

EUTROPHICATION:
RESEARCH AND APPLICATION TO WATER SUPPLY

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Structural dynamic eutrophication models

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This article discusses problems of modelling the seasonal succession of algal species in lakes and reservoirs, and the adaptive selection of certain groups of algae in response to changes in the inputs and relative concentrations of nutrients and other environmental variables. A new generation of quantitative models is being developed which attempts to translate some important biological properties of species (survival, variation, inheritance, reproductive rates and population growth) into predictions about the survival of the fittest, where "fitness" is measured or estimated in thermodynamic terms. The concept of "exergy" and its calculation is explored to examine maximal exergy as a measure of fitness in ecosystems, and its use for calculating changes in species composition by means of structural dynamic models. These models accommodate short-term changes in parameters that affect the adaptive responses (species selection) of algae.

Introduction

Eutrophication models have been developed (Jørgensen 1986) that are able to predict changes in the level of eutrophication due to changes in the "forcing functions", i.e. the input of nutrients to the lake in question. The application of eutrophication models has, however, also demonstrated the shortcomings of current models: due to rapid changes in the composition of algal species it is hardly possible to make predictions about seasonal variations and when the spring and summer blooms will occur. This is regrettable because predictions of seasonal and annual changes in species composition are often more important in lake management than the actual level of eutrophication.

If we follow a general modelling procedure (see, for instance, Jørgensen 1988) we obtain a model describing the processes in the focal ecosystem, but the parameters represent the properties of the state variables (components) as these exist in the ecosystem during the period of examination. They are not necessarily valid for another period of time because we know that ecosystems are able to regulate, modify and change them, if needed, as a response to changes in the prevailing conditions. The latter are determined by the forcing functions and the particular interrelationships existing between the state variables of each ecosystem. Our present models have rigid structures and a fixed set of parameters, so that alterations or replacements of the components are not possible. We need, however, to introduce parameters (properties) that can alter according to changes in the forcing functions affecting an ecosystem and the general set of conditions for the state variables (components) in that ecosystem.

Models that can account for a change in species composition and the ability of the species to alter their properties (i.e. the biological components of the models can adapt to the prevailing conditions imposed on the species), are sometimes called structural dynamic models, to indicate that they are able to accommodate structural changes in the ecosystem. They may also be called the next generation of ecological models, to underline the fact that they are radically different from previous modelling approaches and can do more: they describe changes in species composition.

It could be argued that the natural ability of ecosystems to replace present species with other, better-fitted species, can be modelled by constructing models which encompass all of the actual species known to occur for the entire period of time which the model attempts to cover. However, this approach has two essential disadvantages. Firstly, the model becomes very complex, as for each trophic level it will contain many state variables. Thus the model will also contain many more parameters that have to be calibrated and validated, introducing a large uncertainty in the model and making its application very case-specific (Nors Nielsen 1992a,b). In addition, the model will still be rigid and not possess the property of real ecosystems, where the parameters may alter even if there is no change in species composition.

Later sections of this paper present some results obtained by applying the thermodynamic concept "exergy", as an optimization principle for current changes in the parameters of an ecosystem. Exergy has been used in some kinds of algorithm as a goal function. It expresses the biogeochemical energy (or free energy, or energy able to do mechanical work) of the system, or the distance from thermodynamic equilibrium. First, however, some basic ideas concerning the responses of organisms to changes in their environment are considered, as these have to be incorporated into models of ecosystems and are especially important for modelling the seasonal, short-term dynamics of plankton in lakes and reservoirs.

Ecological structure and species composition

Ecosystems are "soft systems" in the sense that they are able to meet changes in external factors, or impacts with many regulatory processes, on different levels. The results are that only minor changes are observed in the function of the ecosystem. This means that the state variables – but not necessarily the biotic species – are maintained almost unchanged, in spite of changes in external factors.

During recent years there has been wide discussion (Odum 1983; Straskraba 1980) on ways of describing these regulatory processes, particularly those on the ecosystem level, i.e. the changes in ecological structure and the species composition.

Neo-Darwinian theory, expanded to include (1) co-evolution, (2) transfer of knowledge (information) from parents to offspring, (3) the ability of organisms to regulate their environment and thereby the selection pressure on them, (4) D-genes, and modernized according to Brooks *et al.* (1989) and Wiley (1988), describes competition among species. It states that the species which are best fitted to prevailing conditions in the ecosystem will survive. This formulation may be interpreted as a tautology and the following is preferable: life is a matter of survival and growth. Given a particular set of conditions, determined by the external and internal functional properties of the ecosystem, the question is: which of the available species (and there are more available species than are needed) have the combinations of properties required to give the best guarantee for survival and growth? Those species, or rather the particular combination of species, which have the best properties may be denoted the fittest and will be selected. In other words, Darwin's theory may be used to describe changes in ecological structure and the composition of species, but with the present formulation it can not be directly applied quantitatively in ecological modelling.

The problem of describing changes in ecological structure and species composition, using quantitative methods developed by translating the "survival of the fittest" into thermodynamic terms, will be discussed below. In this context it is presented as a hypothesis which attempts to unite the theories of Monod (1970) and Prigogine & Stengers (1979) by explaining ecosystem development and evolution in terms of the concept of exergy.

Hypotheses on survival and growth of organisms under the conditions currently prevailing in an ecosystem

All biological species in an ecosystem are confronted with the question: how is it possible to

grow, or even survive, under the prevailing conditions? The latter are considered to be *all* factors that influence the species, i.e. all external and internal factors, including those originating from other species.

These factors are dynamic; the conditions are steadily changing and there are always many species waiting in the wings, ready to take over if they are better fitted to the emerging conditions than the species dominating in the current prevailing conditions.

