Modelling Biological Processes in the Aquatic Environment

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IIASA Working Paper

WP-79-020

March 1979

Fedra, K. (1979) Modelling Biological Processes in the Aquatic Environment. IIASA Working Paper. WP-79-020 Copyright © 1979 by the author(s). http://pure.iiasa.ac.at/1163/

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MODELLING BIOLOGICAL PROCESSES IN THE AQUATIC ENVIRONMENT
(with special reference to adaptation)

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March 1979
WP-79-20

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Preface

This report addresses some problems of biological aspects in modelling of aquatic ecosystems. The model representation of selected ecological processes in the aquatic environment is discussed with emphasis on biological complexity and an appropriate representation on a holistic level, which means under considerations of lumped and highly aggregated variables and features on a high level of abstraction. The inclusion of adaptation as a basic biological control mechanism in the representation of biological processes within the frame of ecosystem models is advocated and exemplified on the basis of recent literature examples and theoretical considerations.

This report was prepared as a contribution to IIASA's Resources and Environment Area Task 2 "Models for Environmental Quality Control and Management" and in particular to the subtask on "Hydrophysical and Ecological Models for Water Quality"; within the framework of these research tasks, the proposed concepts and modelling strategies should be critically investigated on the basis of actual field data and given application problems in order to estimate their use in the development and application of water quality models.

Abstract

Based on some of the most recent contributions to the field of biological modelling within the frame of ecosystems analysis, some aspects of modelling eco-physiological processes in the aquatic environment are discussed. First, a few rather general comments are made on the predictive capabilities of complex ecosystems models, and the related need to use more realistic and causal descriptions for various complex biological processes. Following this, some ideas and formulations, guided by the above principles, are compiled and discussed. The use of more realistic representations of biological processes, including time-varying parameters, is advocated, and several approaches are compared. Key factors such as temperature, light or nutrients are considered with regard to the basic biological internal control mechanism of adaptation. The inclusion of adaptation phenomena in the representation of, for example, effects of temperature, light dependency of primary production, or nutrient uptake kinetics, is described on different levels of mechanistic detail and complexity, and as a holistic feature. This is also an attempt to reduce dimensionality in complex models by increasing the realism in the description of functionally heterogeneous lumped compartments and thus avoiding separate detailed descriptions of their major component elements. In addition to the adaptation in single-species populations, the problem of community adaptation in multi-species populations, represented in most ecosystem models by lumped variables and averaged parameters, is considered in relation to environmental fluctuations and environmental uncertainty. A concept of environmental tracking is proposed, represented by the relation of parameter values to their governing input variables and state variables, as a major adaptive strategy for biotic systems.

Modelling Biological Processes in the Aquatic Environment

INTRODUCTION

Ecological systems are characterized by a large number of component elements and interrelations, by richness and variety. This complexity and diversity poses principle problems in a deterministic mathematical representation of such ecological systems. On the other hand ecological systems are also characterized by numerous self-organizing and -stabilizing mechanisms, which allow their persistence in a rather hostile - from a thermodynamic point of view - physical environment. These self-organizing capabilities are reflected in an often simple and easy to predict input response behaviour of ecological systems, at least within a specific range of input fluctuations.

Mathematical models of ecological systems are mainly descriptive and basically empirical - especially when they are designed for practical applications in the analysis, control and management of the environment. Although there has been a rapidly progressing development in the field of mathematical modelling, the outcome of most ecosystem models is rarely satisfying: it is either trivial or quite unrealistic compared to real-world observations. Considering the structure of mathematical representations of biological processes within the frame of ecosystem models, we have to admit that these representations are mainly extrapolations of basic physical, chemical and physiological processes and their application to compartments which include a large variety of functionally dissimilar components.

Without a doubt we need more realistic descriptions of the processes determining the behaviour of the compartments in ecosystem models if we want to obtain more reliable predictions, especially considering drastic changes in the input conditions.

The traditional approach to any refinement of our models would be an increase in the level of detail: more variables, more parameters, splitting up of compartments into their component elements. However, such a reductionistic approach is not only illusive from the technical point of view--considering data requirements and computer capacity--but also has to be questioned from a conceptual point of view. Describing and modelling ecological systems by using as many elements as possible is the same as describing the state of a volume of gas by attempting to solve Newtons's equations for all the component molecules. Not only would one have to know the initial state of all the component molecules, but it is also necessary to consider whether the information obtainable, at least in theory, is what we really want to know about the system. Generally we are looking for relevant macro-properties such as the temperature in the gas-example. However, ecological systems are much more complex than an ideal gas, and a basic lesson from systems science tells us that the systems behaviour is not simply the sum of the behaviours of the component elements. This requires the identification of appropriate holistic features of ecological systems for description and modelling. It is ill-conceived to attempt a description of a diverse community or trophic level--the standard biological compartment in an ecosystem model--in terms of the chemical or physiological properties of a single organism using the respective time-invariant parameters. Standard parameters used in ecological models such as maximum growth rates or uptake rates, half-saturation constants or any other rate constant for biological processes have, in fact, to be considered as time-varying, related to various state and input variables of a system.

Reconsidering traditional constants in ecological models, one has to be aware that they are either derived from single-species physiological experiments under steady-state conditions, or if determined from in-situ experiments, averaged over a certain range of measurements. One of the basic mechanisms in the change of a compartment's properties, as described by such parameters, is the mechanism of adaptation of biotic compartments or systems to input variations. Within a certain range of input or state changes, adaptation will result in the stabilization and persistence of certain features of the compartment or the system as a whole. And one of the basic strategies of adaptational responses to input changes will be found in a stragegy of environmental tracking, in other words, in the continuous adjustment of certain properties according to the pattern of environmental changes in time and space.

