10

Structurally Dynamic Models

CHAPTER OUTLINE

10.1. Introduction

Ecological models attempt to capture the characteristics of ecosystems. However, ecosystems differ from most systems because they are extremely adaptive, self-organized, and have a large number of feedback mechanisms. The real challenge of modelling is to answer this question: How can we construct models that are able to reflect these dynamic characteristics? This chapter attempts to answer this question by the use of structurally dynamic models. Section 10.2 focuses on the characteristics of ecosystems and Section 10.3 is devoted to the development of structurally dynamic models (SDMs) or variable parameter models, which are sometimes called the fifth generation of models. The thermodynamic variable eco-exergy (work capacity defined for ecosystems; the definition and presentation are given in Section 10.3) has been applied to develop SDMs in 21 cases (Zhang et al., 2010). The 21 case studies are:

1–8. Eight eutrophication models of six different lakes
  9. A model to explain the success and failure of biomanipulation based on removal of planktivorous fish
 10. A model to explain under which circumstances submerged vegetation and phytoplankton are dominant in shallow lakes

11. A model of Lake Balaton, which was used to support the intermediate disturbance hypothesis
12–15. Small population dynamic models
16. A eutrophication model of the Lagoon of Venice
17. A eutrophication model of the Mondego Estuary
18. An ecotoxicological model focusing on the influence of copper on zooplankton growth rates
19. A model of Darwin's finches
20. A model of the interaction between parasites and birds
21. A model of Lake Fure in Denmark

Sections 10.4–10.6 present three illustrative examples of SDMs; namely 19, 9 and 18 from the previous list of case studies using eco-exergy as a goal function to develop SDMs. The use of this model type will most likely increase in the future in our endeavor to make more adaptive models because reliable predictions can only be made by models with a correct description of ecosystem properties. If our models do not properly describe adaptation and possible shifts in species composition, then the prognoses will inevitably be more incorrect.

10.2. Ecosystem Characteristics

Ecology deals with irreducible systems (Wolfram 1984a,b, Jørgensen, 1990, 1992a,b, 2002, Jørgensen & Fath, 2004b). We cannot design simple experiments to reveal a relationship that can, in all detail, be transferred from one ecological situation and one ecosystem to another situation in another ecosystem. This may be possible with Newton's laws of gravity, because the relationship between forces and acceleration is reducible. The relationship between force and acceleration is also linear, but growth of living organisms is dependent on many interacting factors, which again are functions of time. Feedback mechanisms simultaneously regulate all the factors and rates, interact, and are also functions of time (Straskraba, 1979, 1980).

Table 10.1 shows the hierarchy of regulation mechanisms that are operating at the same time. From this example the complexity alone clearly prohibits the reduction to simple relationships that can be used repeatedly. An ecosystem has so many interacting components that it is impossible to examine all of these relationships. Even if we could,

Table 10.1   The Hierarchy of Regulating Feedback Mechanisms

Level	Explanation of Regulation Process	Exemplified by Phytoplankton Growth
1.	Rate by concentration in medium	Uptake of phosphorus in accordance with phosphorus concentration
2.	Rate by needs	Uptake of phosphorus in accordance with intracellular concentration
3.	Rate by other external factors	Chlorophyll concentration in accordance with previous solar radiation
4.	Adaptation of properties	Change of optimal temperature for growth
5.	Selection of other species	Shift to better fitted species
6.	Selection of other food web	Shift to better fitted food web
7.	Mutations, new sexual recombinations, and other shifts of genes	Emergence of new species or species properties

From Jørgensen, 1988.

it would be impossible to separate one relationship and examine it carefully to reveal its details because the relationship is different when it works in nature with interactions from many other processes and from when it is examined in a laboratory with the relationship separated from the other ecosystem components. The observation that it is impossible to separate and examine processes in real ecosystems corresponds to the examinations of organs that are separated from the organisms in which they are working. Their functions are completely different when separated from their organisms and examined in a laboratory from when they are placed in their right context and in "working" condition.

These observations are indeed expressed in ecosystem ecology — "everything is linked to everything" or "the whole is greater than the sum of the parts" (Pascal and repeated by Allen & Starr, 1982). These expressions imply that it may be possible to examine the parts by reduction to simple relationships, but when the parts are put together they form a whole that behaves differently from the sum of the parts. This statement requires a more detailed discussion of how an ecosystem works. The latter statement is correct because of the evolutionary potential that emerges from living systems. The ecosystem contains the possibility of becoming something different, that is, adapting and evolving. The evolutionary potential is linked to the existence of microscopic freedom, represented by stochasticity and nonaverage

behavior, resulting from the diversity, complexity, and variability of its elements.

Underlying the taxonomic classification is the microscopic diversity, which only adds to the complexity to such an extent that it will be completely impossible to cover all the possibilities and details of the observed phenomena. We attempt to capture at least a part of the reality using models. It is not possible to use one or a few simple relationships, but a model seems the only useful tool when we are dealing with irreducible systems. However, using one model is far from realistic. Using many models simultaneously to capture a more complete image of reality seems the only possible way to deal with complex living systems.

This has been acknowledged by holistic ecology or systems ecology, whereas the more reductionistic style of ecology attempts to understand ecological behavior by analysis of one or a few processes, which are related to one or two components. The results of analyses are expanded to be used in the more reductionistic approaches as a basic explanation of observations in real ecosystems, but such an extrapolation is often invalid and leads to false conclusions. Both analyses and syntheses are needed in ecology, and the analysis is a necessary foundation for the synthesis, but it may lead to wrong scientific conclusions to stop at the analysis. Analysis of several interacting processes may give a correct result of the processes under the analyzed conditions, but the conditions in ecosystems are constantly changing and even if the processes were unchanged (which they very rarely are), it is not possible to oversee the analytical results of so many simultaneously working processes. Our brain simply cannot calculate what will happen in a system where, for example, six or more interacting processes are working simultaneously.

So, reductionism does not consider that the:

1. Basic conditions determined by the external factors for our analysis are constantly changing (one factor is typically varied by an analysis, while all the others are assumed constant) in the real world and the analytical results are not valid in the system context.
2. Interaction from all of the other processes and components may change the processes and the properties of all biological components

significantly in the real ecosystem so the analytical results are invalid.

3. Direct overview of the many simultaneously working processes is not possible and wrong conclusions may result if an overview is attempted.

Therefore, a tool is needed to oversee and synthesize the many interacting processes in an ecosystem. The synthesis may just be "putting together" the various analytical results, but afterward we need to make changes to account for the fact that the processes are working together and become more than the sum of the parts. In other words, there is a synergistic effect or a symbiosis. In Chapter 6, Section 6.4, it was mentioned how important the indirect effects are compared to the direct effects in an ecological network and the emergence of network mutualism.

Modelling can be used as a synthesizing tool. It is our hope that a further synthesis of knowledge will enable us to attain a system-wide understanding of ecosystems and help us cope with the environmental problems that are threatening human survival.

A massive scientific effort is needed to teach scientists how to cope with ecological complexity or even with complex systems in general. Which tools should we use to attack these problems? How do we use the tools most efficiently? Which general laws are valid for complex systems with many feedbacks and particularly for living systems? Do all hierarchically organized systems with many hierarchically organized feedbacks and regulations have the same basic laws? What do we need to add to these laws for living systems?

Many researchers have advocated a holistic approach to ecosystem science (e.g., E. P. Odum, 1953; Ulanowicz, 1980, 1986, 1995). Holism is the description of the system level properties of an ensemble, rather than simply an exhaustive description of all the components. It is thought that by adopting a holistic viewpoint, certain properties become apparent and other behaviors that otherwise would be undetected become visible.

It is, however, clear from this discussion that the complexity of ecosystems has set the limitations for our understanding and for the possibilities of proper management. We cannot capture the complexity and all its details, but we can understand why ecosystems are complex and set up a realistic strategy for gaining sufficient knowledge about

the system — not knowing all the details, but still understanding and knowing the mean behavior and the important reactions of the system, particularly to specified impacts. It means that we can only try to reveal the basic properties behind the complexity.

We have no other choice than to go holistic. The results from the more reductionistic ecological tests are essential in our effort "to get to the root" of the system properties of ecosystems, but we need systems ecology, which consists of many new ideas, approaches, and concepts, to follow the path to the root of the basic system properties of ecosystems. In other words, we cannot find the properties of ecosystems by analyzing all the details because there are simply too many, but we can try to reveal the system properties of ecosystems by examining the entire system.

The number of feedbacks and regulations is extremely high, which makes it possible for the living organisms and populations to survive and reproduce in spite of changes in external conditions.

These regulations correspond to levels 3 and 4 in Table 10.1. Numerous examples can be found in the literature. If the actual properties of the species are changed, then the regulation is called adaptation. Phytoplankton, for instance, is able to regulate its chlorophyll concentration according to available solar radiation. If more chlorophyll is needed because the radiation is insufficient to guarantee growth, then more chlorophyll is produced by the phytoplankton. The digestion efficiency of the food for many animals depends on the abundance of food. The same species may be a different size in different environments, depending on what is most beneficial for survival and growth. If nutrients are scarce, then phytoplankton becomes smaller and vice versa. In this latter case, the change in size is a result of a selection process, which is made possible because of the distribution in size.

The feedbacks are constantly changing, that is, the adaptation itself is adaptable because if a regulation is insufficient, another regulation process higher in the hierarchy of feedbacks (see Table 10.1) will take over. The change in size within the same species is limited. When this limitation has been reached, other species will take over. This implies that the processes and the components, as well as the feedbacks, can be replaced, if needed, to achieve better utilization of the available resources.