A wide spectrum of species, representing different combinations of properties, is available to occupy the ecosystem. The question is: which of these species are best able to survive and grow under the present conditions and which species are best able to survive and grow under new conditions one time-step later, two time-steps later, and so on? The "necessity", in Monod's sense, is given by the prevailing conditions; in order to survive a species must have genes and a phenotype (i.e. properties) which match the prevailing conditions. But the natural

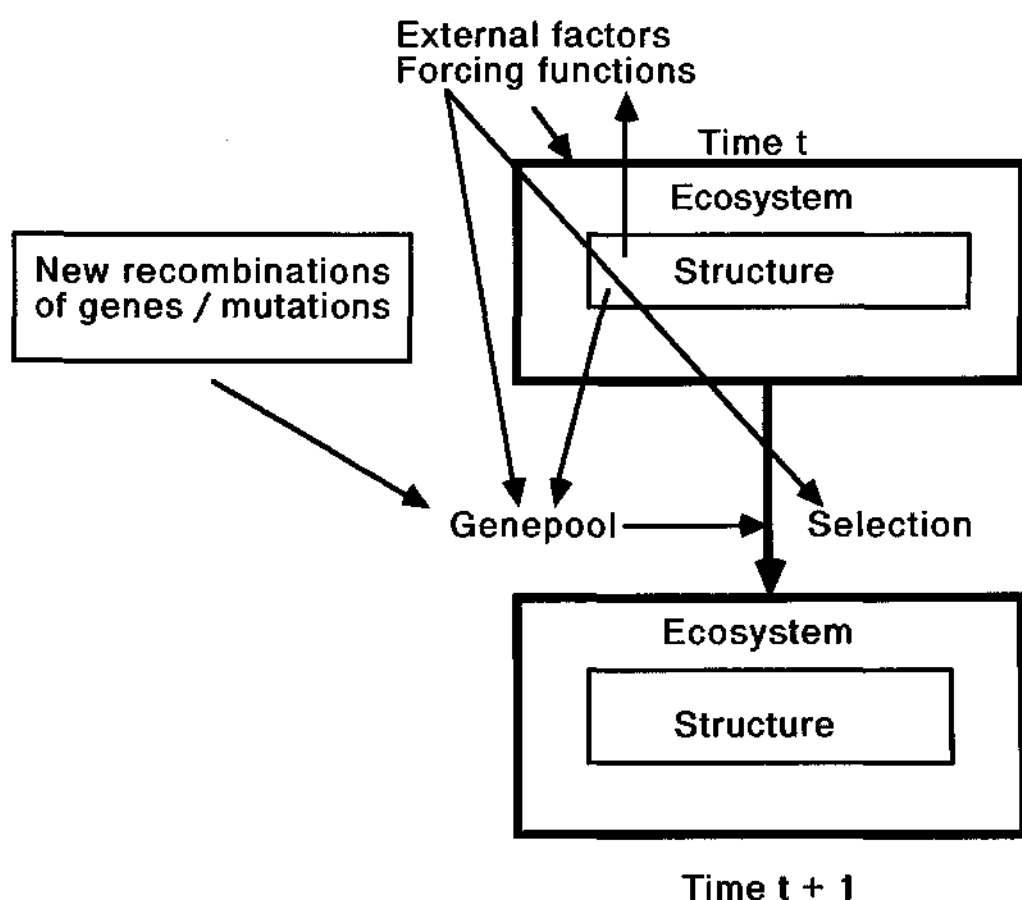


Figure 1. Schematic diagram to show how, in the short term, external factors gradually alter the species composition of an ecosystem such as a lake. The evolutionary development of the ecosystem is, however, more complex. Possible shifts in species composition are determined by the gene pool, which is steadily changed due to mutations and new sexual recombinations of genes; these are tested for fitness, by natural selection. Arrows leading from "structure" to "external factors" and "selection" account for the possibility that a species can modify its own environment and thereby its own selection pressure, and an arrow from "structure" to "gene pool" accounts for the possibility that species can to a certain extent change their own gene pools.

external factors, and the genetic pool available for testing by natural selection, may change by chance. Gradually, new mutations and sexual recombinations emerge and progressively provide new material to be tested against the question: which species are best fitted under the conditions prevailing *now*?

These ideas are illustrated in Figure 1. The external factors steadily alter; some slowly, others relatively quickly and partly at random, e.g. meteorological factors. The species present in the ecosystem are selected from the pool of species available and are represented by the genetic pool which alters by chance, slowly but surely. "Ecological development" is the process of changes with time in nature, caused by the dynamics of external factors, giving the ecosystem sufficient time to react. The ideas behind Figure 1 are analogous with those of Wiley (1988), Brooks *et al.* (1988), Ulanowicz (1980) and Wicken (1988). These authors claim that the following features are characteristic for the evolution of ecosystems from a thermodynamic point of view.

(1). Dollo's Law of an irreversible evolution – in geological time, the same species will never reappear – is valid, because the same situation will not occur again with the same forcing functions and state variables.

(2). The entire ecosystem is evolving because everything is linked to everything else, underpinning the concept of ascendancy.

(3). The past history of the ecosystem is important, because it determines which genes are available to find the best solution to the problem of survival. The history also determines the initial conditions, which are of great importance for the development of the system – compare also with the indirect effect (Patten 1991).

(4). Natural selection is based upon given conditions in the entire ecosystem and is separated from the evolution of the genetic pool. On the other hand, evolution is related to the genetic pool, and is the result of the relationship between the dynamics of the external factors and the dynamics of the genetic pool. The external factors are steadily changing the conditions for survival, and the genetic pool is steadily producing new solutions to the problem of survival.

(5). The most complex ecosystem does not necessarily give the best answer to the problem of survival. Therefore, perhaps, we can not find any relationship between complexity and stability. It does not exist, as was emphasized by May (1981).

Natural selection in ecosystems

Darwin's theory of natural selection presumes that populations consist of individuals which have the following properties.

(i). High reproductive rates: on average, individuals produce more offspring than are needed to simply replace themselves when they die.

(ii). Inheritance: progeny resemble their parents more than they resemble randomly-chosen individuals in the population.

(iii). Variation: individuals vary in heritable traits which influence reproduction and survival, i.e. fitness.