DESCRIPTION vs PREDICTION IN ECOSYSTEM MODELS

Leaving aside the pragmatic arguments against increasing complexity in ecosystem models, there is little doubt that only realistic, that is causal, descriptions can lead to reliable predictions of the future state of a system under a broad range of changed input conditions. In contradiction to this argument, almost all formulations of biological processes used in mathematical ecosystem models are at best semi-empirical, i.e., descriptive, but with little or no explanatory value. As we know, there is little problem in representing almost any given set of data with some mathematical expression without any regard to causal relations and - consequently--predictive power. On the other hand, we know that there is a remarkable trend for highly complex non-linear systems -- which ecological systems are -- to exhibit some kind of simple input response behaviour on a macroscopic level. This can be observed for a specific range of input conditions, the range to which a system is adapted. As a rule, this feature of complex systems allows us to overcome the problem of a realistic and causal description by using the empirically derived input-output relations. This is in general attempted through the use of lumped variables and consequently averaged parameters in such empirical or semi-empirical formulations. The formulation may thus be dependent on the level of averaging and lumping. Nihoul (1975) gives an interesting example from Kelly (1971): the overall behavior of a lumped species component of a system may be quite different from the response of individual species of organisms. Fig.1 shows the rate of nutrient uptake by algae as a function of temperature. Although the rate of each species is found to have a definite temperature optimum and limited range, the total rate increases exponentially within a much larger temperature range, integrating the succession pattern of the individual species.

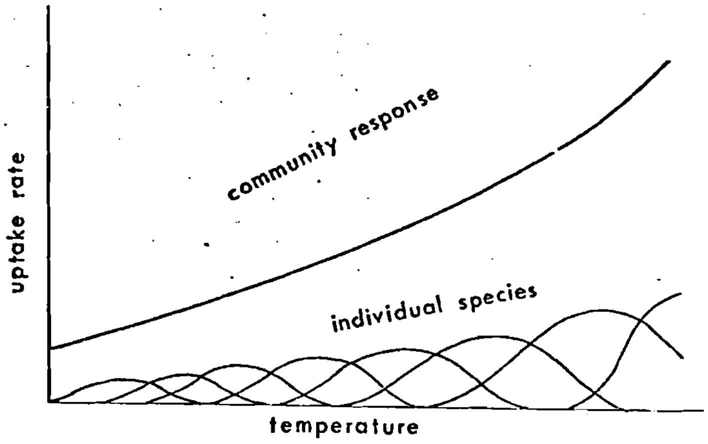

Figure 1. Rate of nutrient uptake as a function of temperature (after Kelly, 1976).

The argument of simple, often linear input response of complex systems is only true -- at least for systems where biotic compartments play a major role, as it is usually the case in ecosystem models -- within a limited, generally unknown range of input variation (and thus state space). Within this range, an empirical model may be descriptive as well as predictive. Outside the empirical range of input fluctuations, for which the parameters are estimated and the model is calibrated, the system may well be subject to changes not only in the parameter values, but also in its structure, so that predictions extrapolated from the input range are no longer reliable. However, this type of prediction would be most important for the model application in control and management problems.

Do let me stress again that if any, only rational models -- following the terminology of Lucan (1964) as discussed in Platt et al. (1977)--should be able to yield predictions outside the range of experimental or observational data. Rational in this context means: based on causal relations, highly structured, with a minimum of arbitrariness, and containing only parameters which are reasonably interpretable in terms of the real world system. Highly structured does not necessarily mean reductionistic with a lot of detail on a micro scale, but refers rather to the network aspect of ecological systems.

In this context it is worthwhile emphasizing the relationship of ecosystem models to experimental data and field observations. It is a rule of thumb--at least for models which are intended to quantitatively represent an ecological system -- that a model cannot be better than its data basis. Such a statement might be questioned in the context of more qualitative models, which are primarily designed to allow insight into the structural and functional relations of a system rather than in quantities. However, a twofold argument is implied: as a straight-forward consequence, a certain quantity and quality of data have to be available for calibration and validation of a model for a given level of accuracy, which is a rather trivial statement. In any case, very little experimental data have been collected with an underlying systems approach up to now. Most ecological studies have concentrated on a few selected variables or parameters, rendering an analysis of the interactions of different groups of values in a system rather difficult, as there are no synoptic data available. One can only plead for increased cooperation between the systems analysist or model builder and the field ecologist in this respect. On the other hand, as a consequence of the above claim for rational models, only magnitudes directly measurable in the system should be represented. Violating this rule will lead to identification problems. Advocating the use of holistic macro-properties -- for example, considering something such as the carrying capacity of a system for a given group -- might therefore lead to some difficulties, since the appropriate holistic properties or macro variables are in many cases not yet identified in a way which allows their direct measurement. In addition, one must keep in mind that the experimental data cannot definitely prove or rule out any theory in a model, if the respective process is not adequately formulated. We have also to keep in mind that many parameters in model representations are, in fact, functions of time and may vary considerably during a series of observations. This variation, of course, results in a "scattering" of the experimental data. Consequently, if the model representation using time-invariant parameters does not account for this variation, various curves could be drawn through the same set of data with equally good fits, rendering the test of validation of a model impossible.

