Opinion

This is a series of contributions, expressing explicit opinions with regard to contemporary topics in limnology. These texts can be based on new books with a large impact, but can also refer to other currently debated topics. Documented reactions to these contributions should be sent to the editor-in-chief; they will be considered for publication in subsequent issues.
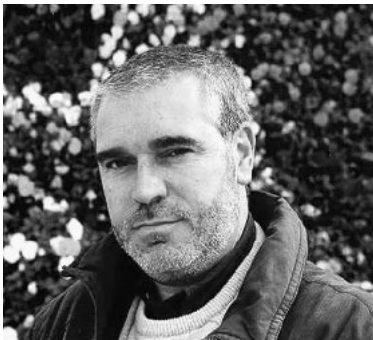
Thermodynamics and ecosystem theory, case studies from hydrobiology

S. E. Jørgensen[1] & J. C. Marques[2]
[1]*DFH, University Park 2, 2001 Copenhagen Ø, Denmark*
[2]*IMAR, Faculty of Science and Technology, Zoological Department, Coimbra University, Coimbra, Portugal*

João Carlos Marques has led the IMAR (Institute of Marine Research Consortium) in Portugal since 1997. IMAR associates presently total approximately 300 researchers distributed in seven research and development units. Since 1989, as Professor of Aquatic Sciences, Dr Marques has been teaching Hydrobiology in Portugal and abroad. His areas of expertise are biological and ecological processes in aquatic ecosystems, systems ecology, and analysis of ecosystem's integrity.
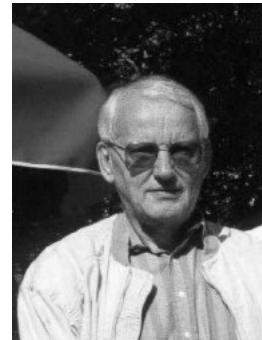
Sven Erik Jørgensen has worked at the Royal Danish School of Pharmacy since 1965 as professor in environmental chemistry. Since 1974, he has been editor-in-chief of the journal *Ecological Modelling* and member of the editorial board of 7 other international journals; he has been president of ILEC since 1994. His areas of expertise are system ecology, ecological modelling and ecological engineering and environmental science.

Introduction

Several papers and books presenting new ideas in system ecology have been published during the last 2–3 decades. The different ideas and approaches look at first glance if they were not consistent. Nevertheless, if we look deeper into the underlying ideas, it becomes evident that the various approaches and hypotheses form a pattern of theories (Jørgensen, 1997) that is able to explain the dynamics of ecosystems. We need probably a number of different complimentary approaches to explain ecosystems (Jørgensen, 1994a), which is not surprising as much simpler physical phenomena, light for instance, needs two different descriptions, namely as waves and as particles.

New ecosystem theories have found a limited application in ecological modelling, for instance in the development of structural dynamic models, i.e. models that account for the adaptation of the biological components in the models; see for instance Jørgensen & Padisak (1996), Jørgensen & de Bernardi (1997, 1998) and Jørgensen (1986, 1992, 1994b and 1997). It is probably necessary if we want to improve the predictive power of our ecological models to apply these ecosystem theoretical approaches much more widely.

If we look into the literature covering general ecology including hydrobiology numerous observations,
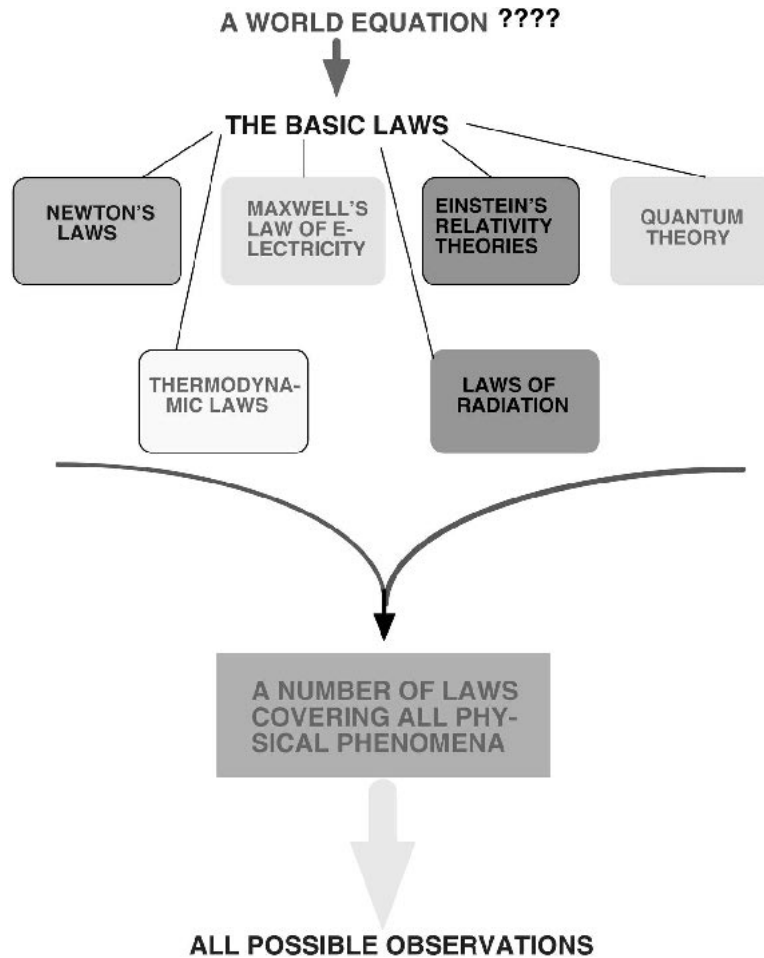
Figure 1. The theoretical network of physics consists of a few fundamental laws (for instance the thermodynamic laws) from which other laws can be derived. All (or almost all) observations can be explained by a fundamental law or a derived law.