Three different concepts have been used to explain the functioning of ecosystems:

1. The individualistic or Gleasonian concept assumes populations respond independently to an external environment.

2. The superorganism or Clementsian concept views ecosystems as organisms of a higher order and defines succession as ontogenesis of this superorganism (Margalef, 1968, 1991). Ecosystems and organisms are different in one important aspect. Ecosystems can be dismantled without destroying them; they are just replaced by others, such as agroecosystems, human settlements, or other succession states. Patten (1981) pointed out that the indirect effects in ecosystems are significant compared to the direct ones, while in organisms, the direct linkages are most dominant. An ecosystem has more linkages than an organism, but most of them are weaker. This makes the ecosystem less sensitive to the presence of all the existing linkages. It does not imply that the linkages in ecosystems are insignificant and do not play a role in ecosystem behavior. The ecological network is of great importance in an ecosystem, but the many and indirect effects give the ecosystem buffer capacities to deal with minor changes.
The description of ecosystems as superorganisms therefore seems insufficient.

3. The hierarchy theory (Allen & Star, 1982) insists that the higher level systems have emergent properties that are independent of the properties of their lower level components. This compromise between the two other concepts seems consistent with our observations in nature.

The hierarchical theory is a very useful tool to understand and describe complex "medium number" systems, such as ecosystems (O' Neill et al., 1975).

During the last decades, there has been a debate over whether "bottom-up" (limitation by resources) or "top-down" (control by predators) effects primarily control system dynamics. The conclusion of this debate seems that *both* effects control the dynamics of the system. Sometimes the effect of the resources may be most dominant, sometimes the higher levels control the dynamics of the system, and sometimes both effects determine the dynamics of the system. This conclusion is nicely presented in *Plankton Ecology* by Sommer (1989).

The ecosystem and its properties emerge as a result of many simultaneous and parallel focal-level processes influenced by even more remote environmental features. It means that the ecosystem will be seen by an observer to be factorable into levels. Features of the immediate environment are enclosed in entities of yet a larger scale and so on. This implies that the environment of a system includes historical factors, as well as immediately cogent ones (Patten, 1981; Jørgensen & Fath, 2004b). The history of the ecosystem and its components is important for the behavior and further development of the ecosystem. This is one of the main ideas behind Patten's indirect effects; the indirect effects account for the "history," while the direct effects only reflect the immediate interactions. The importance of the history of the ecosystem and its components emphasizes the need for a dynamic approach and supports the idea that we will never observe the same situation in an ecosystem twice. The history will always be "between" two similar situations. Therefore, as previously mentioned, the equilibrium models may fail in their conclusions, particularly when we want to look into reactions on the system level.

10.2.1. Ecosystems Show a High Degree of Heterogeneity in Space and Time

An ecosystem is a very dynamic system. All of its components, particularly the biological ones, are steadily changing and their properties are steadily modified, which is why an ecosystem never returns to the same situation. Every point is different from any other point, offering different conditions for the various life forms. This enormous heterogeneity explains why biodiversity is so plentiful on Earth. There is an ecological niche for "everyone" and "everyone" may be able to find a niche where he best fits to utilize the resources.

Ecotones, the transition zones between two ecosystems, offer a particular variability in life conditions, which often results in a particular richness of species diversity. Studies of ecotones have recently drawn much attention from ecologists because they have pronounced gradients in the external and internal variables. This gives a clearer picture of the relation between external and internal variables.

Margalef (1991) claimed that ecosystems are anisotropic; they exhibit properties with different values when measured along axes in different

directions. This means that the ecosystem is not homogeneous in relation to properties concerning matter, energy, and information, and that the entire dynamics of the ecosystem work toward increasing these differences.

These variations in time and space make it particularly difficult to model ecosystems and to capture their essential features. However hierarchy theory applies these variations to develop a natural hierarchy as a framework for ecosystem descriptions and theory. The strength of hierarchy theory is that it facilitates the studies and modelling of ecosystems.

10.2.2. Ecosystems and Their Biological Components Evolve Steadily and Over the Long Term Toward Higher Complexity

Darwin's theory describes the competition among species and states that those species best fitted to the prevailing conditions in the ecosystem will survive. Darwin's theory can, in other words, describe the changes in ecological structure and the species composition, but cannot directly be applied quantitatively in ecological modelling (see the next section).

All species in an ecosystem are confronted with the question: How is it possible to survive or even grow under the prevailing conditions? The prevailing conditions are considered as all factors that influence the species, that is, all external and internal factors including those originating from other species. This explains coevolution, as any change in the properties of one species will influence the evolution of the other species. The environmental stage on which the selection plays out is comprised of all the interacting species, each influencing another.

All natural external and internal factors of ecosystems 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 under the present conditions. There is a wide spectrum of species representing different combinations of properties available for the ecosystem. The question remains: 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 the conditions one time step further, two time steps further,

and so on? The necessity in Monod's (1971) sense is given by the prevailing conditions — species must have genes or phenotypes (properties) that match these conditions to be able to survive. But the natural external factors and the genetic pool available for the test may change randomly or by "chance."

Steadily, new mutations (misprints are produced accidentally) and sexual recombinations (genes are mixed and shuffled) emerge and steadily produce new material to be tested by the question: Which species are best fitted under the prevailing conditions?

These ideas are illustrated in Figure 10.1. The external factors are steadily changed and some even relatively fast and partly at random, such as the meteorological or climatic factors. The species within the system are selected among the species available and represented by the genetic pool, which again is slowly, but surely, changed randomly, or by chance. The selection in Figure 10.1 includes level 4 of Table 10.1. It is a selection of the organisms that possess the properties best fitted to the prevailing organisms according to the frequency distribution.
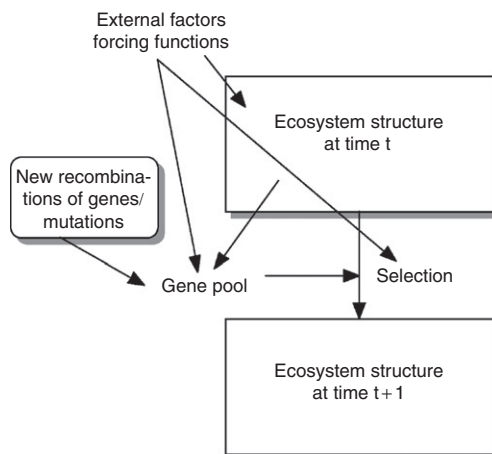

FIGURE 10.1 Conceptualization of how the external factors steadily change the species composition. The possible shifts in species composition are determined by the gene pool, which is steadily changed due to mutations and new sexual recombinations of genes. The development is, however, more complex. This is indicated by arrows from " structure" to "external factors" and "selection" to account for the possibility that the species can modify their own environment and their own selection pressure along with an arrow from "structure" to "gene pool" to account for the possibilities that species can, to a certain extent, change their own gene pool.

Ecological development includes the changes over time in nature caused by the dynamics of the external factors, which gives the system sufficient time to modify its structure and behavior.

Evolution, on the other hand, is related to the genetic pool. It is the result of the relation between the dynamics of the external factors and the dynamics of the genetic pool. The external factors steadily change the conditions for survival, and the genetic pool steadily comes up with new solutions to the problem of survival.

Species are continuously tested against the prevailing conditions (external as well as internal factors) and the better they fit, the better they are able to maintain and even increase their biomass. The specific rate of population growth may even be used as a measure for fitness (Stenseth, 1986). But the property of fitness must be heritable to have any effect on the species composition and the ecological structure of the ecosystem in the long run.

Natural selection has been criticized for being a tautology: Fitness is measured by survival, therefore survival of the fittest means survival of the survivors. However, the entire Darwinian theory including the previously listed three assumptions, cannot be conceived as a tautology, but may be interpreted as follows: Species offer different solutions to survive under prevailing conditions, and the species that have the best combinations of properties to match the conditions also have the highest probability of survival and growth.

Human changes in external factors, that is, anthropogenic pollution, have created new problems because new genes, and hence organisms, fitted to these changes do not develop overnight, while most natural changes have occurred many times previously and the genetic pool is therefore prepared and fitted to meet the natural changes. Life is able to meet most natural changes, but not all of the human changes, because they are new and untested in the ecosystem.

Evolution moves the system toward increasing complexity in the long run. Fossil records have shown a steady increase of species diversity. There may be destructive forces, such as pollution or natural catastrophes, for a short time, but the probability that (1) new and better genes are developed and (2) new ecological niches are utilized will increase with time. The probability will even (again excluding the short time perspective) increase faster and faster, as the probability is roughly

proportional to the amount of genetic material on which the mutations and new sexual recombinations can be developed.

It is equally important to note that a biological structure is more than an active nonlinear system. In the course of its evolution, the biological structure is continuously changed so that its structural map is modified. The overall structure thus becomes a representation of all the information received. Through its complexity, biological structure represents a synthesis of the information with which it has been in communication (Schoffeniels, 1976).

Evolution is maybe the most discussed topic in biology and ecology and millions of pages have been written about evolution and its ecological implications. Today, the facts of evolution are taken for granted and the interest has shifted to more subtle classes of fitness/selection; that is, toward understanding the complexity of the evolutionary processes. One of these classes concerns traits that influence not only the fitness of the individuals possessing them, but also the entire population. These traits overtly include social behaviors, such as aggression or cooperation, and activities that, through some modification of the biotic and abiotic environment feedback, affect the population at large, such as pollution and resource depletion.