When discussing the potential quality of ecosystem models and the prediction limitations, one has to consider the basic modelling strategy of lumping and averaging in relation to basic features of ecosystems such as spatial heterogeneity, functional dissimilarity and diversity, and non-linearities. The effect of certain time-varying inputs on biological processes, for example, is often estimated using an averaged constant input value for a given time step. An example might be the use of a square-wave function for diurnal irradiance, where irradiance I is set equal to the daily average I' for the total photoperiod (Di Toro et al., 1971). This averaging allows the analytical solution of the depth-time integral of the Steele-equation (see p. 29). Kremer and Nixon (1978) have shown that the error introduced by this averaging as compared to a numerical integration of the light/production equation over depth and time, using a realistic light pattern, is non-linear and strongly dependent on the value of the extinction coefficient. Severe discrepancy was found under conditions of clear water and high degrees of photo-inhibition.

Non-linearities in the photosynthesis-light equations are also discussed by Platt et al. (1977). By means of Fourier analysis, the authors conclude from a comparison of variabilities a stabilizing or buffering mechanism in the non-linear response of photosynthesis to light, damping out the environmental fluctuations. Under a fluctuating light regime the total production is less than it would be for the same total amount of energy supplied at constant rates. This effect is rather delicate: if the G^B versus I curve (see Fig.7) had upward or positive curvature rather than downward or negative curvature, the effect of the non-linearity would be completely different, namely destabilizing, enhancing the input fluctuations. Thus a particular non-linearity may be acting as a stabilizing or destabilizing factor in a system subjected to input fluctuations. For an example of stabilizing properties on the ecosystem level, which can be interpreted in the above sense, see Ott and Fedra (1977).

The general argument to be deduced is that any averaging which is part of our traditional compartment modelling approach, but implies linear relations --in case of non-linearities (and in fact all biological processes and interactions are non-linear) may lead to severe distortions in the predictions from a model. This effect of non-linearities together with the largely underestimated significance of spatial heterogeneity, the inherent functional dissimilarity of biotic compartments, and the difficulty to represent such features in a deterministic model cause further limitations on predictability. Considering, for example, the case of a non-linear concentration dependent interaction in a prey-predator system, the representation of the evolution of this system with spatially averaged concentrations will probably fail in the case of a contagious distribution (spatial heterogeneity), for the same basic reason as discussed above for time-heterogeneity. From this point of view, averaging and the implicitly assumed linearity of interactions are in fundamental discrepancy with the nature of biological data. Of course, there is a scale effect in the averaging problem; nevertheless, additional information, describing the range over which the averaging took place is required. A certain magnitude used to describe any property of a given system should not be represented by its mean value alone (which is what we do in deterministic models) but rather by the frequency distribution of the measure in the system which is, in fact, a probability distribution. This concept applies to parameter values as well as to all systems variables. Such an approach will allow consideration of the possible switch or trigger effects of the local or temporal coincidence of extreme values of variables or parameters. Such effects can result in the transition of a systems state to a new region of local stability or equilibrium. Consider, for example, the effect of temperature and dissolved oxygen in their non-linearily combined effect on a population of organisms with a given probability distribution of individual tolerance; coincidence of extreme values could cause a local mortality, triggering a possible collapse of large areas or even whole ecosystems. Such drastic effects could be observed in the case of benthic oxygen deficiency and mass mortality of the benthos in the North Adriatic Sea (Fedra et al., 1976, Ott & Fedra, 1977). A model representation of such phenomena would have to use interacting probability distributions instead of deterministic mean values, predicting the probability of a certain state rather than an averaged dynamic systems behaviour. Instead of a deterministic trajectory in state space over time one might expect dynamic multi-dimensional probability spaces representing a system's potential behaviour. However, the suggestion of such an approach must be seen as a program for future research rather than an actual possibility, since the basic and systematic work on such complex, non-linear stochastic models is far from being completely done.

An example of a stochastic approach to the dynamic modelling of an aquatic ecosystem is found in Tiwari et al. (1978). Besides the theoretical merits in such an approach, a remarkable difference could be documented between the deterministic simulation and the stochastic mean, generated by a Monte Carlo technique. Although the work of Tiwari et al. includes a number of simplifying assumtions, questionable from the biological point of view, it represents an attempt to account for one of the basic features of living systems, namely stochastic variability.

To summarize the above, the present state-of-the-art of modelling complex ecosystems allows a rather accurate description of observed behaviour in many cases. However, this is often due to highly sophisticated parameter estimation techniques, so that modelling has to be considered as more or less complicated curve fitting. However, models are also used as predictive tools, mainly for the management of water quality. From this point of view, the reliability of model predictions has to be questioned: uncertainties are always inherent in the underlying measurements, in the basic modelling strategy of lumping and averaging, and in the poor understanding and consequently poor representation of complex ecological processes. Recent concern about the quantification of model uncertainty (Di Toro and van Straten, in press) can be seen as a first step towards a new and more reliable generation of ecosystem models.

ADAPTATION: INTERNAL CONTROL IN BIOLOGICAL SYSTEMS

To give a definition for introductory purpose, the term adaptation will be used to subsum any deviation counteracting mechanisms, which allow any biotic system to damp its output or stabilize a given property under a certain range of input fluctuations. Adaptation is thus the major mechanism of persistence in a variable and uncertain environment. This broad concept of adaptation implies the existence of internal set points or standards in biosystems, lacking direct outside control, as is envisaged in the concept of the homeostatic plateau (Fig. 2b) and well documented on the organisms level of organization. An analogous concept will be used for the community and ecosystems level as well, related, to a certain

