The Changes of Ecosystem Goal Functions in Stressed Aquatic Communities*

Eugene A. SILOW

*Scientific Research Institute of Biology at State University of Irkutsk,
P.O.Box 24, Lenin str. 3, Irkutsk - 3, 664003, Russia*

Abstract: *The changes of biomass, exergy and structural exergy under the action of various chemical pollution (addition of nutrient compounds, pesticides, chlorinated phenols, oil, heavy metal ions, acidification etc.) are analysed for 50 experimental works with model aquatic ecosystems - microcosms, mesocosms and experimental ponds.*

Structural exergy is shown to remain at constant level or to increase when the allochthonous compounds can be metabolised by ecosystem, or when the ecosystem can adapt itself to the input of toxicant by structural changes. When the substance is too conservative, too toxic or/and is coming in too high concentrations, structural exergy is decreasing, demonstrating the inability of ecosystem to adapt to this influence and irreversibility of changes in ecosystem.

The possibility to use such parameter as structural exergy for estimation of ecosystem state and its changes under various external influences is demonstrated. It reflects the state of ecosystem and can indicate the degree of ecosystem adaptation, decreasing when important for ecosystem functioning components are eliminated.

In experiments with mathematical model of lake Baikal ecosystem exergy content is shown to increase after addition of nutrients and to decrease after addition of phenolic compounds, reflecting the general shifts in ecosystem.

Keywords: *structural exergy, aquatic ecosystems, ecosystems resistance, ecosystems degradation*

1. Introduction

Though the ecosystem health concept itself is criticised (Suter, 1993) the necessity to have measurable parameter, reflecting the state of the ecosystem as the whole and making it possible to estimate the damage of ecosystem changes under precise external influences, is now accepted by the most of ecologists and environmental scientists (Bartell *et al.*, 1992; Costanza *et al.*, 1992).

It seems natural to use one of so called goal functions to characterise the state of the ecosystem and the changes of it under external influences. Among various goal 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

* Received 1997-02-25; accepted 1998-03-27.

others goal functions and relative easiness of computation (Jørgensen, 1992a). Firstly applied in ecological modelling in the end of 70-th (Mejer & Jørgensen, 1979), now exergy is used for the estimation of parameters of ecosystem models and development of models able to predict species composition changes (Jørgensen, 1992b, 1992c; Jørgensen & Nielsen, 1994).

Exergy is defined as the distance between 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 given system from its primary components (in the case of ecological systems - from inorganic chemical compounds). Exergy related to the total biomass measures the possibility of ecosystem to accept and utilise external fluxes of energy. This structural or normalised exergy reflects the degree of ecosystem development or complexity and has such advantages in comparison with the total exergy as independence from the total biomass of the ecosystem and possibility to serve as indicator, demonstrating the level of evolutionary development of organisms the ecosystem consists of.

The relation of exergy content with the trophic status of water body was demonstrated by Salomonsen (1992). The main features of the changes of exergy of ecological systems under the external perturbations were studied in the experiments with water bodies and flows mathematical models, describing processes of eutrophication and toxification (Jørgensen, 1995). The recent work is dedicated to the behaviour of exergy and structural exergy in physical models of aquatic ecosystems - microcosms, mesocosms and experimental ponds under various external perturbations.

2. Model ecosystems description

Experiments with the physical models of ecosystems (model ecosystems) are now one of the most often used tools for ecological risk assessment. The number of experimental works with the model ecosystems has significantly increased during the last two decades when the necessity of the holistic approach to the estimation of effects of external disturbances, particularly chemical pollution, on ecosystems was realised (Odum, 1984; Lundgren, 1985; Gearing, 1989).

Model ecosystems can be divided into three groups: microcosms, mesocosms and experimental ponds. The first, microcosms, are laboratory systems exposed to environmental factors controlled by scientist. Mesocosms are the parts of natural system, completely or partly isolated from it and exposed to the same environmental conditions as the mother ecosystem. Experimental ponds usually are replicate artificial ponds exposed to natural environmental influences. They represent the best possible approach to natural conditions, but they can not be large enough to be oligo-, or, at least, mesotrophic water bodies.

In present study the total number of cases taken into account is 50. There are 28 freshwater and 22 marine ecosystems, among them 21 are oligo-, 14 are meso- and 15 - eutrophic communities according to trophic status.

The volumes of experimental systems varied from 1 300 m³ (Takahashi *et al.*, 1977) to 3.8 l (Taub, 1984), the duration of experiment - from 4 days (Havens, 1994a) to 16 months (Rosemarin *et al.*, 1990). In the most cases the number of replicates in experiment was 2 or 3, ranging from 1 to 6.