rules and correlations have been published during the last decades due to an increasing interest for ecology and environmental sciences. The obvious question is can we develop a theoretical network that would be able to explain these observations, rules and correlations on basis of an accepted pattern of ecosystem theories? In other words, is the time ripe to construct a theoretical network in ecology such as the one in physics, where a few fundamental laws can be applied to derive other laws which can be used to explain all (or almost all) physical observations (see Fig. 1)? We do not know if this is possible in ecology, but assuming that it is the indeed right time to build such a theoretical network in ecology, it should at least be possible to propose a promising direction for our thoughts and to create some fragments of them. This paper attempts to present a fragment of such a theoretical network in

the hope that it will inspire others to work along the same line. Many ecologists must contribute to deepen and enrich these theoretical thoughts which will make ecology a more rigorous science, easier to apply in environmental management context.

We have selected a specific thermodynamic hypothesis to illustrate the possibilities to construct such a theoretical network. Any other central hypothesis could probably equally have been applied. The authors have previously worked with this hypothesis as a goal function in structural dynamic models and as an ecological indicator to assess ecosystem health. Thermodynamics rooted in laws about energy transfer and application is widely applied in ecosystem theory because input, output and cycling of mass and energy are the foundation of all ecological processes. After the hypothesis has been introduced, a few typical observa-
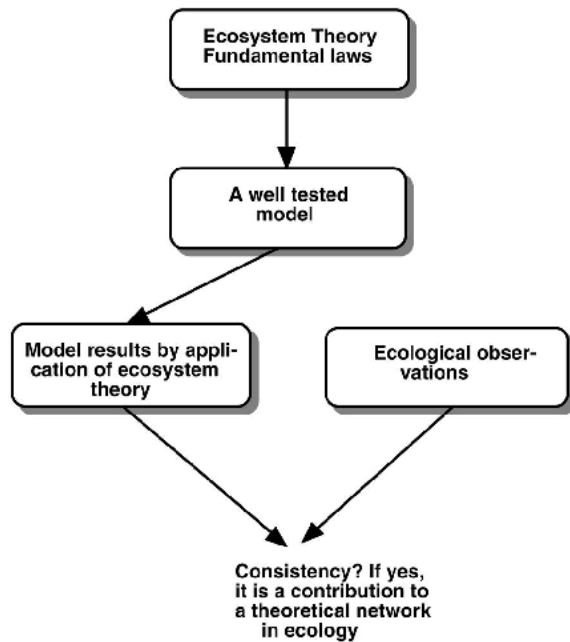
Figure 2. It is not possible to make experiments (with some few exceptions) with entire ecosystems. It is therefore necessary to use well tested models. Application of the fundamental laws leads to statements about ecosystem reactions. These may be compared with observations, and if there is consistency, we have a part of what could be called the 'theoretical ecological network'.

tions, rules and hypotheses which will be shown to be consistent with the thermodynamic hypothesis will be presented. It will be demonstrated that they can be derived from this hypothesis, but as it is difficult to make unequivocal experiments in an ecosystem in contrast to chemical and physical experiments in a laboratory, it has been necessary to apply well-examined models. Figure 2 shows the idea behind the applied procedure.

The applied thermodynamic hypothesis

A flow of energy, or more precisely exergy, which in this case can be seen as energy free of entropy (Jørgensen, 1997) must pass through a system in order to ensure its existence, which means that the system must be open or at least non-isolated. A flow of exergy through the system is also *sufficient* to form an ordered structure (also named a dissipative structure (Prigogine, 1980)). Morowitz (1992) calls this latter formulation the fourth law of thermodynamics, but it would be more appropriate to expand this law to encompass a statement about *which* ordered structure among the possible ones will be selected, or which

factors determine how an ecosystem will grow and develop? A hypothesis to interpret this selection was presented by Jørgensen (1992, 1997), after a former proposition that can be found in Jørgensen & Mejer (1977) and Mejer & Jørgensen (1979). This hypothesis determines the growth of ecosystems, its directions, and its implications for ecosystem properties and development.

Growth may be defined as the increase of a measurable quantity, which in ecology often is presumed to be the biomass. Growth may also be understood as an increase in ordered structure and/or organisation and/or information. Ulanowicz (1986) uses growth and development as the extensive and intensive aspects of the same process. Growth implies increase or expansion, while development focuses on the increase in organisation and/or the amount of information, which is considered independent of the size of the system. In thermodynamic terms, a growing system is moving away from thermodynamic equilibrium. At thermodynamic equilibrium, the system cannot do any work, the components are inorganic and have zero free energy, and all gradients are eliminated. Structure and gradients, resulting from growth and developmental processes, will be found everywhere in the Universe. Second-law dissipation act to tear down the structures and eliminate the gradients, but dissipation cannot operate unless the gradients are there in the first place. An obvious question is therefore: what determines the build-up of gradients? Structure and organisation may be expressed in kJ corresponding to the distance from thermodynamic equilibrium = exergy expressed in energy units.
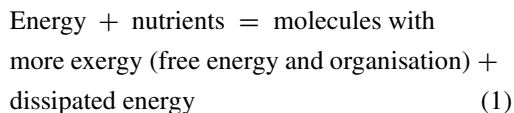
Biological systems may be the best example of systems using many possibilities to move away from thermodynamic equilibrium. It is, therefore, crucial in ecology to know which pathways among the possible ones an ecosystem will select for development. That would be the key to describe the processes characteristic for ecosystem development. Considering the ontic openness presented in Jørgensen et al. (1999), it would be more appropriate to discuss not the selection of components and processes for development of ecosystems, but rather the propensity for directional development (Ulanowicz, 1997). The answer is formulated as a hypothesis in Jørgensen (1988, 1997).