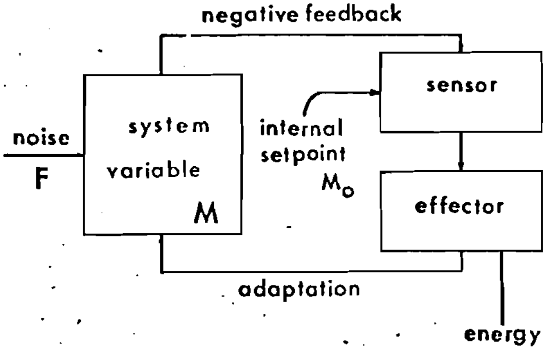

Figure 2. (a) Adaptation as a simplified control system.

degree, to a concept of local stability. However, the lack of outside control of the internal set points or standards to be maintained under fluctuating external conditions has to be seen in relation to the time scales applied: the independent set point on an ecological time scale has to be understood as a result of evolutionary changes and adjustments of the system. In this context, adaptation is found closely related to various aspects of stability and the resilience concept (Holling, 1973) as it subsums the mechanism involved. As much controversy in relation to "stability" is, at least partly, semantic in origin, a short definition of what stability is meant to be in this context is worthwhile to be attempted: with stability I mean the persistence of certain systems variables or structural features in a defined range under a regime of fluctuating input conditions.

This may well include systems subject to "predictable" fluctuations (Slobodkin and Sanders, 1969) as well as systems returning to their former state after certain types of perturbations. Thus two markedly different meanings of the term stability (Steele, 1974) can be included in the stability concept for the purpose of this discussion.

However, with regard to the adaptational mechanisms involved, a distinct relation to the predictability or the probability of certain input changes (environmental uncertainty) and the energetics of the response mechanisms can be noted and will be discussed more thoroughly in the following. Returning to the initial definition of adaptation, it might be convenient to consider two major aspects, namely a physiological and an ecological one. Although it will be attempted to show that both aspects can be described and modelled in the same terms with the same underlying rules and are therefore at least analogous, such a distinction might be necessary and if only to avoid the criticism of a "superorganisms" concept for ecosystems. The basic difference in ecosystems is the lack of heredity; of course there is something like the accumulation of information in terms of structure in at least some ecosystems, but this can only roughly be compared to the genetic information transmission.

Physiological adaptation will be used to describe input dependent changes in the physiology of an organism--if it fulfills the requirements of the above definition--which basically involves biochemical and behavioural mechanisms and is related to the organisms genetics. Ecological adaptation will be used to designate corresponding responses on the systems level, basically involving species and organisms interactions, often density dependent such as competition or predation. Of course both mechanisms, physiological as well as ecological, will inseparably contribute in an ecosystems behaviour; however, they could be distinguished from a conceptual point of view.

On the organisms level, phenotypic design and adaptation can be seen as being mainly means to one end: genetic transmission. However, the ecosystem is the environment for that process. And with regard to the vital necessity of predictability or a somewhat minimized environmental uncertainty for the relative success of the genetic transmission (and thus persistence) the single organism or species is forced into some kind of trade-off contribution to favourable conditions in the overall environment. Mutualism, in a very general sense, could thus be viewed as the species contribution to environment persistence. Nevertheless, many features of ecosystem adaptation can well be understood on a much simpler and more straightforward mechanistic level, without direct relation to evolutionary phenomena, keeping in mind that ecosystems as entities are not subject to evolution <u>sensu stricto</u> themselves, but are rather the reactors within which evolution takes place. Systems adaptation results often enough from the complex network nature of ecosystems, from the cybernetical consequences of tightly coupled nonlinear interrelations and feed-backs.

The spectrum of adaptation processes is fairly large; these can be found from the cellular to the ecosystem level with characteristic response times varying from a few minutes for adaptation in the enzyme machinery of bacteria to millions of years for evolutionary phenomena. With regard to ecosystem modelling, we will have to concentrate on the short- and medium-term phenomena on the individual to the ecosystem level of organization. Such adaptation processes are known, for example, for metabolism, reproduction strategies, or in species interactions. Relevant response time scales will range from a few minutes to a life span in larger vertebrates, which can be several years.

Adaptation in biosystems can be considered as an optimization problem. The available adaptational mechanisms or the possible range of adaptation of a given system could be seen as reflecting the system's--in slightly different terminology--hypothesis on environmental variability. This hypothesis is statistical in nature as a consequence of its evolutionary origin. Optimization now tends to increase the reliability of the "predictions" of environmental variability, because better predictions allow, for example, a decrease in the energetic costs for the adaptational machinery for a given level of error probability. The wider the confidence limits of the predictions for a given error probability, the more adaptational machinery the system needs to maintain in order to be "sure" to persist. To understand the goals of optimization, some consideration must be given to the energy flow aspect of living systems; it should be stressed here that "goals" as well as the above terminology should not be taken as part of a teleological determination approach: they are only a posteriori describing the direction and and results of the processes discussed. The essence of life can be seen in the progression of growth and reproduction or genetic transmission, and thus the creation and maintenance of living order. Energy transfers are the basic requirements of these dissipative processes, and antithermal maintenance is the main problem in living systems. Following Schrödinger (1944), continuous pumping out of "disorder" is necessary to maintain internal order against thermal vibrations. A thermodynamic order function is found in the maintenance to order ratio, in biosystems represented by the relation of total respiration to total biomass (R/B ratio). Related to absolute temperature, the R/B ratio becomes the ratio of entropy increase of maintenance to the entropy of ordered structure. A minimization of this R/B ratio (Margalef, 1968; Morowitz, 1968) or a maximization of the total energy flow itself (Odum, 1971)--both concepts are discussed in the theoretical literature--could be taken as the goal of optimization through adaptation. In this context adaptation has to be seen as the adjustment of the biosystems structure and function to variable input conditions in order to decrease or stabilize the structure specific costs of maintenance in a rather general sense. Homeostatic control with deviation counteracting responses or negative feed-back is responsible for the self-regulation. Referring to Fig. 2a, the set-point is given within the system as part of the systems hypothesis about environmental variability, so that self-correcting homeostasis lacks outside control on the ecological time scale.

