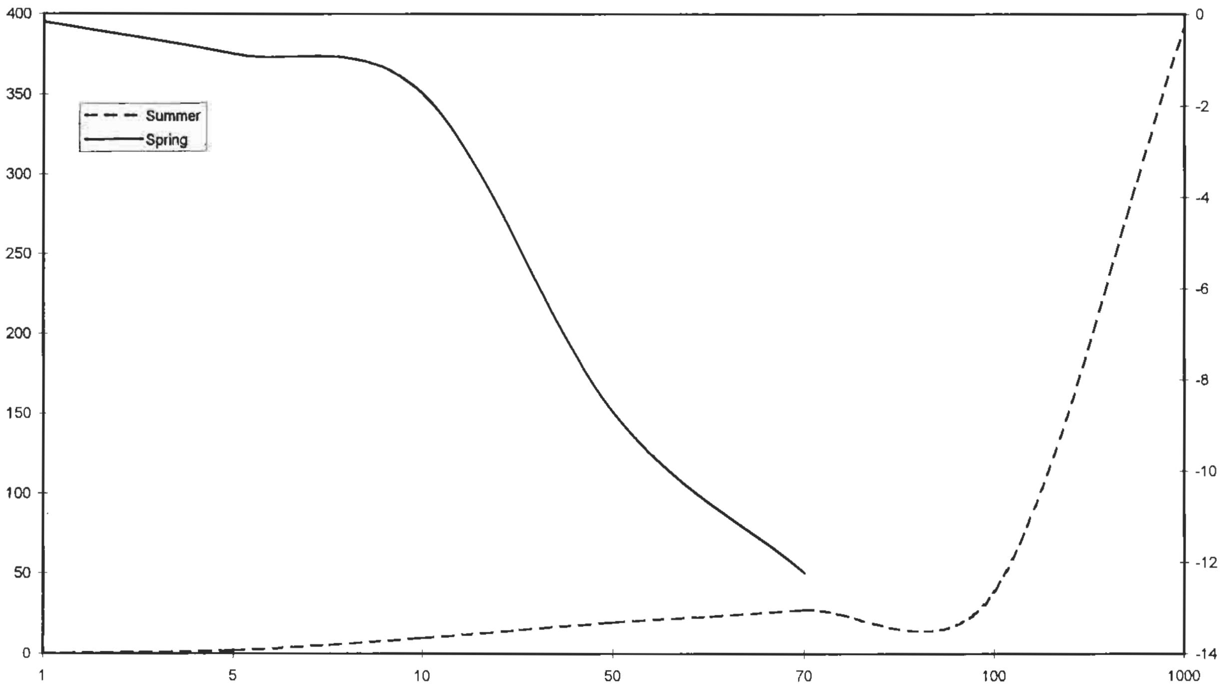

Fig. 3. The effect of nutrients addition (μg l^{-1}) on the change of total biomass (μg l^{-1}) of pelagic community model in spring (right scale) and summer (left scale).