If a system receives a through-flow of exergy (a) the system will utilise this exergy flow to move away from thermodynamic equilibrium and (b) if more than one pathway is available to achieve this, the one yielding most *stored* exergy (measured in J/m^2 or J/m^3) by

the prevailing conditions, i.e. with the most ordered structure and the longest distance to thermodynamic equilibrium, will have a propensity to be selected.

As it is not possible to prove the 1.–3. laws of thermodynamics by deductive methods, the above hypothesis can only be proved by inductive methods. This implies that it should be investigated (and falsification attempted) in as many concrete cases as possible.

The hypothesis may also be considered as an extended version of "Le Chatelier's Principle" (see any textbook in chemistry). Formation of biomass may be described as:

$$\text{Energy} + \text{nutrients} = \text{molecules with more exergy (free energy and organisation)} + \text{dissipated energy} \tag{1}$$

If we pump energy into a system in equilibrium, the system shifts in equilibrium composition in a way to counteract the change. It means that, according to Le Chatelier's Principle, more molecules with more free energy and organisation will be formed. If more pathways are offered, the pathways, that give the most relief, i.e. use most energy and thereby form molecules with most embodied exergy will win according to the hypothesis.

The stored exergy of an ecosystem can be approximated by the following expression:

$$Ex = \sum_{i}^{n} \beta_i c_i, \tag{2}$$

where Ex is the exergy, β_i is a weighting factor dependent on the amount of information that the components carry, c_i is the concentration of the components $i = 1$ to $i = n$. This equation presumes that exergy for the ecosystem is found relatively to the same system at thermodynamic equilibrium at the same temperature and pressure. It means that exergy represents the energy that can do work due to the free energy of the many organic compounds plus the information that the living organisms carry. Table 1 gives the β-values of different types of organised organic matter relatively to detritus which is considered to have no information but only the free energy of the organic matter (in average 18.7 kJ/g). There is nevertheless obviously a lack of discriminating power in the weighting factors given in Table 1, where organisms are considered at very high taxonomic levels. The need for more discriminating weighting factors have in fact, been discussed (Marques et al., 1997) and new methodologies have

Table 1. Approximate number of non repetitive genes

Organisms	Number of information genes*	Conversion factor[a]
Detritus	0	1
Minimal cell (Morowitz, 1992)	470	2.7
Bacteria	600	3.0
Algae	850	3.9
Yeast	2000	6.4
Fungus	3000	10.2
Sponges	9000	30
Moulds	9500	32
Plants, trees	10 000–30 000	30–87
Worms	10 500	35
Insects	10 000–15 000	30–46
Jellyfish	10 000	30
Zooplankton	10 000–15 000	30–46
Fish	100 000–120 000	300–370
Birds	120 000	390
Amphibians	120 000	370
Reptiles	130 000	400
Mammals	140 000	430
Human	250 000	740

[a]Based on number of information genes and the exergy content of the organic matter in the various organisms, compared with the exergy contained in detritus. 1 g detritus has about 18.7 kJ exergy (= energy which can do work). References: Lewin (1994) and Li & Grauer (1991).

*The number of information genes considered needs to be reviewed to take into consideration advances arising from the publication of the draft of the human genome. It will be necessary to appreciate both the scale of challenge of other organisms' genome analysis and the limitations of current gene prediction methods and understanding (see for instance Birney et al. (2001), Tupler et al. (2001) and Wen-Hsiuno et al. (2001)).

been proposed to allow an easier estimation of weighting factors for different types of organisms (Marques et al., 1997; Fonseca et al., 2000). This nevertheless involves difficulties that are not fully understood and overstepped (Fonseca et al., 2000).