A slightly different and very appealing concept for a goal function in evolving--and of course adapting--living systems can be seen in an increase in the probability of persistence. This concept is not so directly related to energy aspects alone; it also involves aspects of information transfer and perception in a very general sense, but the relations of these processes to energy are obvious. Various strategies of increasing the chances of persistence under changing environmental conditions are known and can be thought of, and will be discussed more extensively in the section on adaptation on the community level. However, all these strategies are related to energetic costs, which again results in an energy use optimization problem.

The input range, under which the homeostatic plateau for a given feature can be maintained, is the range of adaptation for the biosystem, reflecting the systems hypothesis on environmental variability. Outside this range positive feedback may result in rapid destabilization and destruction of the system (Fig. 2b). The position and range of the homeostatic plateau has to be seen as the result of the evolutionary adjustment of the system and its component elements to the long-term regime of environmental conditions and internal biological relations. It reflects the current "state of knowledge" of the system about its environment and its variability.

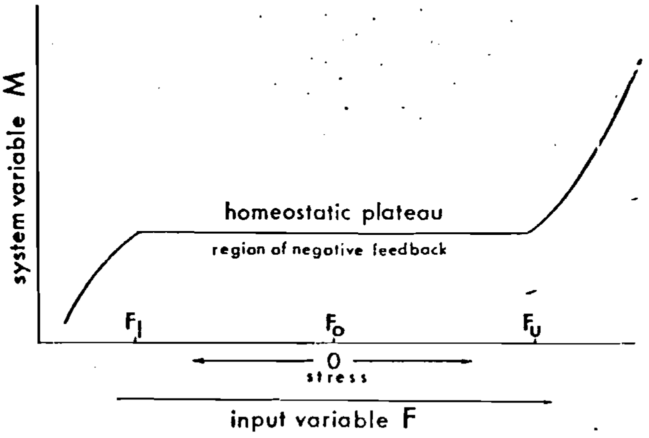

Figure 2b. Concept of the homeostatic plateau: maintenance through deviation-counteracting negative feed-back.

With regard to the mathematical formulation of processes that we are generally concerned with in ecological modelling, adaptation phenomena can in a first approach be reflected in time-varying parameters. Changes in the structure of a system --just consider the disappearance of a certain species or group, or the utilization of a new resource by another group--could also be represented with time-varying parameters. They must simply be temporarily assigned zero values, whenever a certain flow is interrupted.

Considering the traditional compartment approach in ecological modelling, all the state variables that might gain considerable importance within the system under changed input conditions must be included in the model structure *a priori*, necessitating a restriction on the descriptive case or requiring a lot of intuition in designing the model. The realization of structural changes in the model must then either be governed externally by an additional set of boundary conditions, or, much more appealing but perhaps not yet realistic, internally by the formulation of appropriate goal functions. This would allow automatic and internal adaptation of the model structure, given an appropriate computing scheme. A possible example would be prey selection, with different concentration-dependent predation or grazing efforts for different resources, coupled with, for example, a maximum egg production as a goal function. A variable food web structure should result, and the system could be allowed to "learn" an optimized strategy. Using a variable property of an element or a frequency distribution of such a property instead of *a priori* given structural alternatives in the traditional compartment approach would make such a model even more satisfactory from a conceptual point of view. A possible example might be the size distribution in a lumped phytoplankton community, adjusting to size dependent effects such as sinking rate, fecundity, metabolic rates or grazing pressure, in order to optimize the growth strategy of the population for maximum community production in an annual cycle. Such an approach, allowing for internal control explicitly would, in fact, represent structural self-organization in ecosystems (see Radtke and Straskraba, 1977 Straskraba, 1974, and Straskraba and Dvorakova, 1977).

Some recent considerations about structural organization in pelagic ecosystems can be found in Platt & Denman (1977). The authors propose a continuous, steady-state theory for the abundance of pelagic organisms as a function of body size. They conclude, on the basis of the allometric relations of metabolism and growth to weight, from the biomass flow in a community, where the individual organisms are assigned to one of a series of size classes, a regular decrease of total biomass in any size class with increasing size. A certain size dependent balance between catabolism and anabolism will establish a characteristic size distribution under steady-state conditions. With regard to the above example on structural self organization, such a theory can be helpful to use a normalized size-spectrum rather than a number of compartments, representing size classes in a model, to draw conclusions about the influence of functional dynamics on this size spectrum. Another recent example of a continuous model instead of the compartment approach is given in Thomann (1978). In a mass balance model for the bioaccumulation of toxic substances organism size is introduced as an additional variable. The model represents, in terms of the author, an ecological continuum through size dependency; the compartment approach would be a special case of the continuous model, where size dependence is viewed as a very approximate ordering of trophic position.

Without doubt, the above examples represent another step towards more realistic and general representations of ecosystems: using a continuum instead of the compartment approach might not only be less cumbersome in the computational analysis but also avoids one major source of uncertainty in the compartment approach, which is in the assumption of homogeneity within the compartment. Biological compartments in ecosystem models are always characterized by inherent functional dissimilarities of the components and additionally changing composition, and a reductionistic approach, increasing the number of compartments and treating as many as possible separately can hardly be considered an acceptable way for a solution. A more general approach, using holistic features of the elements involved, has to be found, and examples of such approaches will be given in the following sections.