It can be shown that many observations support the various selection models used to describe selection in nature. For example, kin selection has been observed in bees, wasps, and ants (Wilson, 1978). Prairie dogs endanger themselves (altruism) by conspicuously barking to warn fellow dogs of an approaching enemy (Wilson, 1978), and a parallel behavior is observed for a number of species.

Coevolution explains the interactive processes among species. It is difficult to observe coevolution, but it is easy to understand that it plays a major role in the entire evolution process. For example, coevolution of herbivorous animals and plants is an illustrative example. The plants develop toward better seed dispersal and a better defense toward herbivorous animals. In the latter case, selected herbivorous animals are able to cope with the defense. Therefore, the plants and the herbivorous animals will coevolve. Coevolution means that the evolution process cannot be described as reductionistic, but that the entire system is evolving. A holistic description of the system evolution is needed.

Having presented some main features of ecosystem development over time, the next crucial question should be: How can we account for these properties in modelling? Some preliminary results on how to consider levels 4–6 of dynamics (see Table 10.1) will be presented in the next section.

10.3. How to Construct Structurally Dynamic Models and Definitions of Exergy and Eco-exergy

If we follow the modelling procedure proposed in Figure 2.2, then a model that describes the processes in the focal ecosystem will be attained, but the parameters will represent the properties of the state variables as they exist in the ecosystem during the examination period. They are not necessarily valid for another period because we know that an ecosystem can regulate, modify, and change them if needed as a response to changes in the existing conditions determined by the forcing functions and the interrelations between the state variables. Our present models have rigid structures and a fixed set of parameters, so no changes or replacements of the components are possible. We need to introduce parameters (properties) that can change according to changing forcing functions and general conditions for the state variables (components) to optimize continuously the ability of the system to move away from thermodynamic equilibrium. So, we may hypothesize levels 5 and 6 in the regulation hierarchy shown in Table 10.1 that can be accounted for in our model by a current change of parameters, according to an ecological goal function. The idea is to test if a change of the most crucial parameters produces a higher goal function of the system and, if that is the case, to use that set of parameters.

The structurally dynamic model can account for the change in species composition as well as the ability of the species (i.e., the biological components of our models) to change their properties (i.e., to adapt to the existing conditions imposed on the species). The SDM is able to capture structural changes. They are called the next, or fifth, generation of ecological models to underline that they are radically different from previous modelling approaches and can do more; namely, describe changes in species composition.

It could be argued that the ability of ecosystems to replace present species with other (level 6 in Table 10.1), better fitted species, can be

considered by constructing models that encompass all actual species for the entire period that the model attempts to cover. This approach has two essential disadvantages. First, the model becomes very complex, because it will contain many state variables for each trophic level. Therefore, the model will contain many more parameters that have to be calibrated and validated and, as presented in Sections 2.5 and 2.6, this will introduce a high uncertainty to the model and render the application of the model very case specific (Nielsen 1992a,b). In addition, the model will still be rigid and not allow continuously changing parameters, even without changing the species composition (Fontaine, 1981).

Bossel (1992) used his six basic orientors, or requirements, to develop a system model, which can describe the system performance properly. The six orientors are:

1. Existence. The system environment must not exhibit any conditions that may move the state variables out of its safe range.
2. Efficiency. The exergy gained from the environment should exceed the exergy expenditure over time.
3. Freedom of action. The system reacts to the inputs (forcing functions) with a certain variability.
4. Security. The system has to cope with the different threats to its security requirement with appropriate but different measures. These measures either aim at internal changes in the system or at particular changes in the forcing functions (external environment).
5. Adaptability. If a system cannot escape the threatening influences of its environment, then the one remaining possibility consists of changing the system to cope better with the environmental impacts.
6. Consideration of other systems. A system must respond to the behavior of other systems. The fact that these other systems may be of importance to a particular system should be considered with this requirement.

Bossel (1992) applied maximization of a benefit or satisfaction index based upon balancing weighted surplus orientor satisfactions on a common satisfaction scale. The approach is used to select the model structure of continuous dynamic systems and is able to account for the ecological structural properties as presented in Table 10.1. This

approach seems very promising, but has unfortunately not been widely applied to ecological systems.

Straskraba (1979) used biomass maximization as a governing principle. His model computes the biomass and adjusts one or more selected parameters to achieve the maximum biomass at every instance. It has a routine that computes the biomass for all possible combinations of parameters within a given realistic range. The combination that gives the maximum biomass is selected for the next time step and so on. This is an example of an early structurally dynamic model.

Exergy has been used widely as a goal function in ecological models, and a few of the available case studies will be presented and discussed in this section. Exergy has two pronounced advantages as a goal function. (1) Exergy is defined far from thermodynamic equilibrium, and (2) it relates to the state variables, which are easily determined or measured, as opposed to being derived from the flows. As exergy is not a generally used thermodynamic function, we need to explain this concept before we can go any further.

Exergy expresses energy with a built-in measure of quality like energy. Exergy accounts for natural resources and can be considered as fuel for any system that converts energy and matter in a metabolic process (Schrödinger, 1944). Ecosystems consume energy, and an exergy flow through the system is necessary to keep the system functioning — living systems operate far-from-equilibrium. Exergy measures the distance from a reference condition in energy terms, as will be further explained in this section.

Exergy, Ex, is defined by the following equation:

$$Ex = T_o * NE = T_o * I = T_o * (S_{eq} - S) \tag{10.1}$$

where T_o is the temperature of the environment; I is the thermodynamic information, defined as NE; and NE is the negentropy of the system, that is, $= (S_{eq} - S) =$ the difference between the entropy for the system at thermodynamic equilibrium and the entropy at the present state.

Exergy differences can be reduced to differences of other, better known, thermodynamic potentials, which may facilitate the computations of exergy in some relevant cases.

As noted, the exergy of the system measures the contrast — it is the difference in free energy if there is no difference in pressure, as may

be assumed for an ecosystem — against the surrounding environment. If the system is in equilibrium with the surrounding environment, then the exergy is zero.

Since the only way to move systems away from equilibrium is to perform work on them, and since the available work in a system is a measure of the ability, we have to distinguish between the system and its environment or thermodynamic equilibrium. For ecosystems, the prebiotic "inorganic soup" has been used as the reference. Therefore it is reasonable to use the available work, that is, the exergy, as a measure of the distance from thermodynamic equilibrium.

Let us translate Darwin's theory into thermodynamics (Section 10.2), applying exergy as the basic concept. Survival implies biomass maintenance, and growth means biomass increase. It costs exergy to construct biomass and biomass therefore possesses exergy, which is transferable to support other exergetic (energetic) processes. Survival and growth can therefore be measured using the thermodynamic concept exergy, which may be understood as the free energy relative to the environment (Eq. 10.1).

Darwin's theory may therefore be reformulated in thermodynamic terms as follows: *The prevailing conditions of an ecosystem steadily change and the system will continuously select the species and thereby the processes that can contribute most to the maintenance or even growth of the exergy of the system.*

Ecosystems are open systems and receive an inflow of solar energy. The solar energy carries low entropy, while the radiation away from the ecosystem carries high entropy.

If the power of the solar radiation is W and the average temperature of the system is T_1, then the exergy gain per unit of time, ΔEx is:

$$\Delta Ex = T_1 * W\left(\frac{1}{T_0} - \frac{1}{T_2}\right), \tag{10.2}$$

where T_0 is the temperature of the environment and T_2 is the temperature of the sun. This exergy flow can be used to construct and maintain structure far away from equilibrium.

Notice that the thermodynamic translation of Darwin's theory requires that populations have the properties of reproduction, inheritance, and variation. The selection of the species that contributes most to the exergy of the system under the existing conditions requires that there are enough individuals with different properties that a selection

can take place; it means that the reproduction and the variation must be high and that once a change has taken place due to better fitness, it can be conveyed to the next generation.

Notice also that the change in exergy is not necessarily ≥ 0, it depends on the changes of the resources of the ecosystem. The proposition claims, however, that the ecosystem tendency is to move toward the highest possible exergy level under the given circumstances and with the available genetic and species pool (Jørgensen & Mejer, 1977, 1979). Compare Figure 10.2, where the nutrient concentrations of a lake ecosystem decrease and the exergy increases. It is not possible to measure exergy directly, but it is possible to compute it if the composition of the ecosystem is known. Jørgensen and Mejer (1979) showed, by the use of thermodynamics, that the following equation is valid for the components of an ecosystem:

$$Ex = RT \sum_{i=1}^{i=n} \left(C_i \ln \frac{C_i}{C_{eq,i}} - (C_i - C_{eq,i}) \right) \tag{10.3}$$

where R is the gas constant; T is the temperature of the environment (Kelvin); and C_i represents the ith component expressed in a suitable unit, (for phytoplankton in a lake, C_i could be milligrams of a focal nutrient in the phytoplankton per liter of lake water); $C_{eq,i}$ is the concentration of the ith 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 probability of forming a complex organic compound in an inorganic soup (at thermodynamic equilibrium). Morowitz (1968) calculated this probability and found that for proteins, carbohydrates, and fats, the
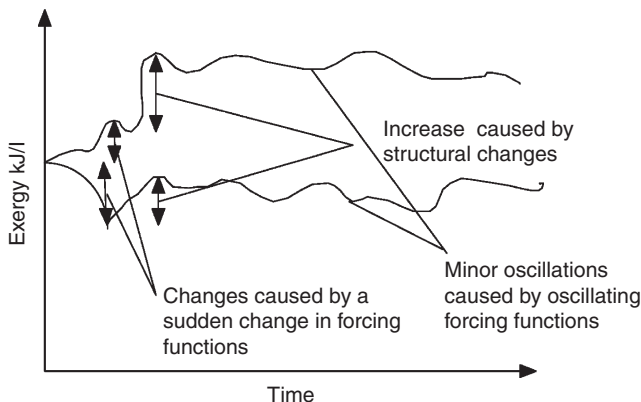

FIGURE 10.2 Exergy response to increased and decreased nutrient concentration.

concentration is about 10^{-86} µg/L, which may be used as the concentration at thermodynamic equilibrium.