Exergy can be converted from detritus equivalents to kJ by multiplication by 18.7. The derivation of Equation (2) shall not be repeated here, but it can be found in Jørgensen et al., (1995), Jørgensen & Padisak (1997, Jørgensen (1997), Jørgensen & De Bernardi (1998) and Jørgensen et al. (2000). Equation (2) is used directly in the calculation of exergy for the models that are applied to explain the ecological observations, rules and correlations following the presented hypothesis here.
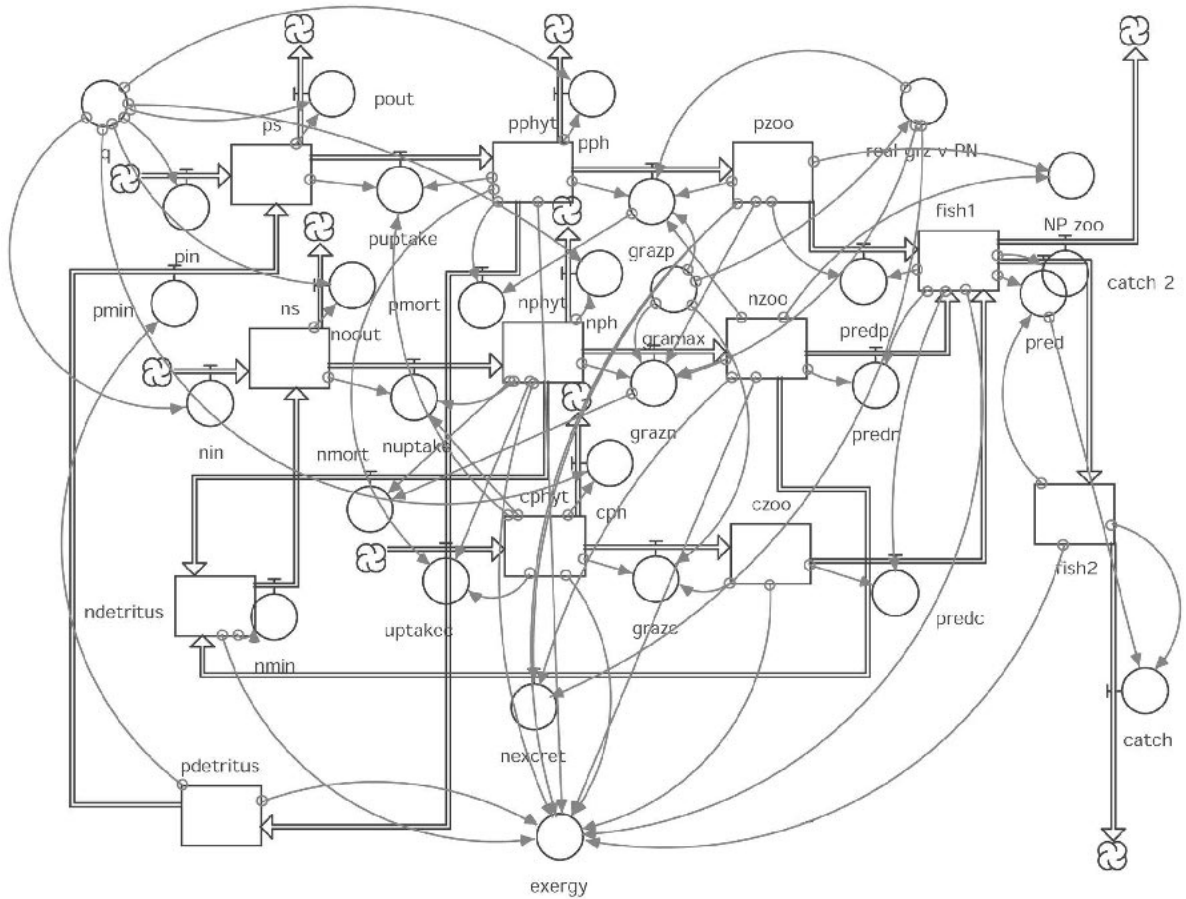
Figure 3. A STELLA model applied to test an observed shift of zooplankton species (Jørgensen, 1997).

Examples of ecological observations that can be derived from the thermodynamic hypothesis by using models

Let us consider a first observation, taking zooplankton as an example. The biochemical differences in body N:P ratio between Cladocera and Copepods is clear (Sterner, 1995). The nitrogen content varies from 8–10% (Andersen & Hessen, 1991), while the mean phosphorus percentage for copepods and cladocerans (especially *Daphnia*) are less than 0.6% and around 1.5%, respectively (Andersen & Hessen, 1991). Cladocerans have evolved rapid growth which requires a higher concentration of nucleic acids (Andersen & Hessen, 1991). Cladocerans are characteristic for relatively higher phosphorus concentrations in lakes where also a lower predation by piscivore fish occurs. By the same phosphorus concentration, how-
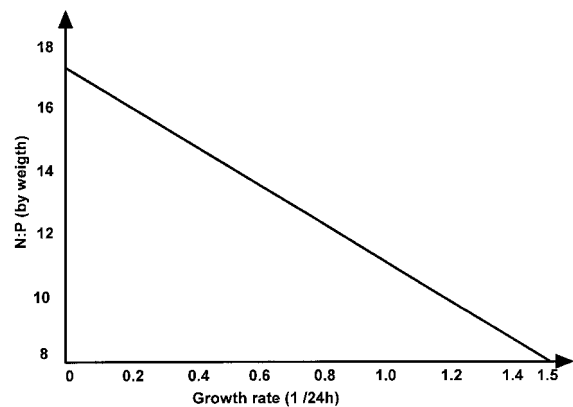

Figure 4. A relationship between growth rate and N:P ratio in zooplankton. This relationship is applied in the model Figure 3.

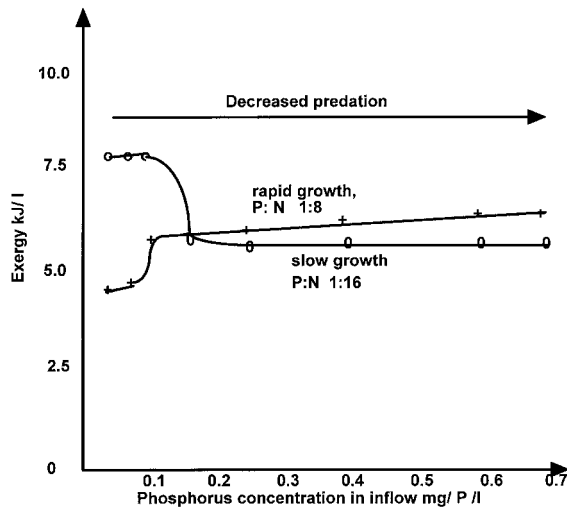ever, increased predation favour cladocerans (Elser et al., 1999).