All three properties are part of the ideas presented here. High reproductive rates are needed to get relatively rapid changes (seasonal and annual) in the species composition, caused by rapid changes in external factors. Variability is represented in the short-term and long-term changes in the genetic pool, and inheritance is necessary for the fitness test to take effect. The species are continuously tested against the prevailing conditions (external as well as internal factors) and the better they are fitted, the better they are able to maintain their biomass and also to grow. Indeed, the specific rate of population growth may be used as a measure of fitness (e.g. see Stenseth 1986). But the property of fitness must be inheritable to have any effect on

the species composition and the ecological structure of the ecosystem.

Man-made changes in external factors, i.e. anthropogenic pollution, has created new problems because new genes fitted to these changes do not develop overnight, although resistance to insecticides, for example, sometimes develops surprisingly fast. Most natural changes have occurred many times previously and the genetic pool is, therefore, prepared to meet the majority of natural changes but not many of the man-made changes, because these are new and untested in the ecosystem.

Survival and growth in terms of exergy

Darwin's theory may be translated into thermodynamic terms, with exergy as the basic concept. Survival implies maintenance of the biomass, and growth means an increase of biomass. The construction of biomass requires exergy, which is transferable to support other exergy-demanding (i.e. energy-demanding) processes. Therefore survival and growth can be measured by the thermodynamic concept, exergy, which is *the amount of free energy relative to the environment*. Thus Darwin's theory may be reformulated in thermodynamic terms as follows:

The prevailing conditions of an ecosystem are steadily changing and the system will continuously select the species that can contribute most to the maintenance of, or even growth of, the exergy of the system.

Ecosystems are open systems, and receive an inflow of solar energy. This carries low entropy, while the radiation from the ecosystem carries high entropy. If the power of the solar radiation is W and the average temperature of the ecosystem is T_o , then the exergy gain per unit of time, $\Delta\Sigma x$, is (Eriksen *et al.* 1976):

$$\Delta\Sigma x = T_o \{W (1/T_o - 1/T_i)\} \quad (1)$$

where T_2 is the temperature of the environment (ecosystem) and T_i is the temperature of the sun. This flow of exergy can be used to construct and maintain structures that are a long way from equilibrium.

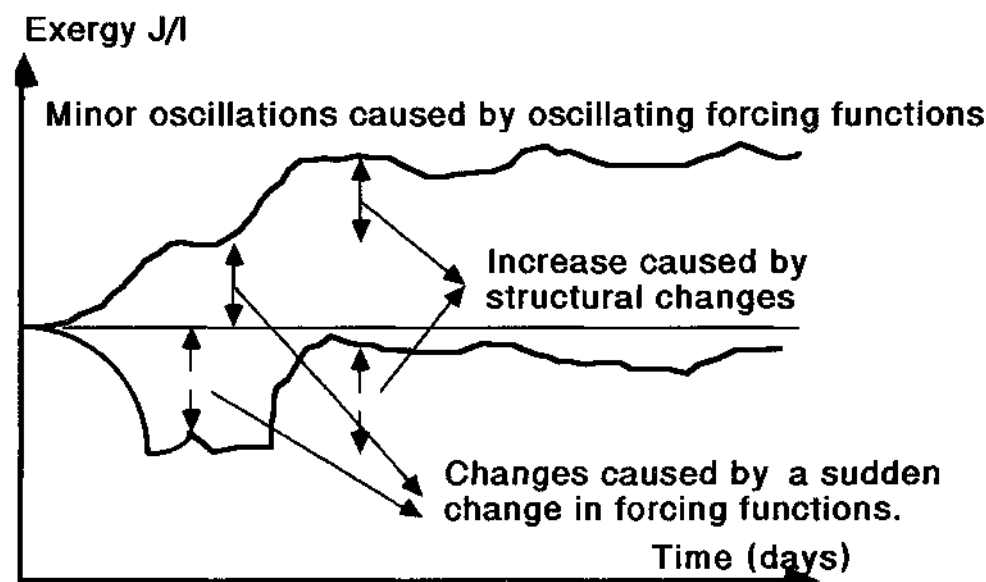


Figure 2. Exergy response to increased and decreased nutrient concentrations.

Thermodynamic translation of Darwin's theory also requires that populations must have the above-mentioned properties of reproduction, inheritance and variation. For selection to occur in favour of species that contribute most to the exergy of a system, under the prevailing conditions, there must be enough individuals with differing properties so that selection can take place. Reproduction and variation must be high so that once a change has occurred due to better fitness, it can be conveyed rapidly to the next generation, at least in the case of algal populations in a lake or reservoir. Furthermore, it should be noted that changes in exergy are not necessarily always positive or zero in value (Fig. 2), depending on changes in the resources of the ecosystem. Nevertheless, general theory supposes that ecosystems attempt to reach the highest possible exergy level under a given set of circumstances, with the available genetic pool ready for this attempt. This is illustrated schematically in Figure 2, which shows the response to changed forcing functions in a eutrophication model.

Calculating exergy

It is not possible to measure exergy but it can be computed, if the composition of the ecosystem is known. From thermodynamics, the following equation is valid for the components of an ecosystem (Mejer & Jørgensen 1979):

$$Ex = RT \sum_{i=1}^n [C_i \times \ln (C_i/C_{eq,i}) - (C_i - C_{eq,i})] \quad (2)$$

where R is the gas constant, T is the temperature (degrees Kelvin) of the environment, C_i represents the i th component expressed in a suitable unit (e.g. milligrams of phytoplankton per litre of lake water), $C_{eq,i}$ is the concentration of the i th component at thermodynamic equilibrium (which can be found in Morowitz (1968)), and n is the number of components. $C_{eq,i}$ is a very small concentration of organic components, corresponding to the very small probability of forming a complex organic compound in an inorganic soup (at thermodynamic equilibrium). Morowitz (1968) has calculated this probability and found that for proteins, carbohydrates and fats the corresponding concentration is about 10^{-60} mg l⁻¹. This figure may be used for mono-cellular species, but at higher trophic levels the probability of cells working together in a more complex organism is several magnitudes lower. Therefore it is relevant to let $C_{eq,i}$ be two magnitudes lower for zooplankton and four magnitudes lower for fish.