The idea of the new generation of models presented here is to continuously locate a new set of parameters (limited for practical reasons to the most crucial, i.e., sensitive parameters) better fitted for the prevailing conditions of the ecosystem. "Fitted" is defined in the Darwinian sense by the ability of the species to survive and grow, which may be measured by the use of exergy (Jørgensen, 1982, 1986, 1988, 1990; Jørgensen & Mejer, 1977, 1979). Figure 10.3 shows the proposed
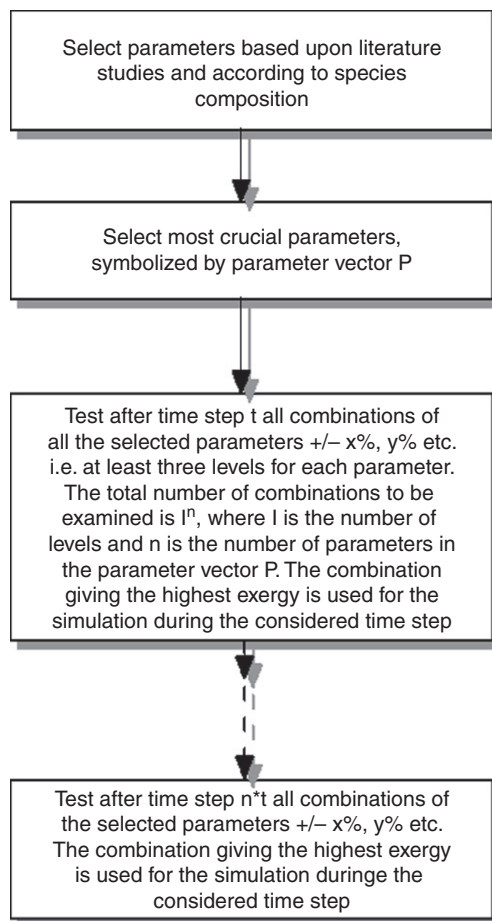

FIGURE 10.3 The procedure used for the development of SDMs.

modelling procedure, which has been applied in the cases presented in Sections 10.4–10.7.

Exergy has previously been tested as a "goal function" for ecosystem development (i.e., Jørgensen, 1986; Jørgensen & Mejer, 1979). However, in all these cases, the model applied did not include the "elasticity" of the system obtained by use of variable parameters; therefore the models did not reflect real ecosystem properties. A realistic test of the exergy principle would require the application of variable parameters.

Exergy is defined as the work the system can perform when it is brought into equilibrium with the environment or another well-defined reference state. If we presume a reference environment for a system at thermodynamic equilibrium — meaning that all the components are: (1) inorganic, (2) at the highest possible oxidation state signifying that all free energy has been utilized to do work, and (3) homogeneously distributed in the system (meaning no gradients) — then the situation illustrated in Figure 10.4 is valid. It is possible to distinguish between chemical exergy and physical exergy. The chemical energy embodied in organic compounds and biological structure contributes most to the exergy content of ecological systems.

Temperature and pressure differences between systems and their reference environments are small in contribution to overall exergy and, for present purposes, can be ignored. We will compute the exergy based entirely on chemical energy: $\Sigma_i(\mu_c - \mu_{c,o})N_i$, where i is the number of exergy-contributing compounds, and c and μ_c are the chemical potential relative to that at a reference inorganic state, $\mu_{c,o}$. Our (chemical) exergy index for a system will be taken with reference to the same system at the same temperature and pressure, but in the form of a prebiotic environment without life, biological structure, information, or organic molecules — the so called inorganic soup.

As $(\mu_c - \mu_{co})$ can be found from the definition of the chemical potential, replacing activities by concentrations we obtain the following expression for chemical exergy:

$$Ex = RT \sum_{i=1}^{i=n} C_i \ln \frac{C_i}{C_{eq,i}} \cdot [ML^2T^{-2}] \tag{10.4}$$

R is the gas constant, T is the temperature of the environment and system (Figure 10.4), c_i is the concentration of the ith component expressed in
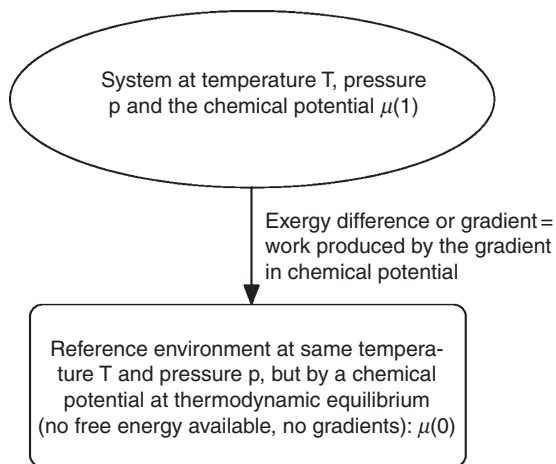
FIGURE 10.4 Illustration of the exergy concept used to compute the exergy index for an ecological model. Temperature and pressure are the same for the both the system and the reference state, which implies that only the difference in chemical potential can contribute to the exergy.

suitable units, $c_{i,eq}$ is the concentration of the ith component at thermodynamic equilibrium, and n is the number of components. The quantity $c_{i,eq}$ represents a very small, but nonzero, concentration (except for $i = 0$, which is considered to cover the inorganic compounds), corresponding to the very low probability of forming complex organic compounds spontaneously in an inorganic soup at thermodynamic equilibrium. The chemical exergy contributed by components in an open system is given by (Jørgensen & Meyer, 1979; Jørgensen, 1982, 2002):

$$Ex = RT \sum_{i=0}^{n} \left[c_i \ln \left(\frac{c_i}{c_{i,eq}} \right) - (c_i - c_{i,eq}) \right] \cdot \left[ML^2 T^{-2} \right] \tag{10.5}$$

The problem in applying these equations is related to the magnitude of $c_{i,eq}$. Contributions from inorganic components are usually very low and can in most cases be neglected. Exergy can be calculated from the elementary composition of the organisms. For our purposes, this is, however, unsatisfactory because compositionally similar higher and lower organisms would have the same exergy, which would not account for the exergy embodied in information. The problem of assessing $c_{i,eq}$ has been discussed and a possible solution proposed by Jørgensen (1997, 2002) and Jørgensen et al. (2000). The essential arguments are

repeated here. The chemical potential of dead organic matter, indexed $i = 1$, can be expressed from classical thermodynamics as:

$$\mu_1 = \mu_{1,eq} + RT \ln \frac{c_1}{c_{1,\,eq}}, [ML^2 T^{-2}\ moles^{-1}] \qquad (10.6)$$

where μ_1 is the chemical potential. The difference $\mu_1 - \mu_{1,eq}$ is known for detritus organic matter, which is a mixture of carbohydrates, fats, and proteins.

By using this particular exergy based on the same system at thermodynamic equilibrium as a reference, the eco-exergy becomes dependent only on the chemical potential of the numerous biochemical components.

It is possible to distinguish in Eq. (1) between the contribution to the eco-exergy from the information and from the biomass. We define p_i as c_i/A, where:

$$A = \sum_{i=1}^{n} c_i \qquad (10.7)$$

is the total amount of matter density in the system. With introduction of this new variable, we get:

$$Ex = A\,RT \sum_{i=1}^{n} p_i \ln \frac{p_i}{p_{io}} + A \ln \frac{A}{A_o} \qquad (10.8)$$

As $A \approx A_o$, eco-exergy becomes a product of the total biomass A (multiplied by RT) and Kullback measure:

$$K = \sum_{i=1}^{n} p_i \ln \left(\frac{p_i}{p_{io}} \right) \qquad (10.9)$$

where p_i and p_{io} are probability distributions, *a posteriori* and *a priori* to an observation of the molecular detail of the system. It means that K expresses the amount of information that is gained as a result of the observations. For different organisms that contribute to the eco-exergy of the ecosystem, the eco-exergy density becomes c RT ln (p_i/p_{io}), where c is the concentration of the considered organism. RT ln (p_i/p_{io}), denoted β, is found by calculating the probability to form the considered organism at thermodynamic equilibrium, which would require that organic matter is formed and that the proteins (enzymes) controlling the life processes in the considered organism have the right amino

acid sequence. These calculations can be seen in Jørgensen and Svirezhev (2005). In the latter reference, the latest information about the β values for various organisms is presented (see Table 10.2). For humans, the β value is 2173, when the eco-exergy is expressed in detritus equivalent or 18.7 times as much, or 40635 kJ/g if the eco-exergy should be expressed as kJ and the concentration unit g/unit of volume or area. One hypothesis, apparently confirmed by observation, is that the β values increase as a result of evolution. To mention a few β values from Table 10.2: bacteria 8.5, protozoa 39, flatworms 120, ants 167, crustaceans 232, mollusks 232, fish 499, reptiles 833, birds 980, and mammals 2127. Evolution has resulted in an increasingly more effective transfer of what we could call the classical work capacity to the work capacity of the information. A β value of 2.0 means that the eco-exergy embodied in the organic matter and the information are equal. As the β values become much bigger than 2.0 the information eco-exergy becomes the most significant part of the eco-exergy of organisms.