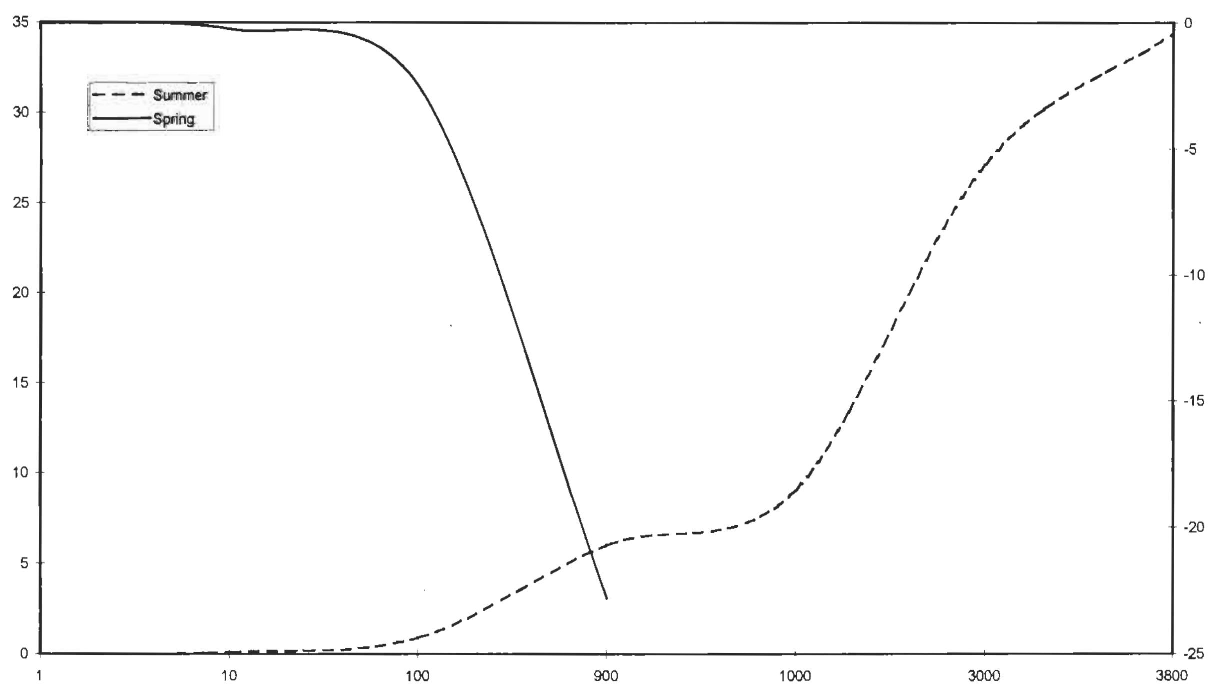

Fig. 4. The effect of phenolic compounds addition(μg l^{-1}) on the change of total biomass (μg l^{-1}) of pelagic community model in spring (right scale) and summer (left scale).

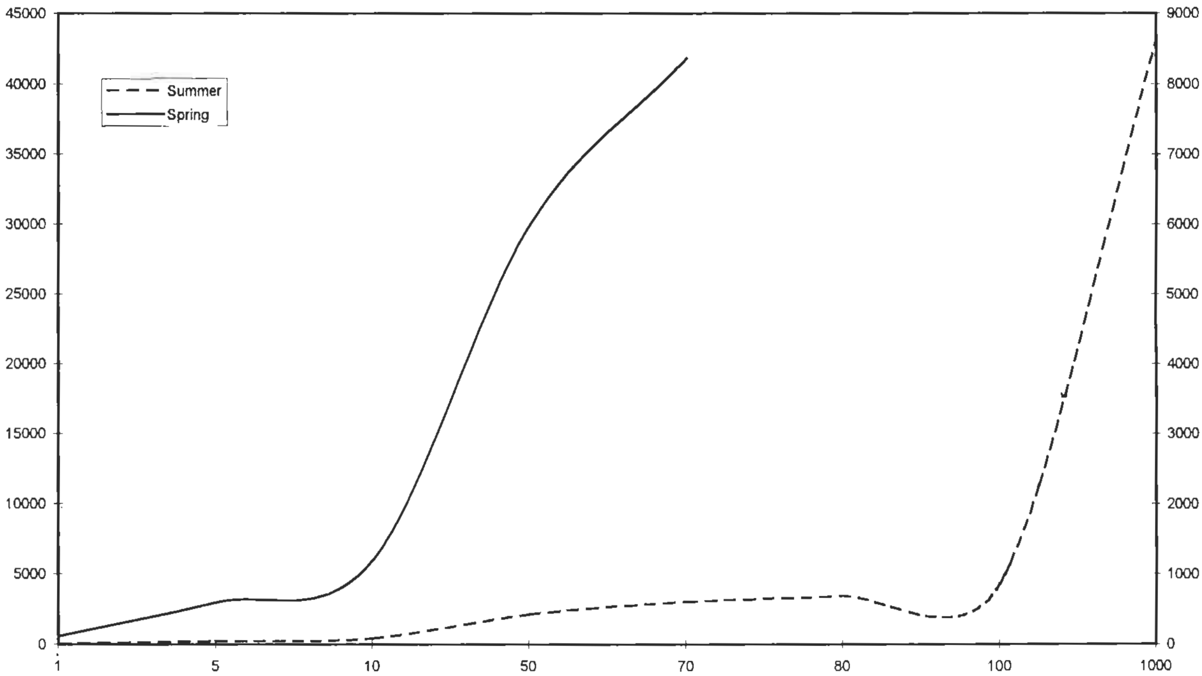

Fig. 5. The effect of nutrients addition (μg l^{-1}) on the change of exergy content (MJ l^{-1}) of pelagic community model in spring (right scale) and summer (left scale).