For more complex compounds such as hormones and genes, the value will be even smaller and, therefore, even if they are present in very small concentrations, they also contribute significantly to the exergy of the ecosystem.

The term $[C_i \times \ln (C_i/C_{eq,i})]$ corresponds to the theoretical minimum work (free energy) required to be done on the ecosystem in order to change its concentration relative to the reference level, and the term $(C_i - C_{eq,i})$ is the work done by the constant concentration's surroundings. Jørgensen *et al.* (1992) show that exergy is always non-negative, independent of whether the system is more or less concentrated than the reference state. In practice the system is more concentrated than the surroundings and the second term ($C_{eq,i}$) becomes negligible, except for the inorganic components, where the equilibrium concentration corresponds to the total concentration.

Equation (2) is valid for systems with an inorganic net inflow and passive outflow. It can be derived from basic thermodynamic equations; e.g. see Mejer & Jørgensen (1979). It is important to emphasize that all computations of exergy have the following shortcomings. They are based on a model and therefore will not be more correct than the model. Hence the results are more appropriate for examining relative differences in exergy by comparing an ecosystem under different conditions. Additionally, like all calculations in thermodynamics, the computations of exergy are based on approximations and assumptions.

The theory behind the application of exergy may be correct – but should of course be considered a hypothesis at this stage – but the practical application of the theory on real ecosystems will suffer from the above-mentioned shortcomings.

Nevertheless the exergy of an ecosystem can be illustrated by a simple example. Consider a pond containing only one species of algae. The phosphorus concentration of the algae is 1 mg l⁻¹ or 0.6 mg l⁻¹ orthophosphate. The temperature is 300K. If we are concerned only with the exergy contribution from the phosphorus compounds, Ex_p , then from equation (2) we find:

$$\begin{aligned} Ex_p &= 8.31 * 300 [(1/31 \ln 10^{-60}) - (1/31 - 10^{-60}/31)] \\ &\quad + (0.61/31 \times \ln 0.6/1.6) - (0.6/31 - 1.6/31)] \\ &= 9214 \text{ mJ l}^{-1} \end{aligned} \quad (3)$$

Similarly, it is possible to calculate the exergy contribution for nitrogen and *all* other compounds, including the contribution originating from the more complex compounds such as hormones and genes. The theoretical definition of exergy implies that we must find the concentrations of all components, calculate the contribution of every component, and add all these contributions to get the total exergy. In practice, however, we can not find the concentrations of all the components, but if we are concerned only with the changes caused by phosphorus, for example, it is sufficient to make the computations shown above to see the *relative changes* in exergy.

Calculations of exergy are often carried out in relation to ecological models, in which case the results will give the exergy of the model ecosystem and not that of a real ecosystem. However, if the model is used in two different situations, i.e. two different sets of external factors are imposed on the model ecosystem, the computations of exergy will give some useful indications of the differences that are likely to occur in a real ecosystem, provided that the model incorporates the essential features of the ecosystem in relation to changes in external factors. Notice that exergy is defined as the free energy of the system relative to the environment and, if the latter is defined as the inorganic soup present on earth 4 billion years ago, the baseline for exergy is the low concentrations of biological components present in this original soup.

Jizhong *et al.* (1992) use exergy computations to produce exergy balances for plants and animals. They distinguish between exergy and anexergy, which is the non-exergetic part of the energy. Jizhong *et al.* compute the exergy efficiency as the ratio between the output exergy + exergy change of the system, and exergy input. They propose to use exergy efficiency as an objective function for optimizing an ecosystem, i.e. the organisms that have a higher efficiency in the use of exergy will be selected for.

Shieh & Fan (1982) have suggested that exergy contents in structurally complicated materials can be estimated as follows, in kcal per kg under standard conditions (1 atmos. pressure and 298.15K):

$$\begin{aligned} &8177.79 [\text{C}] + 5.25 [\text{N}] + 27892.63 [\text{H}] + 4364.33 [\text{S}] - 3173.66 [\text{O}] + 5763.41 [\text{F}] + 2810 [\text{Cl}] \\ &+ 1204.3 [\text{Br}] + 692.5 [\text{I}] - (298.15 S_{\text{ash}} W_{\text{ash}}) + 0.15 [\text{O}] \times (7837.667 [\text{C}] + 33888.889 [\text{H}] + \\ &3828.75 [\text{S}] - 4236.10 [\text{O}] + 4447.37 [\text{F}] + 1790.9 [\text{Cl}] + 681.97 [\text{Br}] + 334.86 [\text{I}] \end{aligned} \quad (4)$$

In equation (4), [C], [H] etc. refers to the respective elements in terms of kg per kg of structurally complicated material, S_{ash} refers to the specific entropy of ash, assumed to have a value of 0.17152 kcal per kg ash °K, and W_{ash} refers to the weight of ash expressed as kg per kg structurally complicated material. If the composition of a particular organic material is known, equation (4) is straightforward to use. However, calculations of this kind do not take into consideration the exergy stored as information. The application of exergy calculations therefore requires that a model, containing all of the focal information for the specific problem, is used simultaneously. As already emphasized, the results are dependent on the accuracy of the model

as well as the accuracy of the computations of exergy.

Structural dynamic models of ecosystems

The aim of the new generation of models presented here is to find a new set of parameters, limited for practical reasons to the most crucial (= sensitive) parameters, which are better fitted for the prevailing conditions of the ecosystem. "Fitted" is defined in the Darwinian sense, as the ability of the species to survive and grow, which may be measured by use of exergy (Mejer & Jørgensen 1979; Jørgensen 1981, 1986; Jørgensen & Mejer 1977, 1979). Figure 3 shows the proposed modelling procedure which has been applied in the cases presented below.