In accordance with the previously presented interpretation of Eqs. (10.8) and (10.9), it is now possible to find the eco-exergy density for a model as:

$$\text{Eco-exergy density} = \sum_{i=1}^{i=n} \beta_i c_i \tag{10.10}$$

The eco-exergy due to the "fuel" value of organic matter (chemical energy) is about 18.7 kJ/g (compared with coal: about 30 kJ/g and crude oil: 42 kJ/g). It can be transferred to other energy forms, such as mechanical work directly, and be measured by bomb calorimetry, which requires destruction of the sample (organism). The information eco-exergy = $(\beta - 1) \times$ biomass or density of information eco-exergy = $(\beta - 1) \times$ concentration. The information eco-exergy controls the function of the many biochemical processes. The ability of a living system to dowork is contingent upon its functioning as a living dissipative system. Without the information eco-exergy, the organic matter could only be used as fuel similar to fossil fuel. Because of the information eco-exergy, organisms are able to make a network of the sophisticated biochemical processes that characterize life. The eco-exergy (of which the major part is embodied in the information) is a measure of the organization (Jørgensen & Svirezhev,

Table 10.2   ß values = Exergy Content Relatively to the Exergy of Detritus

Early Organisms	Plants		Animals
Detritus		1.00	
Virus		1.01	
Minimal cell		5.8	
Bacteria		8.5	
Archaea		13.8	
Protists	Algae	20	
Yeast		17.8	
		33	Mesozoa, Placozoa
		39	Protozoa, amoebae
		43	Phasmida (stick insects)
Fungi, molds		61	
		76	Nemertina
		91	Cnidaria (corals, sea anemones, jelly fish)
	Rhodophyta	92	
		97	Gatroticha
Porifera, sponges		98	
		109	Brachiopoda
		120	Platyhelminthes (flatworms)
		133	Nematoda (round worms)
		133	Annelida (leeches)
		143	Gnathostomulida
	Mustard weed	143	
		165	Kinorhyncha
	Seedless vascular plants	158	
		163	Rotifera (wheel animals)
		164	Entoprocta
	Moss	174	
		167	Insecta (beetles, fruit flies, bees, wasps, bugs, ants)
		191	Coleodiea (Sea squirt)
		221	Lepidoptera (buffer flies)
		232	Crustaceans, Mollusca, bivalvia, gastropodea
		246	Chordata
	Rice	275	
	Gynosperms (incl. pinus)	314	
		322	Mosquito
	Flowering plants	393	
		499	Fish
		688	Amphibia
		833	Reptilia
		980	Aves (birds)
		2127	Mammalia
		2138	Monkeys
		2145	Anthropoid apes
		2173	*Homosapiens*

2005). This is the intimate relationship between energy and organization that Schrödinger (1944) was struggling to find.

Eco-exergy is a result of copying again and again in a long chain of copies where only minor changes are introduced for each new copy. The energy required for the copying process is very small, but it requires a lot of energy to come to the "mother" copy through evolution from prokaryotes to human cells. To cite Margalef (1969, 1991, 1995) in this context:

> evolution provides for cheap — unfortunately often in exact — copies of messages or pieces of information.

The information concerns the degree of uniqueness of entities that exhibit one characteristic complexion that may be described.

Eco-exergy has successfully been used to develop structurally dynamic models in 21 case studies so far. The eco-exergy goal function is found using Eq. (10.10), while the β values are found using Table 10.2.

The application is based on what may be considered thermodynamic translation of survival of the fittest. Biological systems have many possibilities for moving away from thermodynamic equilibrium, and it is important to know along which pathways among the possibilities a system will develop. This leads to the following hypothesis, which is sometimes denoted the ecological law of thermodynamics (Jørgensen & Fath, 2004b). If a system receives an input of exergy, then it will utilize this exergy to perform work. The work performed is first applied to maintain the system (far) away from thermodynamic equilibrium where exergy is lost by transformation into heat at the temperature of the environment. If more exergy is available, then the system is moved further away from thermodynamic equilibrium, which is reflected in growth of gradients. If more than one pathway to depart from equilibrium is offered, then the one yielding the highest eco-exergy storage (denoted Ex) will tend to be selected. In other words, among the many ways for ecosystems to move away from thermodynamic equilibrium, the one maximizing dEx/dt under the prevailing conditions will have a propensity to be selected.

This hypothesis is supported by several ecological observations and case studies (Jørgensen & Svirezhev, 2005; Jørgensen & Fath, 2004; Jørgensen, 2008b). Survival implies maintenance of the biomass, and growth means increase of biomass and information. It costs exergy to

construct biomass and gain information and biomass and information possess exergy. Survival and growth can therefore be measured using the thermodynamic concept eco-exergy, which may be understood as the work capacity the ecosystem possesses.

10.4. Development of Structurally Dynamic Model for Darwin's Finches

The development of an SDM for Darwin's finches illustrates the advantages of SDMs very clearly (see details in Jørgensen & Fath, 2004). The model reflects the available knowledge, which in this case is comprehensive and sufficient to validate even the ability of the model to describe the changes in the beak size as a result of climatic changes, causing changes in the amount, availability, and quality of the seeds that make up the main food item for the finches. The medium ground finches, *Geospiza fortis,* on the island Daphne Major, were selected for this modelling case due to very detailed case-specific information found in Grant (1986). The model has three state variables: seed, Darwin's finches adult, and Darwin's finches juvenile. The juvenile finches are promoted to adult finches 120 days after birth. The mortality of the adult finches is expressed as a normal mortality rate plus an additional mortality rate due to food shortage and an additional mortality rate caused by a disagreement between bill depth and the size and hardness of seeds. Due to a particular low precipitation from 1977 to 1979, the population of the medium ground finches declined significantly and the beak size increased about 6% at the same time. An SDM was developed to describe this adaptation of the beak size due to bigger and harder seeds as a result of the low precipitation.

The beak depth can vary between 3.5 and 10.3 cm according to Grant (1986). The beak size is furthermore equal to the square root of D*H, where D is the diameter and H is the hardness of the seeds. Both D and H are dependent on the precipitation, particularly from January to April. The coordination or fitness of the beak size with D and H is a survival factor for the finches. The fitness function is based on the seed handling time and it influences the mortality as stated above, but it also impacts the number of eggs laid and the mortality of the juveniles. The growth rate and mortality rate of the seeds is dependent on the precipitation and the temperature, which are forcing functions known

as f(time). The food shortage is calculated from the food required by the finches (which is known according to Grant, 1986) and the actual available food according to the state function seed. How the food shortage influences the mortality of the adults and juveniles can be found in Grant (1986). The seed biomass and the number of finches are known as a function of time for the period 1975–1982 (Grant, 1986). The observations of the state variables from 1975 to 1977 were applied for calibration of the model, focusing on the following parameters:

1. The influence of the fitness function on: (a) the mortality of adult finches, (b) the mortality of juvenile finches, and (c) the number of eggs laid.
2. The influence of food shortage on the mortality of adult and juvenile finches is known (Grant, 1986). The influence is therefore calibrated within a narrow range of values.
3. The influence of precipitation on the seed biomass (growth and mortality).

All other parameters are known from the literature (Grant, 1986).

The eco-exergy density is calculated (estimated) as 275 × the concentration of seed + 980 × the concentration of finches (see Table 10.2). Every 15 days, it is decided if a feasible change in the beak size, taking the generation time and the variations in the beak size into consideration, will give a higher exergy. If it is feasible, then the beak size is changed accordingly. The modelled changes in the beak size were confirmed by the observations. The model results of the number of Darwin's finches are compared with the observations in Figure 10.5. The standard deviation between modelled and observed values was 11.6 %. The validation and the correlation coefficient, r^2, for modelled versus observed values, is 0.977. The results of a nonstructural dynamic model would not be able to predict the changes in the beak size, therefore giving values that are too low for the number of Darwin's finches because their beak would not adapt to the lower precipitation yielding harder and bigger seeds. The calibrated model not using the eco-exergy optimization for the SDMs in the validation period 1977–1982 resulted in complete extinction of the finches. A nonstructurally dynamic model — a normal biogeochemical model — could not describe the impact of the low precipitation, while the SDM gave an approximately correct number of finches and could describe the increase of the beak at the same time.
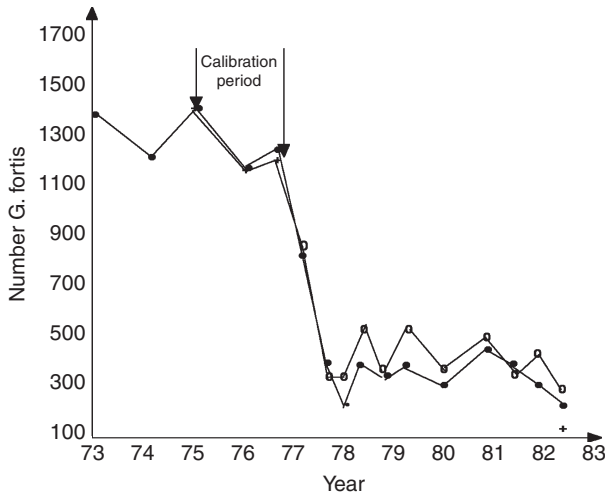
FIGURE 10.5 The observed number of finches (shown with solid dots) from 1973 to 1983, compared with the simulated result (shown with open circles). 1975 and 1976 were used for calibration and 1977 and 1978 for the validation. (The x-axis should indicate 1973 – 1983).