Figure 5. The exergy found by use of the model in Figure 3 is plotted versus the phosphorus concentration in the inflow for a growth rate of 0.15 (1/24 h) (slow growth) with the predation rate giving the highest exergy, indicated by o, and for a growth rate of 1.5 (1/24 h) (rapid growth with the predation rate giving the highest exergy, indicated by +). The predation rate by piscivore fish corresponding to the maximum exergy is decreasing with increasing phosphorus concentration in the inflow.

The model in Figure 3 (STELLA software is applied) is used to show that these observations can be derived from the above mentioned thermodynamic hypothesis. Notice that the model contains a relationship between the growth rate of zooplankton and the P:N ratio that is needed to maintain the growth rate. This relationship is taken from McKee & Knowles (1987); see Figure 4. The exergy has been calculated from the model by (1) variation of the phosphorus concentration in the in flowing water, (2) the growth rate of zooplankton (3) the specific predation rate of piscivore fish. The results are summarised in Figure 5, where:

1. The exergy for a growth rate of 0.15 (1/24 h) (slow growth) is plotted *versus* the in flowing phosphorus concentration with the predation rate giving the highest exergy.
2. The exergy for a growth rate of 1.5 (1/24 h) (rapid growth) is plotted *versus* the in flowing phosphorus concentration with the predation rate giving the highest exergy.

It can be seen that from about 0.15 mg P/l the rapidly growing cladocerans with a high phosphorus concentration becomes dominant which is approximately in agreement with observations. The predation giving the highest exergy is decreasing when the phosphorus input is increasing, which also agrees with observations,
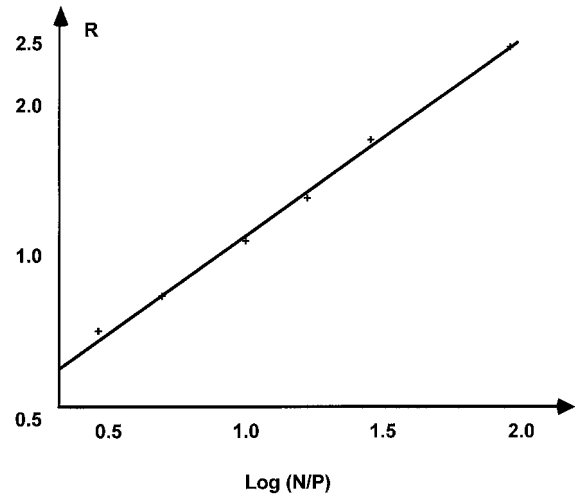

Figure 6. The N/P ratio turn over rates, *R*, is plotted *versus* the logarithm of the N/P ratio. The lines corresponds to observations, while the points indicate model results (Jørgensen, 1997).

i.e. the planktivorous fish become more dominating at higher phosphorus concentration. At the same phosphorus concentration, the highest exergy is obtained at a higher predation rate for the rapid growing species. These results should of course not be considered quantitatively, because the model is only a very coarse representation of the real ecosystem, but should be limited to at the most semi-quantitative interpretations.

We may nevertheless conclude from this case study, that the following questions can be answered on the basis of the thermodynamic hypothesis by use of models:

1. Which is the characteristic growth rate for zooplankton species when we increase the phosphorus input into a lake?
2. Which is the characteristic predation by piscivore fish, when we increase phosphorus input into a lake?
3. If we increase the predation rate, will the rapidly or slowly growing species be favoured?

The same model can be used to derive another observation from the thermodynamic hypothesis. If a source (for instance, a limiting nutrient for plant growth) is abundant, it will typically recycle faster. This appears somehow contradictory since a rapid recycling is not necessary when a given resource is non-limiting. But in fact such observations are totally consistent with the thermodynamic hypothesis. Figure 6 shows the ratio, R, of nitrogen (N) – phosphorus (P) recycling as a function of N/P ratios, according to well-known
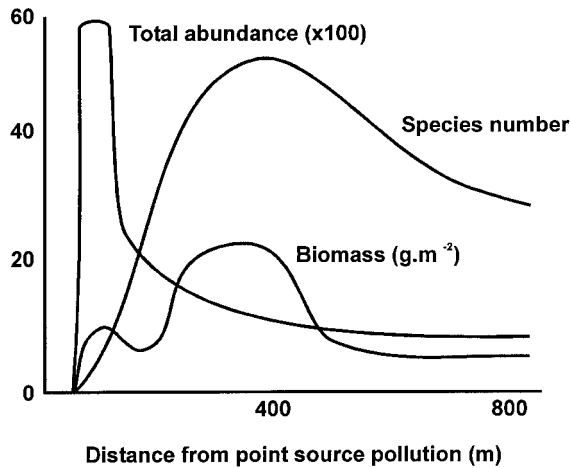
Figure 7. Species number, total abundance of animals, and biomass along a gradient of decreasing sedimentary organic content, expressed as distance from the effluent of seaweed processing plant (adapted from McLusky, 1989). We may observe that population density changes inversely to the biomass, measning that lower individual biomasses correspond to higher population density, and vice-versa.

empirical results (Vollenweider, 1975; Urabe, 1993; Elser & Hassett, 1994). We also plotted on the figure the points corresponding to recycling ratios that provide the highest exergy values for various log (P/N) according to model calculations. The plotted points are almost strictly coinciding with the curve calibrated with empirical observations. This allow us to conclude that observations are in fact in agreement with the thermodynamic hypothesis, and using a well tested eutrophication model it would be actually possible to derive the following rule: if a nutrient is abundant then it will recycle faster.