Part of model ecosystems called "mesocosms" by authors (Fairchild *et al.*, 1992; Webber *et al.*, 1992; Hoagland *et al.*, 1993; Drenner *et al.*, 1993) are experimental ponds according to definition given above. Among the microcosms there are isolated system (Taub, 1984), system consisting from compartments with recirculation (Kersting, 1984), flow - through systems (Oviatt *et al.*, 1977; Heinle *et al.*, 1979; Lynch *et al.*, 1985; Rosemarin *et al.*, 1990). Mesocosms are represented by bags isolated both from atmosphere and sediments (Havens, 1992, 1994a, 1994b), bags open to atmosphere (Takahashi *et al.*, 1977; Grice *et al.*, 1977; Davies & Gamble, 1979; Kuiper, 1977, 1981a, 1981b, 1983; Kuiper & Hansveit, 1984a, 1984b), cylinders open to atmosphere and anchored on sediments (Schauerte *et al.*, 1982; De Costa *et al.*, 1983; Lay *et al.*, 1984; Cuker, 1987; Yasuno *et al.*, 1988; Barmuta *et al.*, 1990; Thompson *et al.*, 1993; Baretta-Bekker *et al.*, 1994).

For the purposes of recent work it was necessary to know reactions of at least two trophic levels to external influence. In the most cases there were only phytoplankton and zooplankton communities responses studied during investigation. Some experiments took into account bacterioplankton (Oviatt *et al.*, 1977; Schauerte *et al.*, 1982; Perez *et al.*, 1983; Kuiper, 1981a; 1983; Kuiper & Hansveit, 1984a, 1984b; Havens, 1994b; Baretta-Bekker *et al.*, 1994) or fishes (Drenner *et al.*, 1993) together with phyto- and zooplankton. The most complete pelagic community experimental study included records of bacterio-, phyto-, zooplankton communities and fishes population dynamics (Azam *et al.*, 1977; Beers *et al.*, 1977; Grice *et al.*, 1977; Koeller *et al.*, 1977; Takahashi *et al.*, 1977, Thomas *et al.*, 1977). In some experiments only benthic communities were studied (Lynch *et al.*, 1985; Notini *et al.*, 1989; Rosemarin *et al.*, 1990). Only few experiments were carried out with the complete ecosystems, consisting of phyto- and zooplankton, benthic invertebrates (Elmgren & Frithsen, 1982) and fishes (Boyle, 1980; Fairchild *et al.*, 1992; Webber *et al.*, 1992). The most complete among them covered bacteria, phytoplankton, zooplankton, phytobenthos, periphyton, zoobenthos and fishes (Giddings *et al.*, 1984).

3. The calculations of exergy

For exergy calculations it was necessary to have the biomasses of ecosystem components. Unfortunately, the biomass of bacteria is given only in one work (Baretta-Bekker *et al.*, 1994), biomass of phytoplankton - in three (Baretta-Bekker *et al.*, 1994; Havens, 1992; 1994a), of zooplankton - in four (Heinle *et al.*, 1979; Baretta-Bekker *et al.*, 1994; Havens, 1992, 1994a). The concentration of zooplankton was expressed practically in all cases in number of individuals per unit of volume, of phytoplankton - in mg of chlorophyll *a* content, sometimes in number of cells per unit of volume (Hurlbert *et al.*, 1972; Schauerte *et al.*, 1982; Lay *et al.*, 1984, 1985a, 1985b; Webber *et al.*, 1992), or as biovolume (Havens & Heath, 1989; Havens, 1994a). Benthic invertebrates quantities were expressed as number of individuals per unit of area. In all these cases the values were recalculated into mg of dry weight per cubic metre on the basis of data known from the literature (Jørgensen *et al.*, 1991).

For the calculation of exergy (mg detritus m⁻³) the equation given by Jørgensen (1994) was used:

$$Ex / RT = \sum_{i=1}^N C_i * f_i$$

where R is the gas constant, T is the absolute temperature, N is the number of components, c_i is the biomass of component i, f_i is the conversion factor corresponding to this component, and depending on the number of genes and number of cell types of given organism. The latter can be found in Jørgensen *et al.* (1995). As it was necessary simply to compare the changes of exergy, it is expressed as Ex/RT throughout the paper. Structural exergy was calculated as relation of Ex/RT to the total biomass of the ecosystem.

Before the presentation of the results it is necessary to point out the main sources of possible errors. They are: insufficient number of replicates in experiments, insufficient number of ecosystem components taken into account (mainly zoo- and phytoplankton), errors of biomass estimations, made on the basis of chlorophyll *a* content, number of zooplankton specimens etc., and, of course, errors raised during the estimation of exergy, as we don't know exact number of informative genes and cell types for the most organisms, but only approximate differences between them. Though estimations presented are rough, they, nevertheless, can provide us with the information concerning the change of exergy and structural exergy in the ecosystem under the external influence.

4. Mathematical model

The basic object of the model is optimisation of interaction of the anthropogenic factors with ecosystem of Baikal, therefore the model was based on the method of disturbances (Silow *et al.*, 1995). The model describes effects of anthropogenic influence on the state of the lake ecosystem components and destruction of pollutants under the action of biotic and abiotic factors.