10.5. Biomanipulation

The eutrophication and remediation of a lacustrine environment do not proceed according to a linear relationship between nutrient load and vegetative biomass, instead they display a sigmoid trend with delay (as shown in Figure 10.6). The hysteresis reaction is completely in
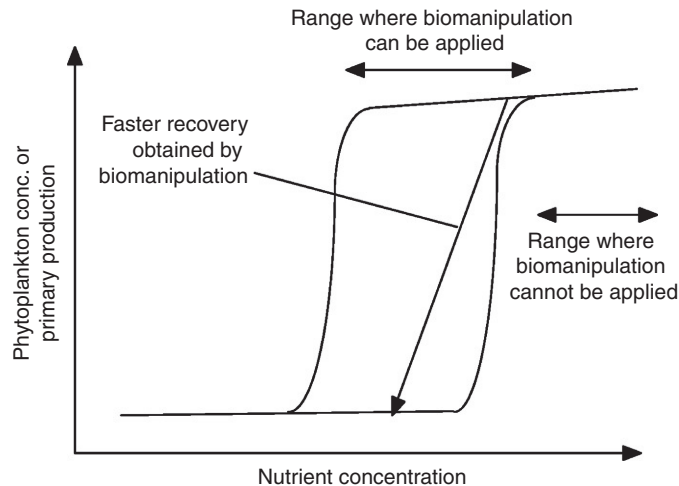
FIGURE 10.6 The hysteresis relation between nutrient level and eutrophication measured by the phytoplankton concentration is shown. The possible effect of biomanipulation is also shown. An effect of biomanipulation can hardly be expected above a certain concentration of nutrients, as indicated on the diagram. The biomanipulation can only give the expected results in the range where two different structures are possible.

accordance with observations (Hosper, 1989; Van Donk et al., 1989) and it can be explained by structural changes (De Bernardi, 1989; Hosper, 1989; Sas, 1989; De Bernardi & Giussani, 1995). A lake ecosystem shows a marked buffering capacity to increasing nutrient level that can be explained by an increasing removal rate of phytoplankton by grazing and settling. Zooplankton and fish abundance are maintained at relatively high levels under these circumstances. At a certain level of eutrophication, it is not possible for zooplankton to increase the grazing rate further, and the phytoplankton concentration will increase very rapidly by slightly increasing concentrations of nutrients. When the nutrient input is decreased under these conditions, a similar buffering capacity to variation is observed. The structure has now changed to a high concentration of phytoplankton and planktivorous fish, which causes a resistance and delay to a change where the second and fourth trophic levels become dominant again.

Willemsen (1980) distinguished two possible conditions:

1. A bream state characterized by turbid water, high eutrophication, low zooplankton concentration, absent of submerged vegetation, large amount of breams, while pike is hardly found at all.
2. A pike state, characterized by clear water and low eutrophication. Pike and zooplankton are abundant and there are significantly fewer bream.

The presence of two possible states in a certain range of nutrient concentrations may explain why biomanipulation has not always been used successfully. According to the observations referred to in the literature, success is associated with a total phosphorus concentration below 50 μg/L (Lammens, 1988) or at least below 100–200 μg/L (Jeppesen et al., 1990), while disappointing results are often associated with phosphorus concentration above this level of more than approximately 120 μg/L (Benndorf, 1987, 1990) with a difficult control of the standing stocks of planktivorous fish (Shapiro, 1990; Koschel et al., 1993).

Scheffer (1990) used a mathematical model based on catastrophe theory to describe these shifts in structure. However, this model does not consider the shifts in species composition, which is of particular importance for biomanipulation. The zooplankton population undergoes a structural change when we increase the concentration of

nutrients; for example, from a dominance of calanoid copepods to small caldocera and rotifers (according to De Bernardi & Giussani, 1995 and Giussani & Galanti, 1995). Hence, a test of SDMs could be used to give a better understanding of the relationship between concentrations of nutrients and the vegetative biomass and to explain possible results of biomanipulation. This section refers to the results achieved by an SDM that aims to understand the previously described changes in structure and species compositions (Jørgensen & De Bernardi, 1998). The applied model has 6 state variables: (1) dissolved inorganic phosphorus; (2) phytoplankton, phyt.; (3) zooplankton, zoopl.; (4) planktivorous fish, fish 1; (5) predatory fish, fish 2; and (6) detritus. The forcing functions are the input of phosphorus, in P, and the throughflow of water determining the retention time. The latter forcing function also determines the outflow of detritus and phyto-plankton. The conceptual diagram is similar to Figure 2.1, except that only phosphorus is considered as nutrient, as it is presumed that phosphorus is the limiting nutrient.

Simulations have been carried out for phosphorus concentrations in the inflowing water of 0.02, 0.04, 0.08, 0.12, 0.16, 0.20, 0.30, 0.40, 0.60, and 0.80 mg/L. For each of these cases, the model was run for any combination of a phosphorus uptake rate of 0.06, 0.05, 0.04, 0.03, 0.02, and 0.01 1/24h and a grazing rate of 0.125, 0.15, 0.2, 0.3, 0.4, 0.5, 0.6, 0.8, and 1.0 1/24h. When these two parameters were changed, simultaneous changes of phytoplankton and zooplankton mortalities were made according to allometric principles (Peters, 1983). The parameters for phytoplankton growth rate (uptake rate of phosphorus) and mortality and for zooplankton growth rate and mortality are made variable to account for the dynamics in structure.

The settling rate of phytoplankton was made proportional to the (length)^2. Half of the additional sedimentation when the size of phyto-plankton increases corresponding to a decrease in the uptake rate was allocated to detritus to account for resuspension or faster release from the sediment. A sensitivity analysis revealed that exergy is most sensitive to changes in these six selected parameters, which also represent the parameters that change significantly by size. The 6 levels selected from the previous list represent an approximate range in size for phytoplankton and zooplankton respectively.

For each phosphorus concentration, 54 simulations were carried out to account for all combinations of the two key parameters. Simulations over 3 years (1100 days) were applied to ensure that steady state, limit cycles, or chaotic behavior would be attained. This SDM approach presumed that the combination with the highest exergy should be selected to represent the process rates in the ecosystem. If exergy oscillates during the last 200 days of the simulation, then the average value for the last 200 days was used to decide on which parameter combination would give the highest exergy. The combinations of the two parameters, the uptake rate of phosphorus for phytoplankton and the grazing rate of zooplankton giving the highest exergy at different levels of phosphorus inputs, are plotted in Figures 10.7 and 10.8. The uptake rate of phosphorus for phytoplankton is gradually decreasing when the phosphorus concentration increases. As seen, the zooplankton grazing rate changes at the phosphorus concentration 0.12 mg/l from 0.4 1/24h to 1.0 1/24h, i.e. from larger species to smaller species, which is according to the expectations.

Figure 10.9 shows the eco-exergy, named on the diagram information, with an uptake rate according to the results in Figure 10.7 and a grazing rate of 1.0 1/24h (called information 1) and 0.4 1/ 24h (called information 2). Below a phosphorus concentration of 0.12 mg/L, information 2 is slightly higher, while information 1 is significantly higher above this concentration. The phytoplankton concentration increases
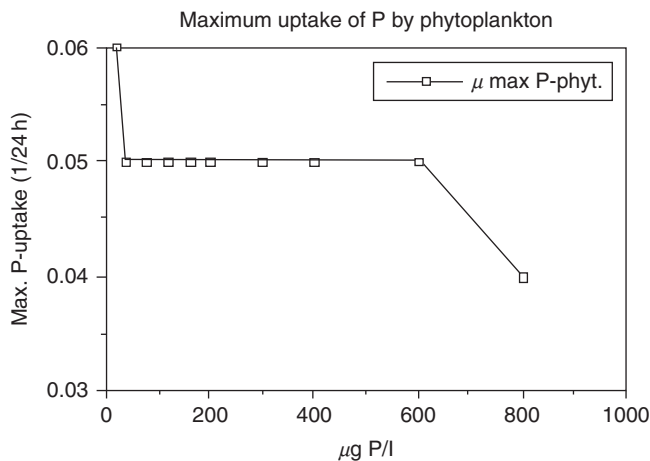

FIGURE 10.7 The maximum growth rate of phytoplankton obtained by the SDM approach is plotted versus the phosphorus concentration.
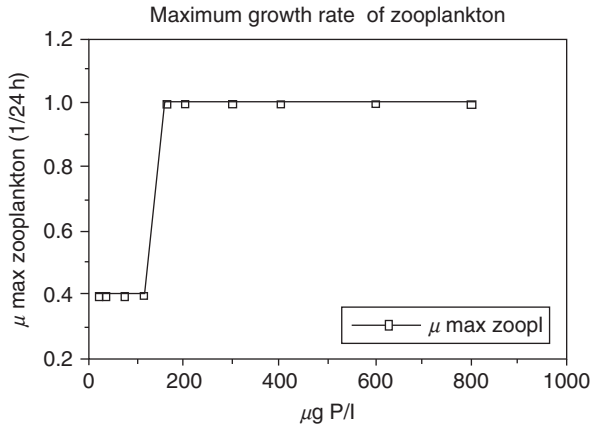
Maximum growth rate of zooplankton