EFFECTS OF TEMPERATURE ON THE ECTOTHERMIC METABOLISM

Among the physical factors in the aquatic environment, temperature has a major impact not only on chemical reactions in general, but especially on all forms of function in organisms. The inclusion of the magnitudes and complexities is therefore of crucial importance. Generally speaking, changes in temperature effect the biochemical structures and processes of organisms by changes in molecular kinetic energy. This results in changed reaction equilibria or changed reaction rates. The rate effect of temperature changes is based on the fraction of molecules in a given population with at least the minimum kinetic energy to be reactive and the related reaction velocity. Even a small change in absolute temperature can influence the proportion of reactive molecules to a considerable extent (Fig. 3).

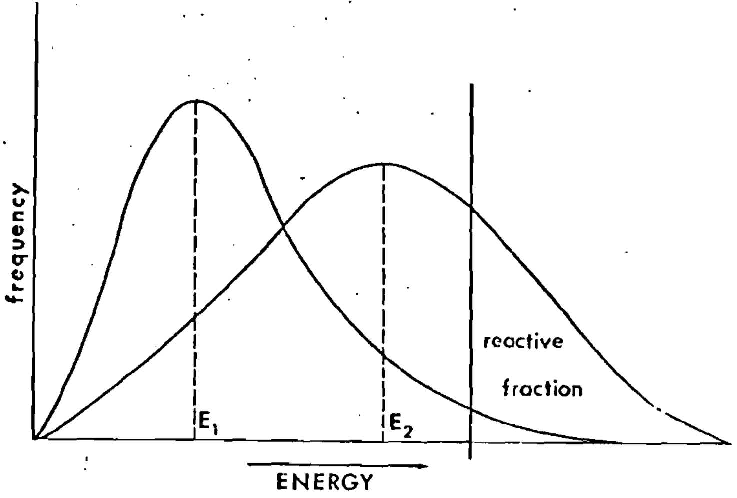

Figure 3. Energy distribution and reactive fraction of a population of molecules for two different temperatures (after Hochachka and Somero, 1973).

With regard to the effects of temperature changes on biotic elements of ecosystems, two terms are of basic importance:

a. the magnitude of the temperature change, and

b. the rapidity of the change, the time scale of variation.

In the aquatic environment, rapid temperature changes with characteristic time scales of less than a day may occur through weather phenomena (e.g., cloud cover), the related effects of wind mixing on thermally stratified water bodies, short-term changes in the inflow in reservoirs or estuaries, or the tidal cycle in coastal marine systems. Such short-term changes may exceed 15-20 °C, for example in the intertidal or in estuaries. Another time course of temperature change is due to the seasonal temperature cycle, most pronounced in mid-latitude, boreal regions of course, where the seasonal changes may well exceed 20 °C.

Following Arrhenius, the relation between temperature and a reaction rate K is described by

$$\frac{d}{dt} \ln K(T) = - \frac{E}{RT^2} , \tag{1.1}$$

where T is temperature in °Kelvin, R is the universal gas constant, and E represents activation energy. To a very good approximation (1.1) leads to an exponential relationship (Di Toro et al. 1977):

$$K(T) = K(20)\theta^{(T-20)} , \tag{1.2}$$

with temperature T in °C, and K(20) is the reaction rate K at 20 °C. (2.2) is consistent with the Q_{10} representation, since

$$\theta^{10} = Q_{10} . \tag{1.3}$$

Values of θ are given around 1.05 to 1.08 for plankton kinetics (Di Toro et al., 1977). Some alternative formulations are discussed by Steele and Mullin (1977). Starting with the allometric size-relationship of any metabolic rate M,

$$M = aB^b \quad , \qquad 0.6 \leq b \leq 1 \quad , \tag{1.4}$$

where B denotes biomass; effects of temperature are generally assumed to influence only the value of a, although some studies have indicated that b might also be a function of temperature (Ikeda, 1970, Champalbert and Gaudy, 1972). Temperature dependency of a is given by

$$a = cQ_{10}^{(0.1T-1)} \quad . \tag{1.5}$$

where c denotes the metabolic rate at 10°C for unit biomass, which is, in fact, a special case of the general representation given in (1.2). An alternative equation, preferred to Q_{10}, was proposed by McLaren (1963):

$$M = g(T + \gamma)^h \quad , \tag{1.6}$$

where g and h are constants governing the mean slope and curvature of the relation, and γ represents a "biological zero", which in effect shifts the temperature scale. However, with regard to adaptation, values of γ would still have to be determined as a function of time, since γ reflects the state of acclimatization.

A temperature reduction factor, based on the assumption of a more or less bell-shaped temperature dependency of respective coefficient rates which specify a temperature optimum for a given process, can also be found in the literature. Halfon and Lam (1978) use such a temperature factor in their description of primary production in terms of phosphorus uptake. A temperature optimum (T_{opt}) as well as an upper (T_u) and lower

(T_i) lethal temperature, is used for the description of the temperature factor TF (see Fig. 4):

$$\tau_1 = (T_u - T)/(T_u - T_{opt}) \qquad (1.7)$$

$$\tau_2 = (T - T_1)/(T_{opt} - T_1) \qquad (1.8)$$

$$TF = 2\left(\frac{1}{\tau_1} + \frac{1}{\tau_2}\right) \qquad (1.9)$$

The relation of primary production to TF is given by

$$G = G_{max} \cdot TF \cdot LF \quad , \qquad (1.10)$$

where G represents primary production in terms of phosphorus uptake, G_{max} its maximum value, and LF the combined influence of light and nutrients.