As a third example, we will address, as starting point, the following question: how does the packing of species in an area derive as a function of individual biomass? Applying the thermodynamic hypothesis, we should expect that individual biomass increase (carrying exergy) rather than population size or respiration (which correspond to the highest dissipation of exergy) would be favoured. Therefore, we should also expect that population density is inversely proportional to the individual biomass of organisms. Figure 7, showing data from empirical observations regarding the variation of total abundance, biomass and number of species of an estuarine benthic community as funtion of the distance to a pollution focus (seee Lusky, 1989) illustrates this expected trend. It is also in accordance with several case studies published by Peters, (1983). The population density may then be expressed as:

$$D = A/W,$$

where *A* is a constant. *D* is approximately proportional to the weight in the exponent – 1 (Peters, 1983).

Let us consider a fourth and final example. A previously developed eutrophication model that have been applied in 25 cases. The model has 21 state variables, when silica is included as nutrient. The carbon, nitrogen, phosphorus and silica cycles are all included in the model. The phosphorus cycle is shown in Figure 8. All details of the model are given in Jørgensen (1976, 1986). This model is particularly well examined for a few shallow Danish lakes and in two cases, it was even possible to validate the prognosis with an acceptable result. This model has been used to answer two illustrative questions, formulated on basis of statements made by Sommer et al. 1986:

1. Under which circumstances will diatoms replace green algae in a eutrophied shallow lake?
2. Under which circumstances will nitrogen-fixing species of filamentous blue-green algae be dominant in a eutrophic shallow lake.

The model was applied for a number of cases from 1 mg P/l to 0.02 mg P/, while silica and nitrogen were constant at 5 mg/l. Two series of simulations were made: (a) for green algae with a high half saturation constant for phosphorus uptake (0.1 mg P/l, characteristic for *Schenodesmus)* and medium growth and settling rates and (b) for diatoms with description of silica uptake, low half saturation constant for phosphorus uptake (0.003 mg P/l.) with a medium growth rate and a high settling rate. In the concentration range from 0.02 mgP/l to about 0.25 mg P/l, the diatoms gave the highest exergy, while green algae gave the highest exergy above 0.25 mg P/l. It is consistent with our observations in Lake Glumsø (see for instance Jørgensen (1997) and with Sommer et al. (1986)). Therefore, the answer to question (1) is (the model results are only used semi-quantitatively): competition for phosphorus leads to a shift from green algae to diatoms in shallow lakes.

The model was similarly tested by three phosphorus concentrations 0.02 mg /l, 0.2 mg /l and 1 mg/l and at 5 different nitrogen concentrations 5 mg/l, 1 mg/l, 0.2 mg/l, 0.05 mg/l and 0.01 mg/l. These 15 cases (3 P concentrations × 5 nitrogen concentrations) were simulated for (a) nitrogen fixing blue-greens (able to nitrogen fix, very low sedimentation rate, relatively low growth rate and for (b) diatoms with
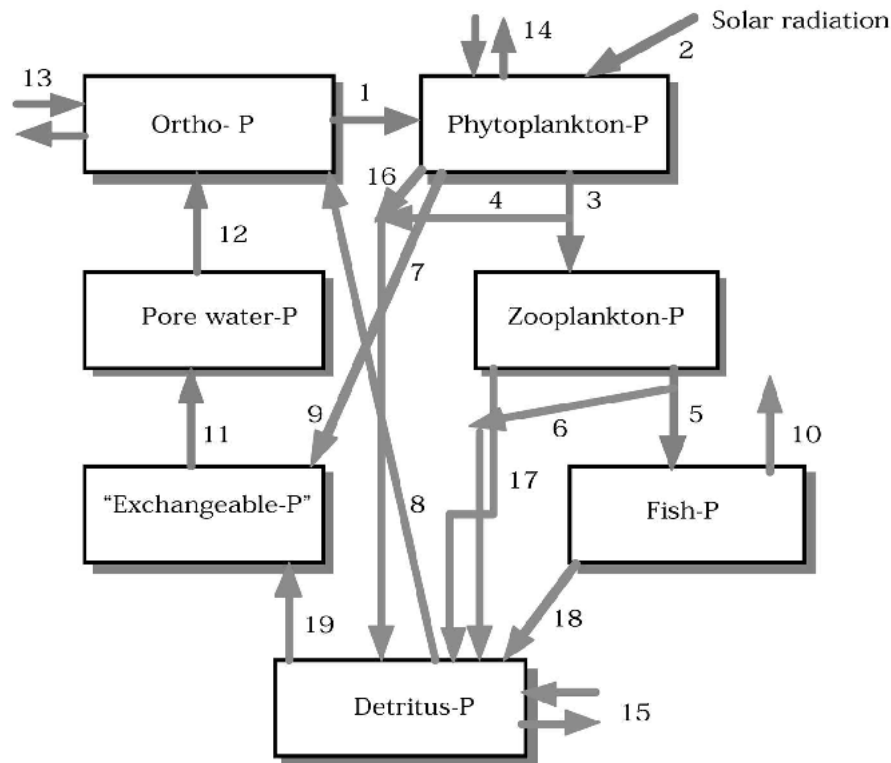
Figure 8. The phosphorus cycle represented in the applied eutrophication model (Jørgensen, 1994b). The processes are: (1) Uptake of phosphorus by algae, (2) Photosynthesis, (3) Grazing with loss of undigested matter, (4), (5) predation with loss of undigested material, (6), (7) and (9) Settling of phytoplankton (8) Mineralisation, (10) Fisheries (11) Mineralisation of phosphorous organic compounds in the sediment, (12) Diffusion of pore water P (13) (14) and (15) are Inputs/outputs, (16), (17) and (18) represent mortalities and (19) is settling of detritus.