Exergy has previously been tested as a "goal function" for ecosystem development, for example by Jørgensen & Mejer (1979), Jørgensen (1986) and Herendeen (1989). However, in all these cases the model applied did not include the "elasticity" of the system, obtained by

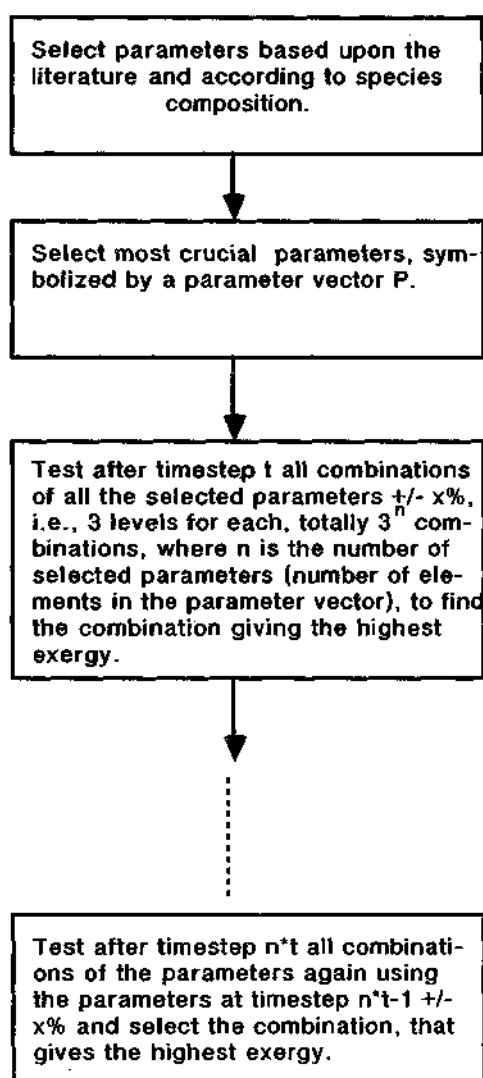


Figure 3. The procedure used to develop structural dynamic models.

using variable parameters, and therefore the models did not reflect the properties of real ecosystems. A realistic test of the exergy principle requires the application of *variable* parameters, used only in the few cases referred to here.

Case 1: algal growth as a variable parameter

In this case the growth of algae was used as the only variable parameter (Jørgensen 1986). This gave a significantly improved validation of the model, which encouraged further investigation of the possibilities for developing and applying such new modelling approaches. Values for the maximum growth rate (μ_{max}), and the respiration rate (F , set equal to $0.15 \mu_{max}$), were changed in the model, relative to values for growth rates previously found by experimental calibration (μ_c). Thus:

$$\mu_{max} = F \times \mu_c \quad (5)$$

The model was run for a series of F values and three levels of phosphorus (and nitrogen) input. As shown in Figure 4, maximum algal growth, giving maximum exergy, decreases when the phosphorus concentration increases, in accord with general ecological observations. When nutrients are scarce, competition between phytoplankton species is dependent on their rates of nutrient uptake. Smaller species have faster uptake rates due to a larger specific surface area and they grow more rapidly. On the other hand, high nutrient concentrations will not favour small species because interspecific competition is based on avoidance of grazing by zooplankton, which favours the larger algae. The results shown in Figure 4 were used to improve the prognosis published in Jørgensen *et al.* (1981, 1986), by introducing selective alteration of the parameters according to the procedure summarized in Figure 3. The standard deviation between model and measurement was significantly reduced, compared to the original prognosis where fixed parameters were applied.

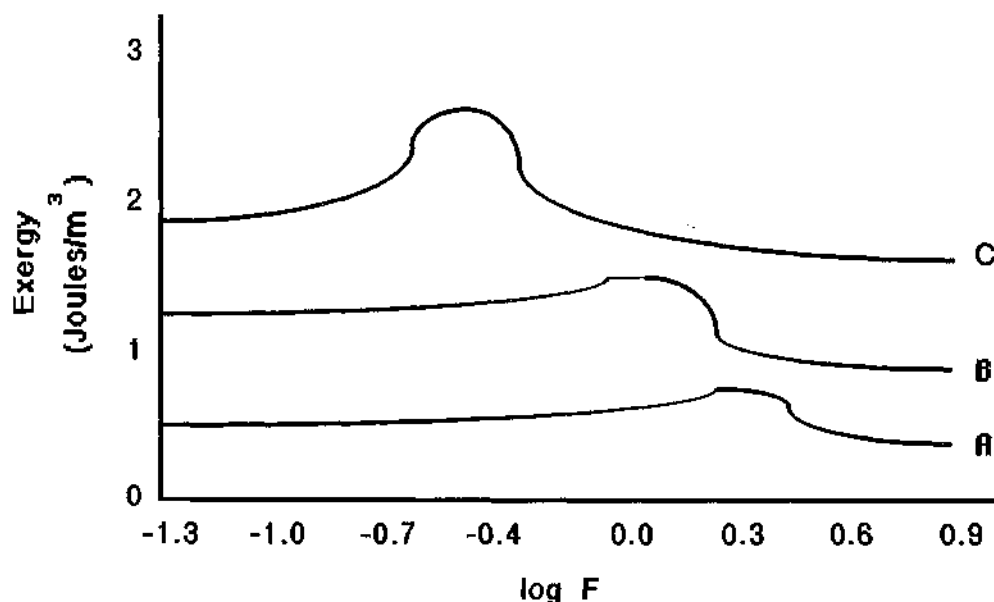


Figure 4. Exergy (joules m^{-3}) plotted against F at different levels (A-C) of phosphorus in a lake, where F is algal respiration rate relative to the maximum growth rate (equation (5), see the text: Case 1). Maximum exergy occurs at different F values for different P-loadings. A represents an oligotrophic lake corresponding to nutrient inputs of 0.04 mg P l^{-1} and 0.3 mg N l^{-1} , B corresponds to nutrient inputs of 1 mg P l^{-1} and 8 mg N l^{-1} , and C corresponds to a hypereutrophic lake where the inputs are 2 mg P l^{-1} and 16 mg N l^{-1} .