The lake water surface is divided into 10 regions, significantly differing by their conditions. In each region the water body is divided into three layers (0-50, 50-250), the layer 250m-bottom was supposed to be homogenous. 21 boxes are thus obtained and ecosystem dynamics within each box (j) is described by an equation:

$$dZ_j^i / dt = \sum_{k=1}^N Q_{ik} Z_j^k + r(Z_j^i) + u_j^i$$

where Z - vector of ecosystem deviation from unperturbed state; Q - mutual influence matrix of ecosystem components; r - functions of the influence of hydro-physical processes on substance export/import in each cell; u - the vector of external influences.

Biotic components described by the model - bacterio-, phyto-, zooplankton, fishes, seal, zoo- and phytobenthos, hydrochemical parameters - water mineralization, nitrogen and phosphorus content, dissolved and particulate organic matter, content of pollutants - phenols, oil products, heavy metals, other anthropogenic influences - catchment of fishes and seal.

The inputs of the model are the input of pollutants with tributaries and precipitation, other economic activity. Model describes both seasonal and annual changes. Information provision is based

on the series of *in situ* field experiments with mesocosms made in different seasons for five years (Silow *et al.*, 1991).

Fig. 1 Effects of addition of phosphorus on lake plankton biomass (1), exergy (2) - left scale, - and structural exergy (3) - right scale. A - initial $0.1 \mu\text{g}\cdot\text{l}^{-1}$ (on the basis of data by De Costa *et al.*, 1983), B - permanent $0.1 \mu\text{g}\cdot\text{l}^{-1}\cdot\text{d}^{-1}$ (on the basis of data by Cuker, 1987).

5. Results

Addition of nutrients caused the following effects. Input of phosphorus (De Costa *et al.*, 1983; Cuker, 1987) resulted in increase of both biomass and exergy of lake plankton (Fig. 1), while structural exergy remained practically at the same level, as the biomasses of the all components of the ecosystem increased in the similar proportion. In experiments with marine plankton community joint addition of phosphate, nitrate and silicate (Baretta-Bekker *et al.*, 1994) caused increase of biomass and exergy of plankton, structural exergy remained at the same level. In microcosms (Heinle *et al.*, 1979) nitrogen addition did not affected biomass, exergy and the structural exergy of the ecosystem. Addition of phosphorus caused the increase of phytoplankton biomass, followed by the growth of copepods biomass and, consequently, increase of grazing, resulted in decrease of the total biomass, when the extra amounts of phosphate were exhausted, and increase of share of zooplankton in it. It was reflected by the growth of exergy and structural exergy.

Input of treated urban sewage (Heinle *et al.*, 1979; Oviatt *et al.*, 1979), where nutrients were the main component, did not significantly influenced the biomasses and caused the increase of exergy in short-term (two-weeks) experiments, as in the previously described case. As a result of it the structural exergy of the system increased. In long-term (170 days) experiment there was no significant changes of the parameters studied.

Fig. 2. Effects of pesticides on aquatic communities biomass and exergy (left scale) and structural exergy (right scale).

A - dimethylamine salt of 2,4-dichlorophenoxyacetic acid, $\text{mg}\cdot\text{l}^{-1}$ (on the basis of data by Boyle, 1980), B - 20 nM Kepone; C - bifenthrin (on the basis of data by Drenner *et al.*, 1993), here exergy content is expressed in 10. (on the basis of data by Perez *et al.*, 1991)

Fig. 3 Effects of cadmium addition ($\mu\text{g}\cdot\text{l}^{-1}$) on marine plankton biomass and exergy (left scale) and structural exergy (right scale) (on the basis of data by Kuiper, 1981b).

When pesticides were added to experimental systems, normalised exergy has decreased only in three cases from 11 studies (Fig. 2). Dimethylamine salt of 2,4-dichlorophenoxy acetic acid (Boyle, 1980) stimulated the growth of algae. The increase of their share in the total biomass was reflected by decrease of structural exergy. The addition of Kepone (Perez *et al.*, 1991) reduced the biomass and grazing pressure of zooplankton due to toxic effect and, consequently, caused the decrease of

structural exergy. Even in these experiments the decrease of structural exergy was not very significant. The addition of toxicant in high concentration (Drenner *et al.*, 1993), which caused complete elimination of zooplankton and fishes and decrease of phytoplankton biomass resulted in sharp fall down of structural exergy.

Fig. 4. Effects of acidification on the lake plankton biomass and exergy (left scale) and structural exergy (right scale). A - on the basis of data by Havens & De Costa (1987), B - on the basis of data by Barmuta *et al.* (1990), C - on the basis of data by Havens (1992), D - on the basis of data by Havens & Heath (1989). In the last case aluminium ($180 \mu\text{g}\cdot\text{l}^{-1}$) was added.