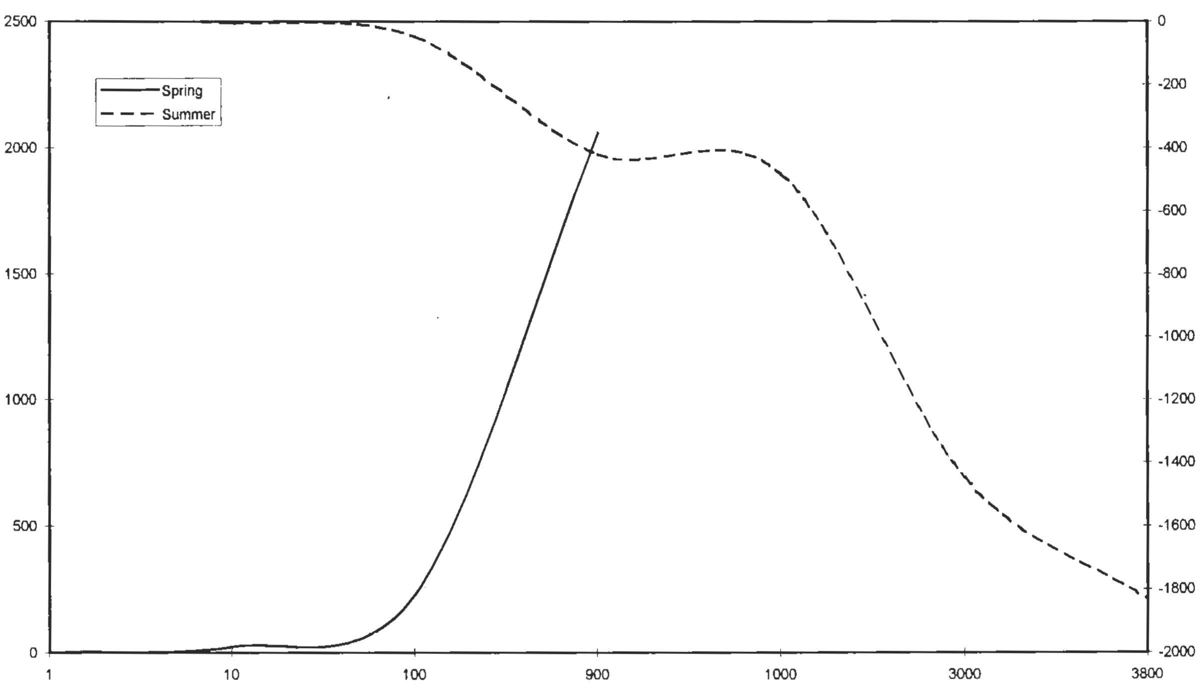

Fig. 6. The effect of phenolic compounds addition (μg l^{-1}) on the change of exergy content (MJ l^{-1}) of pelagic community model in spring (right scale) and summer (left scale).

Table 8
Buffer capacities of the Lake Baikal ecosystem

Buffer capacities for: season	Biomass		Exergy	
	Phenols	Nutrients	Phenols	Nutrients
Spring	−39.53	−5.73	0.44	0.008
Summer	110.38	2.55	−2.07	0.023

External influences caused the decrease of total biomass of the pelagic ecosystem in spring and its increase in summer (Figs. 3 and 4). The ecosystem was destroyed by permanent input of phenols at concentrations of 0.9 mg l^{-1} (in spring) and of 3.8 mg l^{-1} (in summer). The addition of nutrients destroyed spring ecosystem at a concentration of 0.07 mg l^{-1} and was not able to destroy the summer one at a concentration of 1.5 g l^{-1}.

Spring phytoplankton was suppressed by external influences, while biomass of summer phytoplankton increased in response to nutrient addition. It can be connected with the dominance of endemic forms, more sensitive to chemical perturbations than common forms, in the under-ice community. It was shown that phytoplankton of the oligotrophic part of Lake Biwa reacted negatively to addition of nutrients, while phytoplankton of the eutrophic part was stimulated by it (Ischida and Mitamura, 1986). Baikalian phytoplankton reacts similarly, but behaves as oligotrophic during under-ice period and as eutrophic during summer, as endemic Baikalian forms have been adapted to very low level of nutrient content during their evolution. Summer zooplankton, on the contrary, was more sensitive to phenolic additions. It may be explained by higher temperatures of surface water layer during summer, as the most abundant form of Baikalian zooplankton, *Epischura baikalensis*, prefers low temperatures and was more sensitive to toxicant when the temperature was higher. The increase of zooplankton biomass after perturbations during spring may be related to increase of bacterial plankton biomass, as the latter was stimulated by additions of both phenolic compounds and nutrients (Silow, 1990).