Case 2: exergy of half-saturation constants for uptake of silica and phosphorus

This second case focuses on differences in the half-saturation constants for phosphorus and silica, which may play an important role in the selection of different diatoms (see Tilman & Kilham 1976). If the P/Si ratio is low, the diatoms with a low half-saturation constant for phosphorus are selected, while a high Si/P ratio is selective for species with a low half-saturation constant for silica. If the P/Si ratio becomes very low, diatoms may be replaced by green algae.

An examination with a simple single-species model (see Fig. 5) explores the relationship between the Si/P ratio and the half-saturation constants for silica and phosphorus uptake, corresponding to the highest internal exergy value for the system. The results are shown in Figure 6, where the exergy at steady state is plotted against Si/P ratios for two species of algae with different half-saturation constants. The results are completely in accord with chemostat results obtained by Tilman & Kilham (1976), including the shift between the two species at an Si/P ratio of 2 (Fig. 6). These results therefore provide strong support for the maximum exergy principle and for a wider use of this principle in structural dynamic modelling.

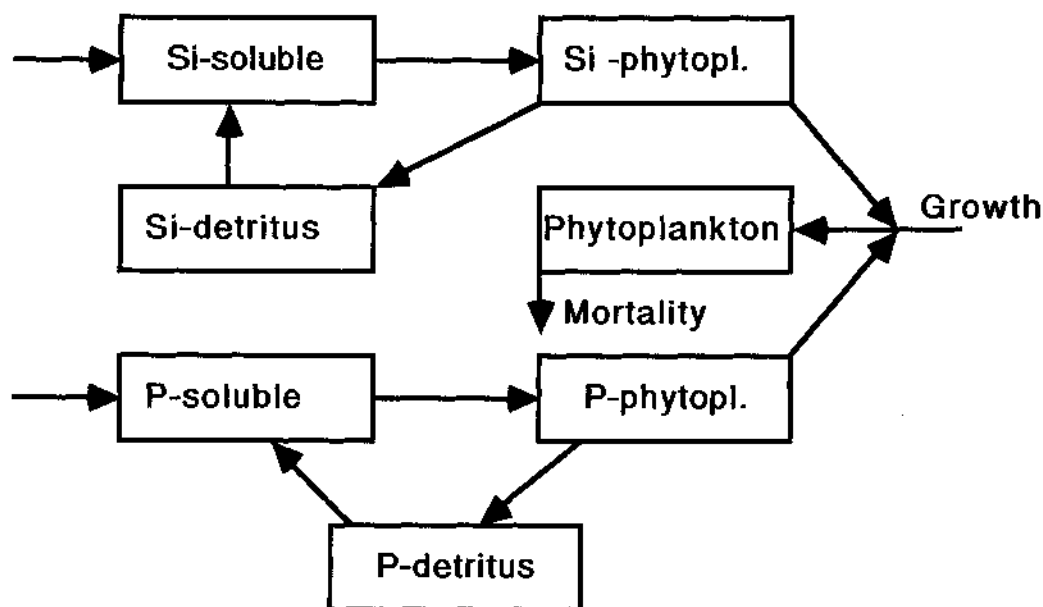


Figure 5. A single-species model (Case 2, see text) applied to show that the results obtained by Tilman & Kilham (1976) are consistent with the maximum exergy principle or the Ecological Law of Thermodynamics. The model has seven state variables. The cycles of silica and phosphorus are independent of each other, while their concentrations in the algae (phytoplankton) determine algal growth.

Case 3: exergy of a model for diatoms and blue-green algae

Nitrogen-fixing species of algae become increasingly predominant as the ratios of nitrogen to phosphorus progressively decrease and phosphorus concentrations increase. A two-species model has been used to simulate these observations. The results are shown in Figure 7, where the internal exergy for diatoms and blue-green algae is plotted against the logarithm of the concentration ratios of nitrogen to phosphorus in the ecosystem, whilst silica is held constant at a relatively high concentration. Exergy was calculated for varying nitrogen and fixed

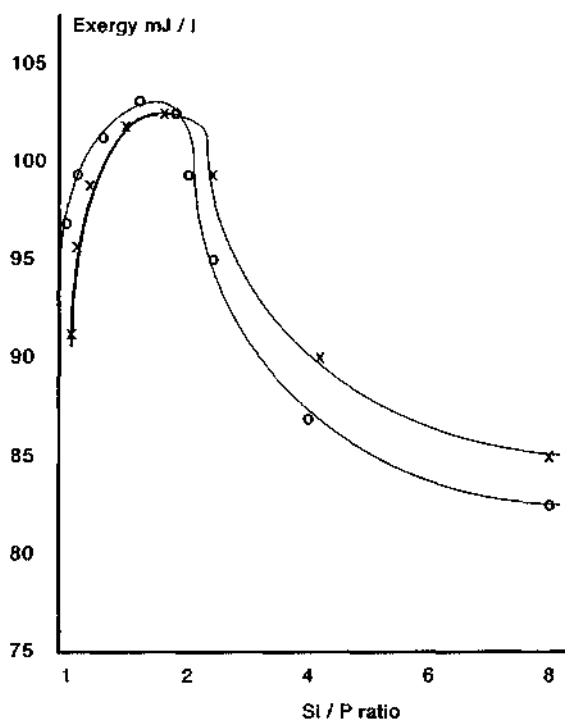


Figure 6. Exergy (mJ l^{-1}) plotted against the ration of silica: phosphorus for two species of algae. X, algae with half-saturation constants of $0.003 \text{ mg P l}^{-1}$ and 0.5 mg Si l^{-1} . O, algae with half-saturation constants of 0.1 mg P l^{-1} and 0.1 mg Si l^{-1} .