Addition of Dursban (Hurlbert *et al.*, 1972) led to the phytoplankton bloom (the biomass of algae in treated ponds was more than 10 times higher than in control ones) due to initial decrease of zooplankton biomass, recovered after receiving extra food source from algae. So, though biomass and exergy content increased, structural exergy remained the same. Carbaryl (Havens, 1994 a) also

affected zooplankton, but mainly cladocerans, which were replaced with copepods and structural exergy decreased very insignificantly. Hexazinone (Thompson *et al.*, 1993 a, 1993 b), permethrin (Yasuno *et al.*, 1988) and dichlobenil (Kersting, 1984) influenced phytoplankton, causing the decrease of its biomass. The structural exergy remained at the initial level due to corresponding decrease of zooplankton biomass.

In the experiments with esfenvalerate (Fairchild *et al.*, 1992; Webber *et al.*, 1992) the direct effects of it resulted in decrease of biomass of crustacean zooplankton, worms and insects. The biomass of phytoplankton and rotifers increased, fishes were not affected or even increased in biomass. So, community adapted to the pollutant and its structural exergy was not changed.

Joint addition of atrazine and bifenthrin (Hoagland *et al.*, 1993) caused decrease of biomasses of both phyto- and zooplankton, but did not affect their relations. As a result of it the structural exergy was not affected.

Addition of chlorinated phenolic compounds (Schauerte *et al.*, 1982; Kuiper & Hansveit, 1984a) toxic for algae caused the decrease of the total biomass of the system, but did not influenced structural exergy, as zooplankton biomass decreased following the biomass of algae. In the case when it changed slower than algae biomass decrease, the increase of structural exergy was observed.

3,4-dichloroaniline (Kuiper & Hansveit, 1984 b) caused the decrease of phytoplankton biomass in low, and mortality of zooplankton in high concentrations. As a result of it structural exergy increased after addition of it in low concentrations (it is necessary to note, that later it was to decrease, following the lack of food for zooplankton) and decreased after high-dose addition. Experiments with other chlorinated organic compounds toxic for zooplankton (Lay *et al.*, 1984, Lay *et al.*, 1985 a) also showed the decrease of structural exergy.

Long-term exposure of experimental ecosystem to oil input (Giddings *et al.*, 1984) resulted in fluctuations of structural exergy, slight increase of exergy, practically constant biomass at concentrations less than 4 mg·l⁻¹, higher input caused total elimination of fishes, phytobenthos, significant decrease of zooplankton, reflected in the fall of all three parameters. The similar processes took place in the experiments with constant high-level input of oil to marine experimental ponds (Elmgren & Frithsen, 1982), where sufficient decrease of structural exergy, reflecting the degradation of ecosystem was observed.

Addition of 5-nitrofuroic acid (Kuiper, 1983) caused some increase of phytoplankton biomass and did not affect zoo- and bacterioplankton, so structural exergy changed insignificantly. Benzene (Lay *et al.*, 1985 b) addition resulted in complete elimination of zooplankton and, consequently, fall of structural exergy, though biomass has been increased. Addition of streptomycin sulphate (Taub, 1984) caused structural exergy increase, connected with the replacement of daphnia population by more numerous ostracods.

In long-term experiments with hexachlorobiphenil and atrazine (Lynch *et al.*, 1985) slight decrease of plant biomass and some increase of animal biomass were observed, structural exergy was not affected. Trichloroguaiacol (Rosemarin *et al.*, 1990) additions did not caused any direct toxic effect, though the abundance of molluscs and worms increased, while the number of insects and crustaceans

decreased. No changes of structural exergy were observed. Arsenate additions (Notini *et al.*, 1989) severely affected *Fucus* population and caused its replacement with the filamentous algae as the dominant primary producers. The shift in community structure from herbivorous gastropods and crustaceans to detritivorous bivalves and gastropods as well as enhancement of fish production was observed. Structural exergy increased, while the total biomass decreased.

Copper addition (Havens, 1994 a, 1994 b) caused decrease both in biomass and exergy. Affecting mainly phytoplankton it caused decrease of its biomass, followed by decrease of zooplankton biomass. Structural exergy was not affected, as decrease of zooplankton biomass was proportional to decrease of phytoplankton one. But it is necessary to note that the duration of this experiment was only 4 days. When experiment lasted two weeks and concentration of copper was high enough to cause toxification of zooplankton significant decrease of structural exergy was observed.

Cadmium (Kuiper, 1981 b) was toxic for zooplankton and caused the decrease of zooplankton biomass and increase of phytoplankton one due to lowering of grazing pressure. Structural exergy of the ecosystem decreased (Fig. 3).

Addition of mercury influenced ecosystems in the similar way. When the concentrations of mercury added were too low to cause direct toxic action the decrease of structural exergy was nevertheless observed, connected with the inhibition of zooplankton development rate and fish growth.