The changes of exergy of ecosystem due to addition of pollutants are presented in Figs. 5 and 6. Addition of nutrients is shown to increase the exergy content of the model ecosystem in both summer and spring, while phenols caused the growth of exergy content in spring and decrease of it in summer. The summer decrease connected with the mortality of summer zooplankton, as input of zooplankton to the total exergy content is much higher. The increase of exergy under external influences is in accordance with the results of model experiments, where the increase of exergy due to nutrient enrichment and toxication was demonstrated (Jørgensen, 1995). The case of exergy decrease after addition of phenols in summer can be observed as the immediate reaction (as the duration of experiment was only 90 days), also described in the work cited.

The higher sensitivity of under-ice community may also be connected with different exergy content in planktonic community in spring and summer. Using data concerning seasonal dynamics of the Lake Baikal ecosystem components from 1967 to 1974 (Beckman and Afanasyeva, 1977; Shimaraev and Afanasyeva, 1977; Starikov, 1977b; Popovskaya, 1978; Kozhov, 1998), it is possible to calculate the difference between exergy content in summer and spring planktonic community. It equals 805 ± 92 g detritus m^{-2}, or about 1/3–1/4 of the total exergy content.

4. Buffer capacities

It is also interesting to compare buffer capacities for different seasons for the various response parameters studied. The buffer capacity quantifies the ability of the ecosystem to react pliably to external factors, being the ecological expression of Le Chatelier's principle. It can be calculated as

(Jørgensen, 1995):

$$\beta = \delta(\text{forcing function})/\delta(\text{state variable}). \quad (12)$$

It is possible to calculate buffer capacities for various state variables, e.g. for individual components, phytoplankton and zooplankton; or for the whole ecosystem, biomass and exergy buffer capacities.

Buffer capacities, calculated for the model of ecosystem, also demonstrate higher sensitivity of the spring community, than the summer one (Table 8). It is clearly seen, that exergy buffer capacity is more realistic than that of the biomass. The latter shows the spring community to be more resistant to nutrient additions than the summer one (judging by absolute values), while exergy buffer capacity indicates that spring community is three times more sensitive than summer one.

5. Conclusion

Though the models described in this work are relatively simple, they are shown to produce results, which can be useful both for theory and practice.

Static size conversion model of the Lake Baikal ecosystem has demonstrated higher sensitivity of top trophic levels to external influences and necessity to take these levels into account during monitoring works.

Model of anthropogenic disturbances of the Lake Baikal ecosystem based on field experiments has shown higher sensitivity of under-ice community than the summer one. It can be related to: (1) differences in abiotic environmental conditions (temperature, light regime etc.); (2) the different species composition of phytoplankton, as the dominant species of the spring community are shown to be less resistant to pollutants than those of the summer community; (3) different exergy content in planktonic community (mainly due to differernt biomasses of zooplankton).

Exergy is shown to decrease under the action of conservative pollutant and increase after addition of nutrients and phenolic compounds, reflecting the general shift in ecosystem. Exergy buffer capacity seems to be a more realistic measure for pliability of ecosystem reaction to external factors than biomass buffer capacity.

Though this work does not pretend to be the basis for response parameters selection, it indicates the necessity of further studies of properties of such parameters as exergy, and ways of applying them to the needs of modern ecology.

Acknowledgements

The author is very grateful to Professor Sven Erik Jørgensen for the initiation and constant support of this work and to Dr Boris Kompare for the useful discussion of it. Special thanks to Danish Ministry of Education and Research that granted the author the possibility to work at the Royal Danish School of Pharmacy. This research was also supported by the grant of the Russian Foundation for Fundamental Researches.

References

Afanasyeva, E.L., 1977. The Biology of Baikalian Epischura. Nauka, Novosibirsk, p. 144 (in Russian).

Beckman, M. Yu., Afanasyeva, E.L., 1977. Distribution and production of Macrohectopus. In: Votintsev, K.K. (Ed.), Pelagial of the Lake Baikal Biological Productivity and its Variability. Nauka, Novosibirsk, pp. 76–98 (in Russian).