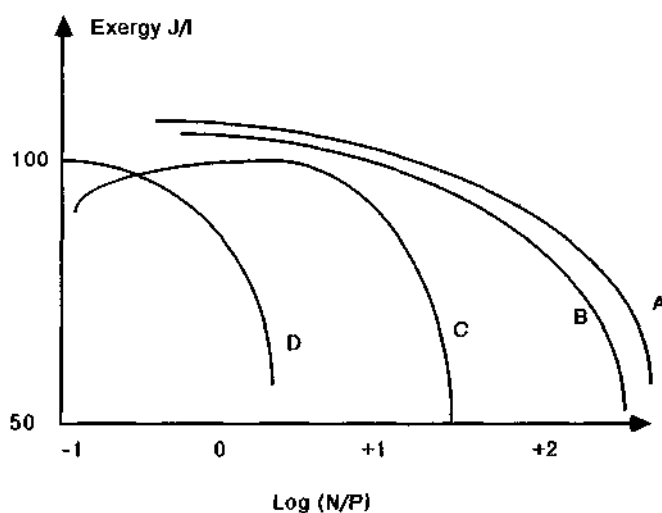


Figure 7. Internal exergy (joules l^{-1}) for diatoms and blue-green algae plotted against the logarithm of concentration ratios for nitrogen:phosphorus, when silica is kept constant at a relatively high concentration. A represents diatoms and B represents blue-green algae at a concentration of 0.02 mg P l^{-1} . C represents diatoms and D represents blue-green algae at a concentration of 1.0 mg P l^{-1} .

phosphorus concentrations of 1.0 mg P l^{-1} (curves A and B, Fig. 7) and 0.02 mg P l^{-1} (curves C and D, Fig. 7). Blue-green algae give the highest exergy at low N/P ratios when $P = 1.0 \text{ mg l}^{-1}$, while the diatoms give the highest exergy at all other situations. This accords with the appearance of blue-green nitrogen-fixing algae in eutrophic lakes with high phosphorus concentrations.

Case 4: exergy of a model for diatoms and green algae

Diatoms are dominant in many tropical lakes at the high rates of precipitation which usually occur during the summer. This is surprising because diatoms usually have a high settling rate and, as the retention time under these conditions is often low, diatoms should be relatively poor competitors. However, the very heavy rains stir up the photosynthetic layers, thereby reducing the tendency of diatoms to settle out and providing an opportunity for them to move, from time to time, into layers that offer the most favourable light conditions.

Table 1 shows the results of a two-species model for the exergy of diatoms and green algae. Under given circumstances of temperature, retention time and ratios of silica to phosphorus, the dominance of diatoms gives the highest internal exergy for a tropical ecosystem (reservoir) in the summer rainy season, while a distribution between the two classes of algae gives the highest exergy in the winter dry period. These theoretical results agree with an actual case reported by T. Tundisi (*pers. comm.*, 1988)

Table 1. The ratios of diatoms to green algae at maximum exergy, calculated for summer and winter conditions in a tropical reservoir.
(Q = flow, V = volume; Q/V = relative retention time).

Season	Simulation characteristics	Ratio
Summer	Very low settling rate $Q/V = 0.1$ No light limitations	∞
Winter	Normal settling rate $Q/V = 0.02$ Light limitations	6:4

Case 5: exergy of a model for nitrogen and phosphorus turnover

Another examination of structural changes in an ecosystem is based on a model similar to the one shown schematically in Figure 5, except that nitrogen and phosphorus were considered instead of silica and phosphorus. All rates were given average values (growth, mortality and mineralization) for the nitrogen and phosphorus cycles. All rates were multiplied by the same factor in each of the two cycles and the inputs of nitrogen and phosphorus were varied. The factors giving the highest exergy were found, and the ratios between the corresponding nitrogen and phosphorus turnover rates were calculated. The results are summarized in Figure 8, where the turnover ratios are plotted against the N/P concentration ratios, and they are completely in accord with Vollenweider (1975). The latter considered it a paradox that the higher the ratio of N/P, the higher was the turnover rate of nitrogen to phosphorus, as it may be argued that relatively high nitrogen concentrations make it unnecessary to have a rapid turnover of nitrogen.

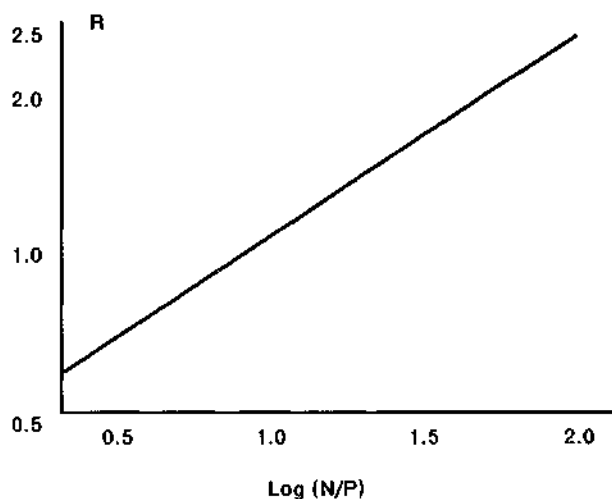


Figure 8. The ratio of nitrogen:phosphorus turnover (R) at maximum exergy, plotted against the logarithm of concentration ratios for nitrogen:phosphorus. Note that both scales are logarithmic, making the relationship almost linear.

Conclusions

The five cases referred to above all show that the principle of maximum exergy agrees with the observed selection and seasonal succession of algal species in natural ecosystems. Therefore it would be an obvious step to use the principle to predict the short-term natural selection and sequence of events that will occur under given circumstances, i.e. to develop structural dynamic models, as was attempted in the first case above. The results obtained so far are promising for a wider application, but far more experience is needed before a general application of this approach to structural dynamic modelling can be recommended.