A similar approach is found in Najarian and Harleman (1975); their temperature-dependency curve for phytoplankton nutrient (nitrogen) uptake was fitted by Leonov (in preparation), and is also shown in Figure 4:

$$R_T = \frac{0.009(e^{0.288T} - 1)}{1 + .009\ e^{0.288T}} - \frac{7.94 \cdot 10^{-11}\ (e^{0.626T} - 1)}{1 + 7.94 \cdot 10^{-11}\ e^{0.626T}} \qquad (1.11)$$

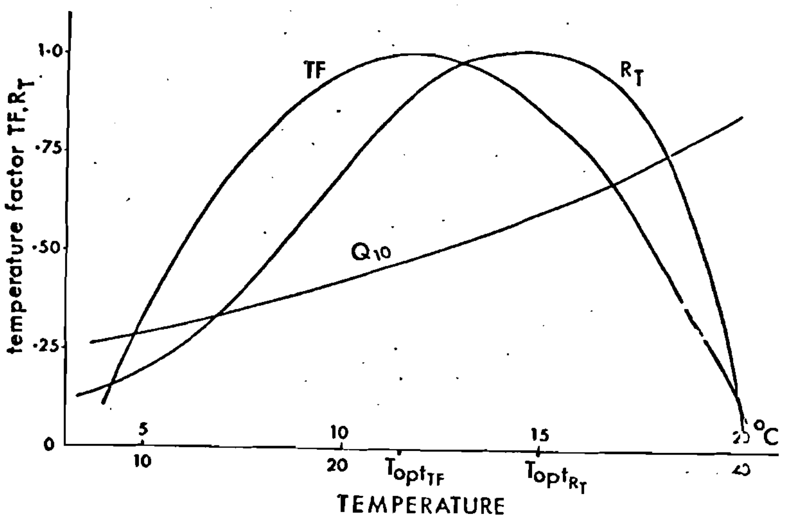

Figure 4. Temperature factors TF (Halfon and Lam, 1978, upper temperature scale) and R_T (Najarian and Harleman, 1975, lower temperature scale) as a function of temperature. T_{opt} denotes the optimum temperature for nutrient uptake in phytoplankton. For comparison, a Q_{10} relationship with approximately the same mean as TF and a Q_{10}-value of 2.0 is included (upper temperature scale).

An alternative representation is found in Cloern (1978), and deals more realistically with the physiology of the temperature effect on a biological process, i.e., primary production. The growth rate of the flagellate *Cryptomonas ovata* is described as

$$G' = G_{max}(T)\frac{I}{I_{opt}(T)}\exp\left(1 - \frac{I}{I_{opt}(T)}\right) , \qquad (1.12)$$

where G' is the specific growth rate in units/day^{-1}, e.g., (1.12) is essentially Steele's (1962, 1965) equation for photosynthesis light response, modified through the description of the parameters

G_{max} and I_{opt} as functions of temperature T (°C). The parameters are thus made time-variable and relate to a major forcing. The following expressions are given in Cloern (1978):

$$G_{max}(T) = 0.02 \exp (0.17\ T) \tag{1.13}$$

$$I_{opt}(T) = 0.06 \exp (0.22\ T) \tag{1.14}$$

The inclusion of (1.13) and (1.14) in (1.12) results in a rather complex set of curves, when G' is plotted as a function of temperature for different values of I (Figure 5). A sigmoid pattern with an absolute decrease in G' in the high temperature range results, which steepens with increasing light level. The model thus predicts an optimum temperature for specific growth rate, which decreases exponentially with insolation. Although the predictions of the model would be questionable for short-term variations in insolation under low temperature conditions, the general pattern can be interpreted as a coupled low light/temperature adaptation of photosynthesis, taking into account the most obvious coupling of the daily average in light input and temperature in the yearly cycle, e.g., (1.12) describes the medium-term adaptational response to the seasonal input change (see p. 24).

In many ecological models the effect of temperature on metabolic rates and processes of ectothermic or poikilothermic organisms are represented by simple Q_{10} relationships, where the Q_{10} value is defined by

$$Q_{10} = \frac{M_2}{M_1}^{\left(\frac{10}{T_2 - T_1}\right)} , \tag{1.14}$$

and

$$M_2 = M_1 \cdot Q_{10}^{\left(\frac{T_2 - T_1}{10}\right)} , \tag{1.15}$$

where M_1 and M_2 denote metabolic rates at temperature T_1 and T_2, respectively. The Q_{10} values as reported in the literature