FIGURE 10.8 The maximum growth rate of zooplankton obtained by the SDM approach is plotted versus the zooplankton concentration.
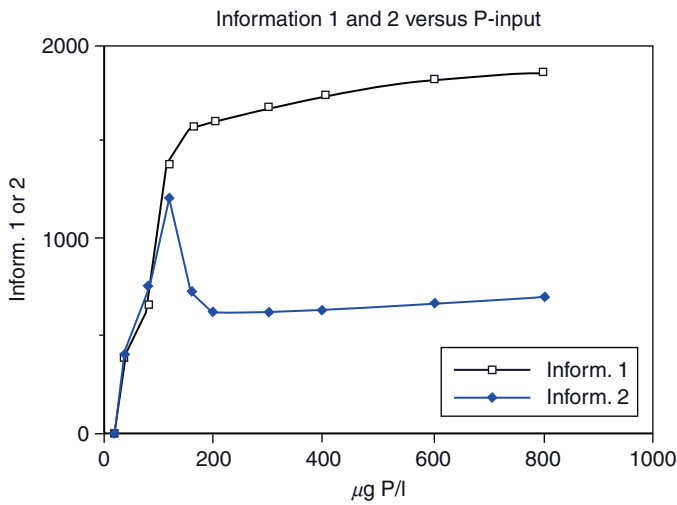
Information 1 and 2 versus P-input

FIGURE 10.9 The exergy is plotted versus the phosphorus concentration. Information 1 corresponds to a maximum growth rate of 1 1/24h and information 2 corresponds to a maximum zooplankton growth rate of 0.4 1/24h. The other parameters are the same for the two plots, including the maximum phytoplankton growth rate (uptake of P) is taken from Figure 10.7 as a function of the phosphorus concentration.

for both parameter sets with increasing phosphorus input, as shown Figure 10.10, while the planktivorous fish shows a significantly higher level by a grazing rate of 1.0 1/24h when the phosphorus concentration is ≥ 0.12 mg/L (= valid for the high exergy level). Below this concentration, the difference is minor. The concentration of fish 2 is higher for case 2 corresponding to a grazing rate of 0.4 1/24h for phosphorus concentrations below 0.12 mg/L. Above this value, the differences are minor, but at a phosphorus concentration of 0.12 mg/L the level is
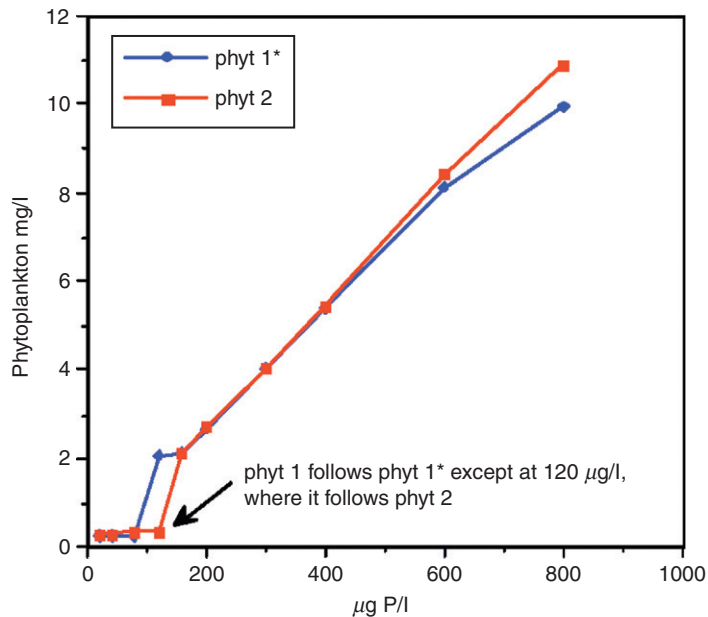
FIGURE 10.10 The phytoplankton concentration as a function of the phosphorus concentration for parameters corresponding to "information 1" and "information 2"; see Figure 10.9. The plot named "phyt 1*" coincides with "phyt 2," except for a phosphorus concentration of 0.12 mg/L, where the model shows limit cycles. At this concentration, information 1* represents the higher phytoplankton concentration, while information 2 represents the lower phytoplankton concentration. Notice that the structural dynamic approach can explain the hysteresis reactions.

significantly higher for a grazing rate of 1.0 1/24h, particularly for the lower exergy level, where the zooplankton level is also highest.

If it is presumed that eco-exergy can be used as a goal function in ecological modelling, then the results seem to explain why we observe a shift in grazing rate of zooplankton at a phosphorus concentration in the range of 0.1–0.15 mg/L. The ecosystem selects the smaller species of zooplankton above this level of phosphorus because it means a higher level of the eco-exergy, which can be translated to a higher rate of survival and growth. It is interesting that this shift in grazing rate produces only a small rise in the level of zooplankton, while the exergy index level rises significantly higher by this shift, which may be translated as survival and growth for the entire ecosystem. Simultaneously, a shift from a zooplankton, predatory fish dominated system to a system dominated by phytoplankton and particularly by planktivorous fish takes place.

It is interesting that the levels of eco-exergy and the four biological components of the model for phosphorus concentrations at or below 0.12 mg/L parameter combinations are only slightly different for the two parameter combinations. This explains why biomanipulation is more successful in this concentration range. Above 0.12 mg/L the differences are much more pronounced and the exergy index level is clearly higher for a grazing rate of 1.0 1/24h. It should therefore be expected that the ecosystem, after the use of biomanipulation, easily falls back to the dominance of planktivorous fish and phytoplankton. These observations are consistent with the general experience of success and failure of biomanipulation.

An interpretation of the results points toward a shift at 0.12 mg/L, where a grazing rate of 1.0 1/24h yields limit cycles. It indicates an instability and probably an easy shift to a grazing rate of 0.4 1/24, although the exergy level is on average highest for the higher grazing rate. A preference for a grazing rate of 1.0 1/24h at this phosphorus concentration should therefore be expected, but a lower or higher level of zooplankton is dependent on the initial conditions.

If the concentrations of zooplankton and fish 2 are low and high for fish 1 and phytoplankton, that is, the system is coming from higher phosphorus concentrations, then the simulation produces with high probability a low concentration of zooplankton and fish 2. When the system is coming from high concentrations of zooplankton and of fish 2, the simulation illustrates with high probability a high concentration of zooplankton and fish 2, which corresponds to an eco-exergy index level slightly lower than obtained by a grazing rate of 0.4 1/24h. This grazing rate will therefore still persist. As it also takes time to recover the population of zooplankton and particularly of fish 2; and in the other direction of fish 1, these observations explain the presence of hysteresis reactions.

This model is considered to have general applicability and has been used to discuss the general relationship between nutrient level and vegetative biomass and the general experiences by application of biomanipulation. When the model is used in specific cases, it may be necessary to include more details and change some of the process descriptions to account for the site specific properties, which is according to general modelling strategy. It could be considered to include two state variables

to cover zooplankton, one for the bigger and one for the smaller species. Both zooplankton state variables should have a current change of the grazing rate according to the maximum value of the goal function.

This model could probably also be improved by introducing size preference for the grazing and the two predation processes, which is in accordance with numerous observations. In spite of these shortcomings of the applied model, it has been possible to give a qualitative description of the response to changed nutrient level and biomanipulation, and even to indicate an approximately correct phosphorus concentration where the structural changes may occur. This may be due to an increased robustness by the SDM approach.

Ecosystems are very different from physical systems mainly due to their enormous adaptability. It is therefore crucial to develop models that are able to account for this property, if we want reliable model results. The use of goal functions such as eco-exergy to simulate fitness offers a good way to develop a new generation of models, which are able to consider the adaptability of ecosystems and to describe shifts in species composition. The latter advantage is probably the most important because a description of the dominant species in an ecosystem is often more essential than assessing the level of the focal state variables.

It is possible to model competition between a few species with very different properties, but the SDM approach makes it feasible to include more species even with only slightly different properties, which is impossible by the usual modelling approach (see also the unsuccessful attempt by Nielsen, 1992a,b). The rigid parameters of the various species make it difficult for the species to survive under changing circumstances. After some time, only a few species will still be present in the model, which is different in reality, where more species survive because they are able to adapt to the changing circumstances. It is important to capture this feature in our models. The SDMs seem promising when applied in lake management, as this type of model could explain our experiences with biomanipulation. It has the advantage compared with catastrophe models, which can also be used to explain success and failure of biomanipulation that it is able also to describe the shifts in species composition expressed by the size.