description of silica uptake, low half saturation constant for phosphorus uptake (0.003 mg P/l.), a medium growth rate and a high settling rate. Results are shown in Figure 9 and it can be concluded at least qualitatively, that relative nitrogen depletion favours a shift from diatoms to nitrogen-fixing species. It may be semi-quantitatively possible to state that by a N:P ratio below about 3 there is a clear tendency to a higher exergy for the nitrogen-fixing blue greens.

Discussion and conclusion

The general idea behind this paper is to demonstrate that the time is ripe to develop a more rigorous ecology. We do have sufficient knowledge about the behaviour of ecosystems to be able to explain many observations, rules and regressions on the basis of ecosystem theory. In this paper, we considered a thermodynamic hypothesis and we have shown that it is possible to use it to explain several hydrobiological

observations, mainly from lake studies. This approach has of course limitations, because we used models and these cannot consider all factors but rather those processes and components considered most important for the focal problem to be solves or elucidated. Moreover, the theory applied is only considered a hypothesis which implies that we could also use the consistency opposite, i.e. as a support for the hypothesis. This was actually the case when Jørgensen & Padisak (1996) showed the consistency between the intermediate disturbance hypothesis and the thermodynamic hypothesis presented in this paper, and also when Jørgensen & De Bernardi (1999) showed that the phosphorus concentration (from about 0.05 to about 0.125 mg P/l) when only biomanipulation is applicable is consistent with the thermodynamic hypothesis. But these two rules can now be included in the network, where the thermodynamic hypothesis has a central position.

Physics uses the same idea, i.e. to build a logical network of all observations with the most fundamental
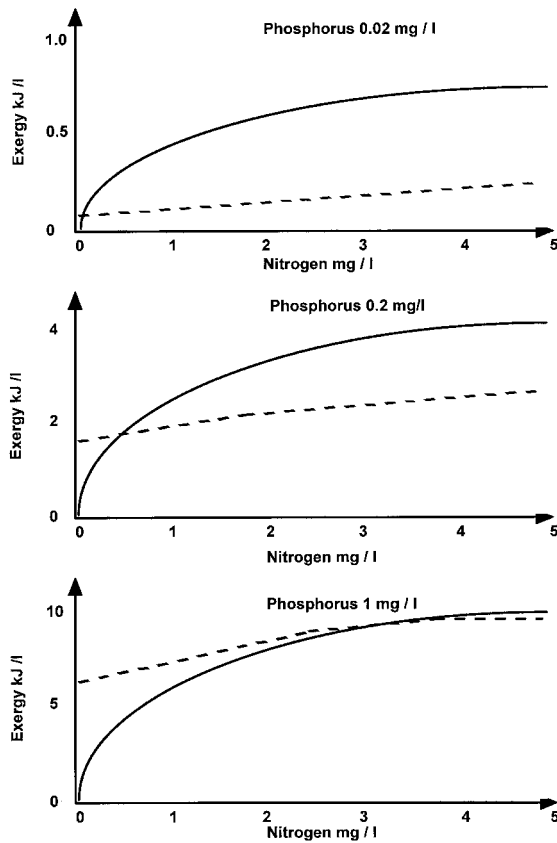
Figure 9. Exergy obtained by application of the complex eutrophication model (The P-cycle is shown Figure 8) is plotted *versus* the nitrogen concentration in the inflow for three different phosphorus concentrations in the inflow. The full lines represent diatoms and the dotted lines nitrogen-fixing blue–greens.

laws as nodes in the network. Slowly, but certainly, physics has build up a theoretical network. This means that all parts of physics are linked together in a system which can also be applied to test a new hypothesis: does it fit into the logic network? If not, there has to be a very strong support for the hypothesis to be accepted because it requires the network to be changed to a certain extent. If so the network is made larger or stronger.

Ecology as we may understand from numerous publications every year does not offer such a theoretical network and, therefore, all the observations and rules appear like lonely island in a huge ocean. In fact, there are no or at the most only a few links between the various observations, laws and rules. Recent progresses in ecosystem theory including the application of thermodynamics in ecology, may nevertheless allow us also in ecology to build a theoretical network

also in ecology. This paper intended to show a very small fragment of this network to illustrate that the time is ripe to develop it. The effort of many researchers during several years will of course be necessary to develop this theoretical network through a stepwise approach. It cannot be done overnight, but it is important for the progress in ecology and for the application of environmental sciences in a management context that we get started as soon as possible to develop a general theoretical network in ecology.

References

Andersen, T. & D. O. Hessen, 1991. Carbon, nitrogen, and phosphorus content of freshwater zooplankton. Limnol. Oceanogr. 36: 807–814.