Experimental acidification of aquatic ecosystems to pH 4.5 caused some increase (Fig. 4a, b) or slight decrease (Fig. 4c, d) of the total biomass. Exergy content remained at the same level (Fig. 4a), slightly (Fig. 4b, c), or significantly (Fig. 4d) decreased. In all cases the structural exergy decreased significantly, as acidification was toxic for zooplankton and caused serious structural changes in plankton community. Addition of aluminium (Fig. 4d) caused no effect, or it was not such significant as the effect of acidification.

6. Discussion

It is clearly seen, that addition of compounds, which can be utilised by the community usually does not cause decreases of structural exergy. It is demonstrated in experiments with the nutrients and treated sewage. Some compounds (Dursban, dimethylamine salt of 2,4-dichlorophenoxy acetic acid, nitrofuroic acid) stimulated the growth of algae. It was followed by the increase of consumers biomass and structural exergy did not significantly changed.

When compound depressed the primary production processes by inhibition of phytoplankton (permethrin, atrazine, chlorinated phenolic compounds, copper in low concentrations), the lack of food for zooplankton caused the corresponding decrease of its biomass and structural exergy remained at the same level or increased. Arsenate addition caused the elimination of principal primary producer *Fucus*, but it was replaced by filamentous algae and the structural exergy was not decreased, in spite of the changes in the community structure. In some cases the substance added was toxic for some groups of consumers. The reduction of their biomass was compensated by increase of biomass of other animals. E.g., cladocerans were replaced with copepods after addition of Carbaryl, and with ostracods after addition of streptomycin, crustaceans, worms and insects were replaced with

rotifers and fishes under the action of esfenvalerate, insects and crustaceans were replaced with molluscs and worms in the presence of trichloroguaiacol. These examples can be observed as the cases of ecosystem adaptation to external influences reflected by stability or rise of structural exergy level.

In all cases discussed above there were no significant decreases of structural exergy, so possibilities of ecosystem to use external resources remained at the same level, in spite of disturbances. Changes in the structure and composition of ecosystems always led to supporting the stability of existing structural exergy level. The decreases of total exergy observed in some experiments were connected with the availability of resources.

When added substances were very toxic or unmetabolized, e.g. Kepone, cadmium, mercury, inorganic acids, or the substances were introduced in high concentrations (copper, bifenthrin, chlorinated organic compounds, benzene, oil) the decrease of structural exergy was observed. Often it indicated the sufficient degradation of ecosystem, elimination of its component or even entire trophic levels. Sometimes it was observed when the toxicant was added in sublethal concentrations, e.g. low concentrations of mercury inhibited the crustacean zooplankton development rate and the growth of fishes.

In calculation experiments with mathematical model described above, addition of nutrients lead to increase of biomass and exergy content after addition of nutrients (phosphates and nitrates) and decrease of them after addition of phenolic compounds. Unfortunately the results of the model calculation are relative, not absolute data, so assessment of structural exergy changes is impossible.

7. Conclusion

Recent work demonstrates the possibility to use such parameter as structural exergy for estimation of ecosystem state and its changes under various external influences. It reflects the state of ecosystem and can indicate the degree of ecosystem adaptation, falling down when important for ecosystem functioning components are eliminated.

Structural exergy seems to remain at constant level or to increase when the allochthonous compounds can be metabolised by ecosystem, or when the ecosystem can adapt itself to the input of toxicant by structural changes.

When the substance is too conservative, too toxic or/and is coming in too high concentrations, structural exergy is falling down, demonstrating the inability of ecosystem to adapt to this influence and irreversibility of changes in ecosystem.

Acknowledgements

The author is very grateful to Prof. Sven E. Jørgensen, the initiator and supervisor of recent presentation, and to his collaborators, especially to Dr. Søren N. Nielsen, both from Royal Danish School of Pharmacy (Copenhagen, Denmark), for useful discussions and constant help during the performance of this research. The recent work was supported by the Danish Ministry of Education and Research.