Borgman, U., 1985. Predicting the effect of toxic substances on pelagic ecosystems. Sci. Total Environ. 44, 111–121.

Ischida, N., Mitamura, O., 1986. Utilization of nitrogenous nutrients by natural phytoplankton in enriched lake waters. Jap. J. Limnol. 47, 345–350.

Jørgensen, S.E., 1992a. Integration of the Ecosystem Theories: A Pattern. Kluwer Academic, Dordrecht/Boston/London, p. 383.

Jørgensen, S.E., 1992b. Parameters, ecological constraints and exergy. Ecol. Modell. 62, 163–170.

Jørgensen, S.E., 1992c. Development of models able to account for changes in species composition. Ecol. Modell. 62, 195–208.

Jørgensen, S.E., 1994. Review and comparison of goal functions in system ecology. Vie et Milieu 44, 11–20.

Jørgensen, S.E., 1995. Exergy and ecological systems analysis. In: Patten, B.C., Jørgensen, S.E. (Eds.), Complex Ecology: the Part–Whole Relation in Ecosystem. Prentice Hall PTR, Englewood Cliffs, p. 568—584.

Jørgensen, S.E., Nielsen, S.N., 1994. Models of the structural dynamics in lakes and reservoirs. Ecol. Modell. 74, 39–46.

Kozhov, M.M., 1998. Lake Baikal and its Life, 2nd ed. Backhuys, Leiden.

Kozhova, O.M., Silow, E.A., 1998. The current problems of Lake Baikal ecosystem conservation. Lakes Reserv. Res. Manag. 3, 19–33.

Mejer, H.F., Jørgensen, S.E., 1979. Energy and ecological buffer capacity. In: Jørgensen, S.E. (Ed.), State of the Art in Ecological Modelling. International Society for Ecological Modelling, Copenhagen, pp. 829–846.

Odum, E.P., 1985. Trends expected in stressed ecosystems. BioScience 35, 419–422.

Popovskaya, G.I., 1978. The phytoplankton. In: Galazy, G.I. (Ed.), Problems of Baikal. Nauka, Novosibirsk, pp.158–169 (in Russian).

Shimaraev, M.N., Afanasyeva, E.L., 1977. The influence of temperature conditions on inter-annual changes of pelagic zooplankton. In: Votintsev, K.K. (Ed.), Pelagial of the Lake Baikal Biological Productiveness and its Variability. Nauka, Novosibirsk, pp. 61–76 (in Russian).

Silow, E.A., 1990. Complex Model Experiment in Aquatic Ecotoxicology: Application to the Lake Baikal, PhD Thesis. Institute of Aquatic Biology, Kiev, p. 150 (in Russian).

Silow, E.A., Stom, D.J., 1989a. The use of mesocosms for aquatic ecosystem modelling. Biol. Sci. (Biol. Nauki) 2, 101–109 (in Russian).

Silow, E.A., Stom, D.J., 1989b. Model experiment in aquatic toxico-ecology. Hydrobiol. J. 26, 83–87.

Silow, E.A., Rudykh, A.R., Stom, D.J., 1989. An ecotoxicological experiment under the ice in Lake Baikal. Hydrobiol. J. 25, 98–100.

Silow, E.A., Stom, D.J., Basharova, N.A., et al., 1990. The influence of biogenous elements on the components of the Lake Baikal plankton community. Acta Hydrochim. Hydrobiol. 19, 629–634.

Silow, E.A., Gurman, V.J., Stom, D.J., Rosenraukh, D.M., Baturin, V.A., 1995. Mathematical models of Lake Baikal ecosystem. Ecol. Modell. 82, 27–39.

Starikov, G.V., 1977a. Comephoridae of the Lake Baikal. Nauka, Novosibirsk, p. 104 (in Russian).

Starikov, G.V., 1977b. Dynamics of number, biomass and production of *Comephorus* sp. In: Votintsev, K.K. (Ed.), Pelagial of the Lake Baikal Biological Productiveness and its Variability. Nauka, Novosibirsk, pp. 105–115 (in Russian).

Votintsev, K.K., 1978. Bioenergetic structure of pelagic ecosystem. In: Galazy, G.I. (Ed.), Problems of Baikal. Nauka, Novosibirsk, pp. 258–265 (in Russian).