Birney, E., A. Bateman, M.E. Clamp & T.J. Hubbard, 2001. Mining the draft human genome. Nature, 15 February 2001: 827–828.

Elser, J. J., D. R. Dobberfuhl, N. A. MacKay & J. H. Schampel, 1999. Organisms Size, Life History and N:P Stoichiometry. In Readings in Ecology. Oxford University Press, Oxford: 237–254.

Elser, J. J. & R. P. Hassett, 1994. A stoichiometric analysis of the zooplankton-phytoplankton interactions in marine and freshwater ecosystems. Nature 370: 211–213.

Jørgensen, S. E., 1976. A eutrophication model for a lake. Ecol. Modell. 2: 147–165.

Fonseca, J. C., J. C. Marques, A. A. Paiva, A. M. Freitas, **X. X.** Madeira & S. E. Jørgensen, 2000. Nuclear DNA in the determination of weighting factors to estimate exergy from organisms biomass. Ecol. Modell. (in press).

Jørgensen, S. E., 1986. Structural dynamic model. Ecol. Modell. 31: 1–9.

Jørgensen, S. E., 1988. Use of models as an experimental tool to show that structural changes are accompanied by increased exergy. Ecol. Modell. 41: 117–126.

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

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

Jørgensen, S. E., 1994b. Fundamentals of Ecological Modelling (2nd edn). Developments in Environmental Modelling, 19. Elsevier, Amsterdam: 628 pp.

Jørgensen, S. E., 1997. Integration of Ecosystem Theories: A Pattern. 2nd edn. Kluwer Academic Publishers, Dordrecht: 400 pp. (1st edn, 1992).

Jørgensen, S. E. & H. F. Meyer, 1977. Ecological buffer capacity. Ecol. Modell. 3: 39–61.

Jørgensen, S. E., S. N. Nielsen & H. Mejer, 1995. Energy, environ, exergy and ecological modelling. Ecol. Modell. 77: 99–109.

Jørgensen, S. E. & J. Padisák, 1996. Does the intermediate disturbance hypothesis comply with thermodynamics? Hydrobiologia 323: 9–21.

Jørgensen, S. E. & R. De Bernardi, 1997. The application of a model with dynamic structure to simulate the effect of mass fish mortality on zooplankton structure in Lago di Annone. Hydrobiologia 356: 87–96.

Jørgensen, S. E. & R. De Bernardi, 1998. The use of structural dynamic models to explain successes and failures of biomanipulation, Hydrobiologia 379: 147–158.

Jørgensen, S. E., B. C. Patten & M. Straskraba, 1998. Ecosystem emerging: 3. Openness. Ecol. Modell. 117: 41–64.

Jørgensen, S. E., B. C. Patten & M. Straskraba, 2000. Ecosystem emerging: 4. Growth. Ecol. Modell. (in press).

Lewin, B., 1994. Genes V. Oxford University Press, Oxford: 620 pp.

Li, W.-H. & D. Grauer, 1991. Fundamentals of Molecular Evolution. Sinauer, Sunderland, Massachusetts: 430 pp.

Marques, J. C., M. A. Pardal, S. N. Nielsen & S. E. Jørgensen, 1997. Analysis of the properties of exergy and biodiversity along an estuarine gradient of eutrophication. Ecol. Modell. 102: 155–167.

McKee, *X.* & **X.** Knowles, 1987. Levels of proteins, RNA, DNA, glycogen and lipids during growth and development of *Daphnia magna* Straus. Freshwat. Biol. 18: 341–351.

Mejer, H. F. & S. E. Jørgensen, 1979. Energy and ecological buffer capacity. In Jørgensen, S. E. (ed.), State-of-the-Art of Ecological Modelling. Environmental Sciences and Applications 7. Proceedings of a Conference on Ecological Modelling, 28 August–2 September 1978, Copenhagen. International Society for Ecological Modelling, Copenhagen: 829–846.

Morowitz, H. J., 1992. Beginnings of Cellular Life. Yale University Press, New Haven.

Peters, R. H., 1983. The Ecological Implications of Body Size. Cambridge University Press, Cambridge.

Prigogine, I., 1980. From Being to Becoming: Time and Complexity in the Physical Sciences. Freeman, San Fransisco, CA: 260 pp.

Sommer, U., Z. M. Gliwicz, W. Lampert & A. Duncan, 1986. The PEG model of seasonal succession of planktonic events in fresh water. Arch. Hydrobiol. 106: 433–471.

Tupler R., G. Perini & M.R. Green, 2001. Expressing the human genome. Nature, 15 February 2001: 832–833.

Ulanowicz, R. E., 1986. Growth and Development. Ecosystems Phenomenology. Springer-Verlag, New York: 204 pp.

Ulanowicz, R. E., 1997. Ecology, the Ascendent Perspective. Columbia University Press, New York: 201 pp.

Urabe, J., 1993. N and P cycling coupled with grazers' activities: food quality and nutrient release by zooplankton. Ecology 74: 2337–2350.

Vollenweider, R. A., 1975. Input-output models with special reference to the phosphorus loading concept in limnology. Schweiz Z. Hydrol. 37: 53–84.

Wen-Hsiuno, L., G. Zhenglong, W. Haidong & A. Nekrutenko, 2001. Evolutionary analysis of the human genome. Nature, 15 February 2001: 847–849.