References

- Azam, F., Vaccaro, R. F., Gillespie, P. A., Moussali, E. I., and Hodson, R. E. 1977. Controlled ecosystem pollution experiment: effect of mercury on enclosed water columns. II. Marine bacterioplankton. *Marine Science Communications*. 3: 313 - 329.
- Baretta-Bekker, J. G., Riemann, B., Baretta, J. W., and Rasmussen, E. Koch. 1994. Testing the microbial loop concept by comparing mesocosm data with results from a dynamical simulation model. *Marine Ecology Progress Series*. 106: 187 - 198.
- Barmuta, L. A., Cooper, S. D., Hamilton, S. K., Kratz, K. W., and Melack, J. M. 1990. Responses of zooplankton and zoobenthos to experimental acidification in a high - elevation lake (Sierra Nevada, California, U. S. A.). *Freshwater Biology*. 23: 571 - 586.
- Bartell, M. S., Gardner, R. H., and O'Neil, R. V., 1992. Ecological risk estimation. Lewis Publishers, Boca Raton / Ann Arbor / London / Tokyo. 252 pp.
- Beers, J. R., Reeve, M. R., and Grice, G. D. 1977. Controlled ecosystem pollution experiment: effect of mercury on enclosed water columns. IV. Zooplankton population dynamics and production. *Marine Science Communications*. 3: 355 - 394.
- Boyle, T. R. 1980. Effects of the aquatic herbicide 2,4-DMA on the ecology of experimental ponds. *Environmental Pollution*. 21: 35 - 49.
- Cuker, B. E. 1987. Field experiment on the influences of suspended clay and P on the plankton of a small lake. *Limnol. Oceanogr.* 32: 840 - 847.
- Davies, J. M., and Gamble, J. C. 1979. Experiments with large enclosed ecosystems. *Phil. Trans. R. Soc. Lond. B*. 286: 523 - 544.
- De Costa, J., Janicki, A., Shellito, G., and Wilcox, G. 1983. The effect of phosphorus additions in enclosures on the phytoplankton and zooplankton of an acid lake. *Oikos*. 40: 283 - 294.
- Costanza, R., Norton, B. G., and Haskell, B. D. (eds.) 1992. Ecosystem health: new goals for environmental management. Island Press, Washington. 269 pp.
- Drenner, R. W., Hoagland, K. D., Smith, D., Barcello, W. J., Johnson, P. C., Palmieri, M. A., and Hobson, J. F. 1993. Effects of sediment-bound bifenthrin on gizzard shad and plankton in experimental tank mesocosms. *Environmental Toxicology and Chemistry*. 12: 1297 - 1306.
- Elmgren, R., and Frithsen, J. B. 1982. The use of experimental ecosystems for evaluating the environmental impact of pollutants: a comparison of an oil spill in the Baltic sea and two long-term, low-level oil addition experiments in mesocosms. In G. D. Grice & M. R. Reeve (eds.), *Marine mesocosms: biological and chemical research in experimental ecosystems*. Springer-Verlag, New York / Heidelberg / Berlin. pp.153 - 165.
- Fairchild, J. F., La Point, T. W., Zajicek, J. L., Nelson, M. K., Dwyer, J. and Lovely, P. A. 1992. Population-, community- and ecosystem-level responses of aquatic mesocosms to pulsed doses of a pyrethroid insecticide. *Environmental Toxicology and Chemistry*. 11: 115 - 129.

- Gearing, J. N. 1989. The role of aquatic microcosms in ecotoxicological research. In S. A. Levin, M. A. Harwell, J. R. Kelly & K. D. Kimball (eds.), *Ecotoxicology: problems and approaches*. Springer-Verlag, New York / Berlin / Heidelberg / London / Paris / Tokyo . pp. 411- 472.
- Giddings, J. M., Franko, P. J., Cushman, R. M., Hook, L. A., Southworth, G. R., and Stewart, A. J. 1984. Effects of chronic exposure to coal-derived oil on freshwater ecosystems: II. Experimental ponds. *Environmental Toxicology and Chemistry* .3: 465 - 488.
- Grice, G. D., Reeve, M. R., Koeller, P., and Menzel, D. W. 1977. The use of large volume, transparent, enclosed sea-surface water columns in the study of stress on plankton ecosystems. *Helgolander wiss. Meeresunters*. 30: 118 - 133.
- Havens, K. E. 1992. Acidification effects on the algal-zooplankton interface. *Can. J. Fish. Aquat. Sci.* 49: 2507 - 2514.
- Havens, K. E. 1994a. An experimental comparison of the effects of two chemical stressors on a freshwater zooplankton assemblage. *Environmental Pollution*. 84: 245 - 251.
- Havens, K. E. 1994b. Structural and functional responses of a freshwater community to acute copper stress. *Environmental Pollution*. 86: 259 - 266.
- Havens, K. E., & De Costa, J. 1987. Freshwater plankton community succession during experimental acidification. *Arch. Hydrobiol.* 111: 37 - 65.
- Havens, K. E., and Heath, R. T. 1989. Acid and aluminium effects on freshwater zooplankton: an in situ mesocosm study. *Environmental Pollution*. 62: 195 - 211.
- Heinle, D. R., Flemer, . A., Huff, R. T., Sulkin, S. T., and Ulanowicz., R. E. 1979. Effects of perturbations on estuarine microcosms. In R. F. Dame (ed.), *Marsh-estuarine systems simulation*, University of South Carolina Press, Columbia. 119 - 141.
- Hoagland, K. D., Drenner, R. W., Smith, J. D. and Cross, D. R. 1993. Freshwater community responses to mixtures of agricultural pesticides: effects of atrazine and bifenthrin. *Environmental Toxicology and Chemistry* .12: 627 - 637.
- Hurlbert, S. H., Mulla, M. S., and Wilson, H. R. 1972. Effects of organophosphorous insecticide on the phytoplankton, zooplankton, and insect populations of fresh-water ponds. *Ecological Monographs* 42: 269 - 299.
- Jørgensen, S. E. 1992a. Integration of ecosystem theories: a pattern. Kluwer Academic Publishers, Dordrecht / Boston / London. 383 pp.
- Jørgensen, S. E. 1992b. Parameters, ecological constraints and exergy. *Ecological Modelling*. 62: 163 - 170.
- Jørgensen, S. E. 1992c. Development of models able to account for changes in species composition. *Ecological Modelling* 62: 195 - 208.
- Jørgensen, S. E. 1994. Review and comparison of goal functions in system ecology. *Vie Milieu*. 44: 11 - 20.
- Jørgensen, S. E. 1995. Exergy and ecological systems analysis. In B. C. Patten & S. E. Jørgensen, (eds.), *Complex ecology: the part-whole relation in ecosystem*. Prentice Hall PTR, Englewood Cliffs. pp. 568 - 584.