References

- Brooks, D. R., Collier, J., Maurer, B. A., Smith, J. D. H. & Wiley, E. O. (1989). Entropy and information in evolving biological systems. *Biology and Philosophy*, **4**, 407-432.
- Brooks, D. R., Cumming, D. D. & LeBlond, P. H. (1988). Dollo's law and the second law of thermodynamics: analogy or extension? In *Entropy, Information and Evolution: New Perspectives on Physical and Biological Evolution* (eds B. H. Weber, D. J. Depew & J. D. Smith), pp. 189-224. MIT Press, Cambridge, Massachusetts.
- Eriksson, B., Eriksson, K. E. & Wall, G. (1976). *Basic Thermodynamics of Energy Conversions and Energy Use*. Institute of Theoretical Physics, Göteborg, Sweden.
- Herendeen, R. (1989). Energy intensity, residence time, exergy, and ascendancy in dynamic ecosystems. *Ecological Modelling*, **48**, 19-44.
- Jizhong, Z., Shijun, M. & Hinman, G. W. (1992). Ecological exergy analysis: a new method for ecological energetics research. *Ecological Modelling*, in press.
- Jørgensen, S. E. (1982). A holistic approach to ecological modelling by application of thermodynamics. In *Systems and Energy* (eds W. Mitsch et al.), pp. 61-72. Ann Arbor.
- Jørgensen, S. E. (1986). Structural dynamic model. *Ecological Modelling*, **31**, 1-9.
- Jørgensen, S. E. (1988). *Fundamentals of Ecological Modelling*. Elsevier, Amsterdam.
- Jørgensen, S. E. & Meyer, H. F. (1977). Ecological buffer capacity. *Ecological Modelling*, **3**, 39-61.
- Jørgensen, S. E. & Meyer, H. F. (1979). A holistic approach to ecological modelling. *Ecological Modelling*, **7**, 169-189.
- Jørgensen, S. E., Mejer, H. F. & Friis, M. (1978). Examination of a lake model. *Ecological Modelling*, **4**, 253-279.
- Jørgensen, S. E., Nors-Nielsen, S. & Jørgensen, L. A. (1991). *Handbook of Ecological Parameters and Ecotoxicology*. Elsevier, Amsterdam.
- Jørgensen, S. E., Patten, B. & Straskraba, M. (1992). Ecosystem emerging. *Ecological Modelling*, **60**, in press.

- Jørgensen, S. E., Jørgensen, L. A., Kamp-Nielsen, L. & Mejer, H. F. (1981). Parameter estimation in eutrophication modelling. *Ecological Modelling*, **13**, 111-129.
- Jørgensen, S. E., Kamp-Nielsen, L., Christensen, T., Windolf-Nielsen, J. & Westergaard, B. (1986). Validation of a prognosis based upon a eutrophication model. *Ecological Modelling*, **32**, 165-182.
- May, R. M. (Editor) (1981). *Theoretical Ecology: Principles and Applications*. 2nd Edition. Blackwell Scientific Publications, Oxford.
- Mejer, H. F. & Jørgensen, S. E. (1979). Energy and ecological buffer capacity. In *State-of-the-Art of Ecological Modelling. Environmental Sciences and Applications, 7th Proc. Conf. Ecological Modelling, 28th August - 2nd September 1978* (ed. S. E. Jørgensen), pp. 829-846. International Society for Ecological Modelling, Copenhagen.
- Monod, J. (1972). *Chance and Necessity*. Random House, New York.
- Morowitz, H. J. (1968). *Energy Flow in Biology*. Academic Press, New York.
- Nors-Nielsen, S. (1992a). Modelling the structural dynamical changes in a Danish shallow lake. *Ecological Modelling* (in press).
- Nors-Nielsen, S. (1992b). Optimization of exergy in a structural dynamical model. *Ecological Modelling*, (in press).
- Odum, H. T. (1983). *Systems Ecology*. Wiley Interscience, New York.
- Patten, B. C. (1991). Network ecology: indirect determination of the life-environment relationship in ecosystems. In *Theoretical Studies of Ecosystems: The Network Perspective* (eds M. Higgashi & T. P. Burns), pp. 288-351. Cambridge University Press.
- Prigogine, I. & Stengers, I. (1979). *La Nouvelle Alliance*. Gallimard, Paris.
- Shieh, J. H. & Fan, L. T. (1982). Estimation of energy (enthalpy) and energy (availability) contents in structurally complicated materials. *Energy Resources*, **6**, 1-46.
- Stenseth, N. C. (1986). Darwinian evolution in ecosystems: a survey of some ideas and difficulties together with some possible solutions. In *Complexity, Language, and Life: Mathematical Approaches* (eds J. L. Casti & A. Karlqvist), pp. 105-129.
- Straskraba, M. (1980). The effects of physical variables on freshwater production: analyses based on models. In *The Functioning of Freshwater Ecosystems* (eds E. D. Le Cren & R. H. McConnell), pp. 13-31.
- Tilman, D. & Kilham, S. S. (1976). Phosphate and silicate growth and uptake kinetics of the diatoms *Asterionella formosa* and *Cyclotella meneghiniana* in batch and semi-continuous culture. *Journal of Phycology*, **12**, 375-383.
- Ulanowicz, R. E. (1980). An hypothesis on the development of natural communities. *Ecological Modelling*, **85**, 223-245.
- Vollenweider, R. A. (1975). Input-output models with special reference to the phosphorus loading concepts in Limnology. *Schweizerische Zeitschrift für Hydrologie*, **37**, 53-84.
- Wicken, J. S. (1988). Thermodynamics, evolution, and emergence: ingredients for a new synthesis. In *Entropy, Information and Evolution: New Perspectives on Physical and Biological Evolution* (eds B. H. Weber, D. J. Depew & J. D. Smith), pp. 139-172. MIT Press, Cambridge, Massachusetts.
- Wiley, E. O. (1988). Entropy and evolution. In *Entropy, Information and Evolution: New Perspectives on Physical and Biological Evolution* (eds B. H. Weber, D. J. Depew & J. D. Smith), pp. 173-188. MIT Press, Cambridge, Massachusetts.