10.6. An Ecotoxicological Structurally Dynamic Models Example

The conceptual diagram of the ecotoxicological model used to illustrate an SDM is shown in Figure 10.11. This model is presented by Jørgensen (2009) in Devillers (2009). The model software STELLA was used for the model simulation results. Copper is an algaecide causing an increase in the mortality of phytoplankton (Kallqvist & Meadows, 1978) and a decrease in the phosphorus uptake and photosynthesis. Copper also reduces the carbon assimilation of bacteria. The literature changes these three model parameters: growth rate of phytoplankton,
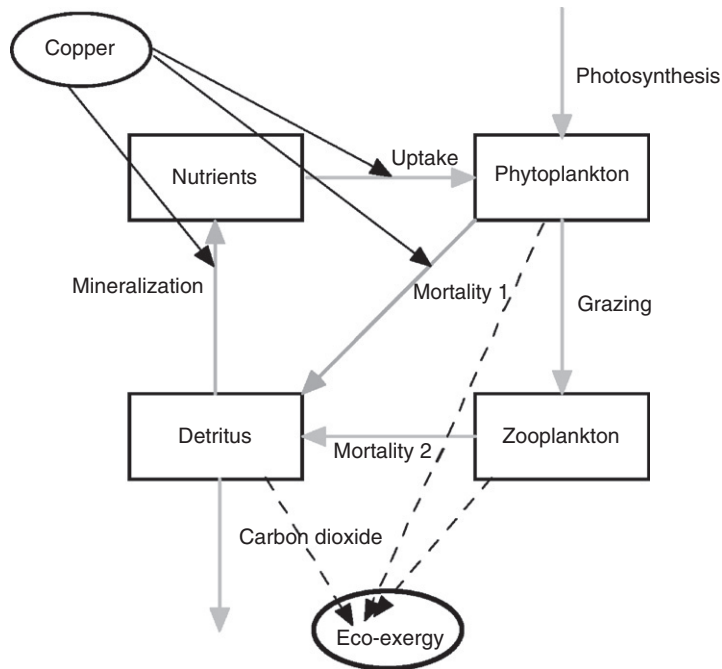

FIGURE 10.11 Conceptual diagram of an ecotoxicological model focusing on the influence of copper on the photosynthetic rate, phytoplankton mortality rate, and the mineralization rate. The boxes are the state variables, the thick gray arrows symbolize processes, and the thin black arrows indicate the influence of copper on the processes and the calculation of eco-exergy from the state variables. Due to the change in these three rates, it is advantageous for the zooplankton and the entire ecosystem to decrease its size. The model is therefore made structurally dynamic by allowing zooplankton to change their size and the specific grazing rate and the specific mortality rate according to allometric principles. The size yielding the highest eco-exergy is currently found.

mortality of phytoplankton, and mineralization rate of detritus with increased copper concentration (Havens, 1999). As a result, the zooplankton is reduced in size, which, according to allometric principles, means an increased specific grazing rate and specific mortality rate. It has been observed that the size of zooplankton in a closed system (e.g., a pond) is reduced to less than half the size at a copper concentration of 140 mg/m^3 compared with a copper concentration less than 10 mg/m^3 (Havens, 1999). In accordance with allometric principles (Peters, 1983), it would result in a more than doubled grazing and mortality rate.

The model shown in Figure 10.11 was made structurally dynamic by varying the zooplankton size and using an allometric equation to determine the corresponding specific grazing and mortality rates. This equation expresses that the two specific rates are inversely proportional to the linear size (Peters, 1983). Different copper concentrations from 10 mg to 140 mg/m^3 are found by the model in which zooplankton size yields the highest eco-exergy. In accordance to the presented SDM approach, it is expected that the size yielding the highest eco-exergy would be selected. The results of the model runs are shown in Figures 10.12, 10.13, and 10.14. The specific grazing rate, the size yielding the highest eco-exergy, and the eco-exergy are plotted versus the copper concentration in these three figures.
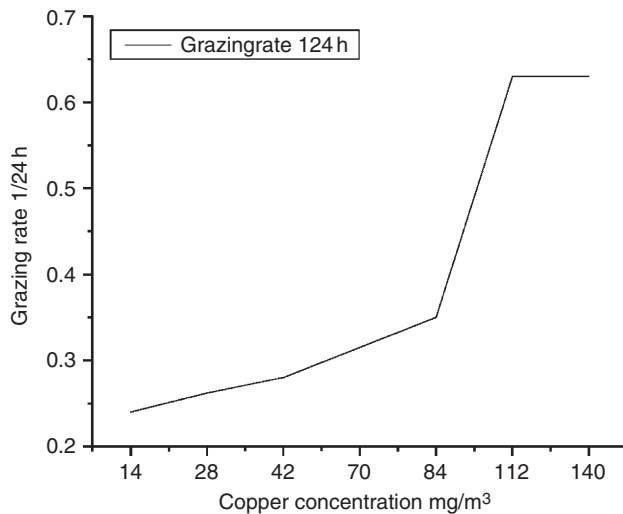

FIGURE 10.12 The grazing rate that yields the highest eco-exergy is shown at different copper concentrations. It increases more rapidly as the copper concentration increases. But at a certain level, it is impossible to increase the eco-exergy further by changing the zooplankton parameters because the amount of phytoplankton becomes the limiting factor for zooplankton growth.
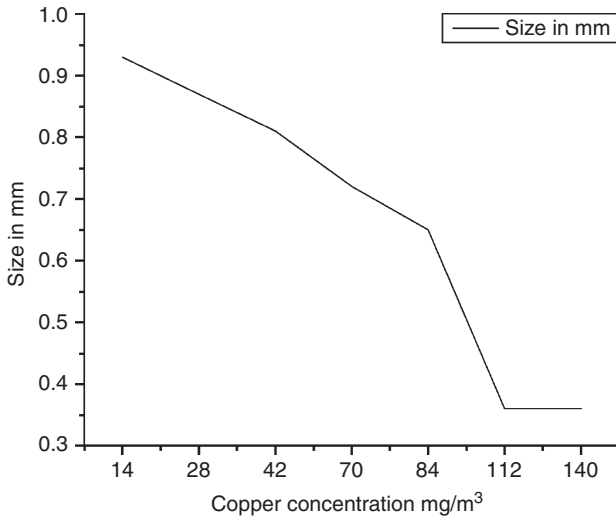
FIGURE 10.13 The zooplankton size that yields the highest eco-exergy is plotted versus the copper concentration. The size decreases more rapidly as the copper concentration increases. But at a certain level, it is impossible to increase the eco-exergy further by changing the zooplankton size because the amount of phytoplankton becomes the limiting factor for zooplankton growth.
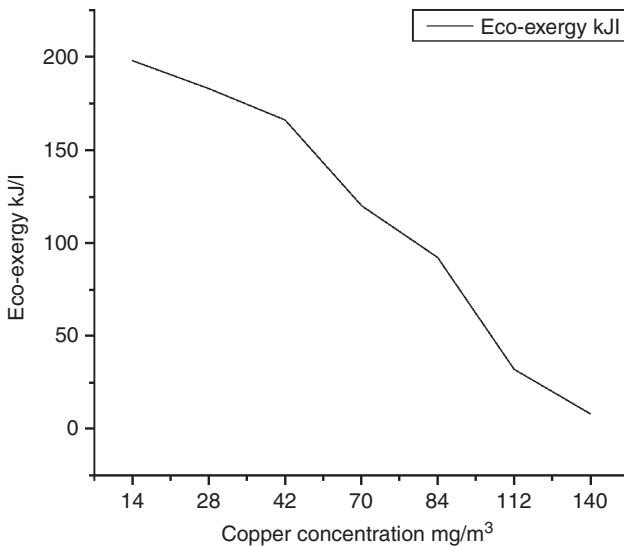

FIGURE 10.14 The highest eco-exergy obtained when varying the zooplankton size is plotted versus the copper concentration. The eco-exergy decreases almost linearly with increasing copper concentration. The discrepancy from a nearly linear plot may be due to model uncertainty, discontinuous change of the copper concentration, and the zooplankton size.

As expected, the eco-exergy, even at the zooplankton size, yields the highest eco-exergy that decreases with increased copper concentration due to the toxic effect on phytoplankton and bacteria.

From the literature, we see the selected size at 140 mg/m^3 is less than 0.4 mm, which is less than one half the size (0.93 mm) at 10 mg/m^3 (see

Figure 10.13). The eco-exergy decreases from 198 kJ/L at 10 mg/m^3 to 8 kJ/L at 140 mg/m^3. The toxic effect of the copper, in other words, results in an eco-exergy reduction to about 4% of the original eco-exergy level, which is a very significant toxic effect. If the zooplankton was not adaptable to the toxic effect by changing its size and the parameters, then the reduction in eco-exergy would have been even more pronounced already at a lower copper concentration. It is therefore important for the model results that the model is made structurally dynamic and accounts for the change of parameters when the copper concentration is changed.

Zooplankton is changing in size in the presented ecotoxicological case. It is an advantage that SDMs can approximately predict the changes in species' properties, but it is an even more important advantage that the state variables are predicted closer to the observations by the SDMs than by biogeochemical models because the organisms are able to adapt to the existing conditions. The toxic effect of copper would have been more pronounced if a nonstructurally dynamic model was applied, which would inevitably have illustrated concentrations of zooplankton that were too small.

Problems

1. Discuss why it would be beneficial to apply an SDM to describe the consequences of (a) global warming, (b) invading species, and (c) an oil spill.
2. Explain why it would not be beneficial to apply an SDM for construction of a subsurface wetland (e.g., the model of a subsurface wetland presented in Chapter 7)
3. Explain why it would advantageous to develop new model types that would be a hybrid of (a) IBM and SDMs, (b) ANN and SDMs, and (c) spatial models and SDMs.
4. Which factors determine the interval between two optimizations of eco-exergy? How could we quantify these factors?
5. Under what circumstances would it be sufficient to use optimization of biomass for the description of the structural changes instead of eco-exergy?