- Jørgensen, S. E. and Nielsen, S. N. 1994. Models of the structural dynamics in lakes and reservoirs. *Ecological Modelling*. 74: 39 - 46.
- Jørgensen, S. E., Nielsen, S. N., and Jørgensen, L. A. 1991. Handbook of ecological parameters and ecotoxicology. Elsevier, Amsterdam. 1263 pp.
- Jørgensen, S. E., Nielsen, S. N., and Mejer, H. 1995. Emergy, environ, exergy and *Ecological Modelling*. *Ecological Modelling*. 77 : 99 - 109.
- Kersting, K. 1984. Normalised ecosystem strain: a system parameter for the analysis of toxic stress in (micro-)ecosystems. *Ecological Bulletins*. 36 : 150 - 153.
- Koeller, P.A., and Wallace, G. T. 1977. Controlled ecosystem pollution experiment: effect of mercury on enclosed water columns. V. Growth of juvenile chum salmon (*Oncorhynchus keta*). *Marine Science Communications*. 3: 395 - 406.
- Kuiper, J. 1977. An experimental approach in studying the influence of mercury on a North Sea coastal plankton community. *Helgolander wiss. Meeresunters*. 30: 652 - 665.
- Kuiper, J. 1981a. Fate and effects of mercury in marine plankton communities in experimental enclosures. *Ecotoxicology and Environmental Safety*. 5: 106 - 134.
- Kuiper, J. 1981b. Fate and effects of cadmium in marine plankton communities in experimental enclosures. *Marine Ecology Progress Series*. 6: 161 - 174.
- Kuiper, J. 1983. Fate and effects of 5-nitrofuric acid-2 (NFA) on a marine plankton in experimental enclosures. In W. E. Bishop, R. D. Cardwell & B. B. Heidolph (eds.), *Aquatic Toxicology and Hazard Assessment: Sixth Symposium*, ASTM, Baltimore: 171 - 179.
- Kuiper, J. and Hansveit, A. O. 1984a. Fate and effects of 4-chlorophenol and 2,4-dichlorophenol in marine plankton communities in experimental enclosures. *Ecotoxicology and Environmental Safety*. 8: 15 - 33.
- Kuiper, J. and Hansveit, A. O. 1984b. Fate and effects of 3,4-dichloroaniline (DCA) in marine plankton communities in experimental enclosures. *Ecotoxicology and Environmental Safety*. 8: 34 - 54.
- Lay, J. P. 1987. Influence of chemicals upon plankton in freshwater systems. *Chemosphere*. 16: 581 - 588.
- Lay, J. P., Schauerte, W., and Klein, W. 1984. Effects of trichloroethylene on the population dynamics of phyto- and zooplankton in compartments of a natural pond. *Environmental Pollution*. 33 : 75 - 91.
- Lay, J. P., Schauerte, W., Mueller, A., Klein, W., and Korte, F. 1985a. Long-term effects of 1,2,4-trichlorobenzene on freshwater plankton in an outdoor-model ecosystem. *Bull. Environ. Contam. Toxicol.* 34: 761 - 769.
- Lay, J. P., Schauerte, W., Peichl, L., Klein, W., and Korte, F. 1985b. Influence of benzene on the phytoplankton and on *Daphnia pulex* in compartments of an experimental pond. *Ecotoxicology and Environmental Safety*. 10 : 218 - 227.
- Lundgren, A. 1985. Model ecosystems as a tool in freshwater and marine research. *Arch. Hydrobiol. Suppl.* 70 : 157 - 196.

- Lynch, T. R., Johnson, H. E., and Adams, W. J. 1985. Impact of atrazine and hexachlorobiphenil on the structure and function of model stream ecosystems. *Environmental Toxicology and Chemistry*. 4: 399 - 413.
- Mejer, H. F., and Jørgensen, S. E. 1979. Energy and ecological buffer capacity. In S. E. Jørgensen (ed.), *State of the art in Ecological Modelling*. International Society for *Ecological Modelling*. Copenhagen. pp.829 - 846.
- Notini, M., Nageli, B., Hangstroem, A., and Grahn, O. 1977. An outdoor model simulating a Baltic Sea littoral ecosystem. *Oikos*. 28: 2-9.
- Notini, M., Rosemarin, A., and Landner, L. 1989. Enclosure studies on Baltic Sea littoral ecosystems. In H. Løkke, H. Tyle & F. Bro-Rasmussen (eds.), *1st European Conference on Ecotoxicology*, Politeknisk Forlag, Odense. pp. 345-361.
- Odum, E. P. 1984. The mesocosm. *BioScience*. 34: 558 - 562.
- Oviatt, C. A., Perez, K. T., and Nixon, S. W. 1977. Multivariate analysis of experimental marine ecosystems. *Helgolander. wiss. Meeresunters.* 30: 30 - 46.
- Oviatt, C. A., Nixon, S. W., Perez, K. T., and Buckley, B. 1979. On the season and nature of perturbations in microcosm experiments. in R. F. Dame (ed.), *Marsh-estuarine systems simulation*. University of South Carolina Press, Columbia. pp.143 - 164.
- Perez, K. T., Davey, E. W., Lackie, N. F., Morrison, G. E., Murphy, P. G., Soper, A. E., and Winslow, D. L. 1983. Environmental assessment of a phthalate ester, di(2-ethylhexyl)phthalate, derived from a marine microcosm. In W. E. Bishop, Cardwell, R. D., and Heidolph, B. B. (eds.). *Aquatic toxicology and hazard assessment: Sixth symposium, ASTM, Baltimore* : 180 - 191.
- Perez, K. T., Morrison, G. E., Davey, E. W., Lackie, N. F., Soper, A. E., Blasco, R. J., and Winslow, D. L. 1991. Influence of size on fate and ecological effects of Kepone in physical models. *Ecological Applications*. 1: 237 - 248.
- Rosemarin, A., Notini, M., Soederstrom, M., Jensen, S., and Landner, L. 1990. Fate and effects of pulp mill chlorophenolic 4,5,6-trichloroguaiacol in a model brackish water ecosystem. *The Science of the Total Environment*. 92: 69 - 89.
- Salomonsen, J. 1992. Examination of properties of exergy, power and ascendancy along a eutrophication gradient. *Ecological Modelling*. 62 : 171 - 181.
- Schauerte, W., Lay, J. P., Klein, W., and Korte, F. 1982. Influence of 2, 4, 6-trichlorophenol and pentachlorophenol on the biota of aquatic systems. *Chemosphere* .11 : 71 - 79.
- Silow, E. A., Stom, D. J., Basharova, N. A., et al. 1991. Influence of biogenous elements on 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., and Baturin, V. I. 1995. Mathematical models of lake Baikal ecosystem. *Ecological Modelling*. 82: 27 - 39.
- Suter II, G. W. 1993. A critique of ecosystem health concepts and indexes. *Environmental Toxicology and Chemistry*. 12: 1533 - 1539.

- Takahashi, M., Wallace, G. T., Whitney, F. A., and Menzel, D. W. 1977. Controlled ecosystem pollution experiment: effect of mercury on enclosed water columns. I. Manipulation of experimental enclosures. *Marine Science Communications*. 3: 291 - 312.
- Taub, F. 1984. Synthetic microcosms as biological models of algal communities. In L. E. Schubert (ed.), *Algae as ecological indicators*. Academic Press, London. pp.363 - 394.
- Thomas, W. H., Seibert, D. L. R., and Takahashi, M. 1977. Controlled ecosystem pollution experiment: effects of mercury on enclosed water columns. III. Phytoplankton population dynamics and production. *Marine Science Communications*. 3 : 331 - 354.
- Thompson, D. G., Holmes, S. B., Wainio-Keizer, K., MacDonald, L., and Solomon, K. R. 1993a. Impact of hexazinone and metilsulfuron methyl on the phytoplankton community of a mixed-wood/boreal forest lake. *Environmental Toxicology and Chemistry* .12 : 1695 - 1707.
- Thompson, D. G., Holmes, S. B., Wainio-Keizer, K., MacDonald, L., and Solomon, K. R. 1993b. Impact of hexazinone and metilsulfuron methyl on the zooplankton community of a boreal forest lake. *Environmental Toxicology and Chemistry*. 12 : 1709 - 1717.
- Webber, E. C., Deutsch, W. G., Bayne, D. R., and Seesock, W. C. 1992. Ecosystem-level testing of a synthetic pyrethroid insecticide in aquatic mesocosms. *Environmental Toxicology and Chemistry* 11: 87 - 105.
- Yasuno, M., Hanazato, T., Iwakuma, T., Takamura, K., Ueno, R., and Takamura, N. 1988. Effects of permethrin on phytoplankton and zooplankton in an enclosure ecosystem in a pond. *Hydrobiologia*. 59: 247 - 258.