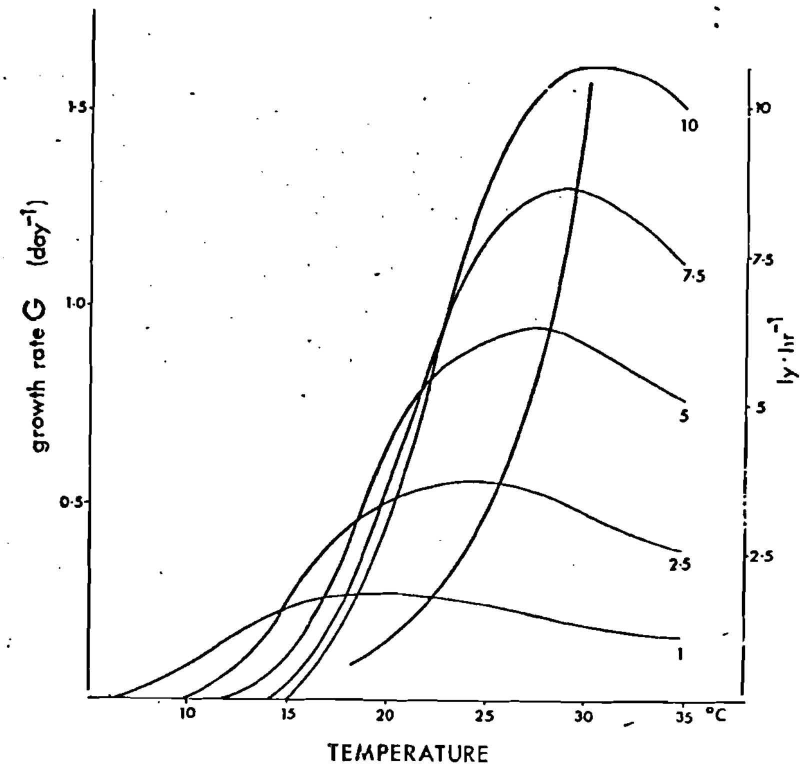

Figure 5. Specific growth rate (day $^{-1}$) of *Cryptomonas ovata* as a function of temperature after 2.7 for different light levels (ly*hr^{-1}). The exponential curve indicates the relation of optimum temperature to light level.

After: Cloern, 1978.

(see Mullin and Brooks, 1970), usually vary around 2. Consequently, each 10°C change in temperature would lead to a two-fold change in metabolic rate. However, many poikilotherms exhibit the ability to compensate metabolically for changes in temperature within a certain range. Again, as stated in a previous section, metabolic adaptation may occur over several time courses of different orders of magnitude. Through evolution, species adapt to different temperatures or temperature regimes; compensatory patterns can be observed on a medium time scale for phenotypic acclimation processes; furthermore, organisms have been found to be capable of almost immediate temperature compensation. The latter pattern is primarily characteristic of poikilotherms under a special regime of temperature fluctuations, i.e., rapid and often large temperature changes as in, for example, intertidal zones (see Newell, 1976) or very shallow bodies of water. A typical compensation pattern of an intermediate-time scale, during the course of the year is shown in Figure 6.

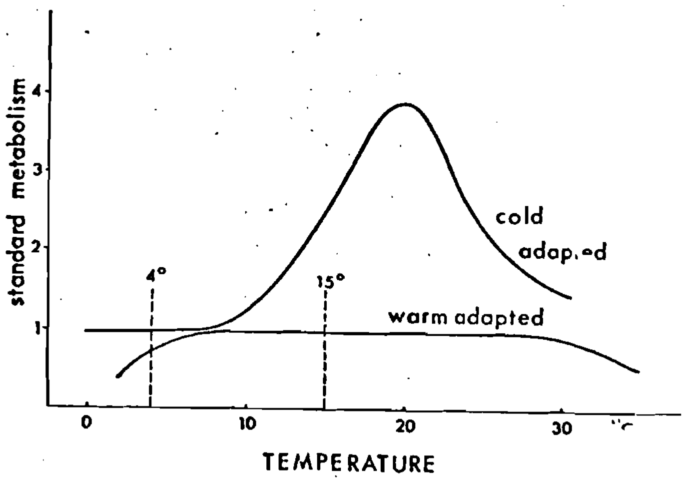

Figure 6. Range of adaptation as a function of seasonal temperature regime.

After: Newell and Pye, 1970.

Adaptation patterns depend primarily on the time scale of the temperature input variation. Short-term changes can be met by means of behavior in motile organisms, thus influencing distribution patterns. However, when such behavioral mechanisms are inadequate as, for example, in all sessile organisms, biochemical adaptation will take place. Somero and Hochachka (1976) discuss several potential biochemical mechanisms of rate compensation, based on considerations of velocity control of the underlying enzymatic reactions. Four such control mechanisms are discussed:

1. changes in enzyme concentrations;
2. changes in substrate and cofactor concentration;
3. modulation of enzyme activities;
4. formulation of new enzyme variants with different catalytic efficiencies.

Different response times are characteristic of these mechanisms, and for practical purposes one can assume that combinations of these quantitative and qualitative strategies are applied. They result in damping the output variations induced by temperature input variations, as compared to the simple Q_{10} relationship. Generally, the longer the time available for the organism to adapt to a changed environmental temperature, the closer the organism will adjust its metabolism to what one might call its standard level (see Figures 6, 2b). Many organisms show a characteristic temperature range, within which at least partial independence of the metabolism from temperature changes--at least seasonal--can be observed. Generally, this range will correspond to the temperature range of the organisms habitat. Adaptation to a given temperature T_2 will, therefore, be a function not only of the time scale of the temperature change, but also of the relation of the actual temperature T_2 to the boundary values of possible adaptation, say, T_{min} and T_{max} and T_o, which represent the average habitat temperature. Using a simple exponential relation and including the time-element and a time-varying temperature coefficient, we get

$$M_{2(t)} = M_o \cdot \theta_{(t)}^{(T_o-T_2)} \qquad (1.16)$$

with M_o representing the standard metabolism (Figure 6); θ is a temperature coefficient and will be a function of T_2 in relation to some upper and lower limiting or lethal temperature boundaries of a temperature range for adaptation, as well as of the temperature history of the system and approach unity with time.

In reconsidering the underlying biochemical mechanisms, adaptability requires an ensemble of possible mechanisms to persist under different environmental (temperature) states. The question of whether these mechanisms are constitutive, inducible or selective (Conrad, 1976), is only relevant for the relation of the mechanisms to the time scales and predictability of the environmental changes. The basic and most general feature of adaptability, as will be documented at different levels of organization, is found in the availability of several "behavioral" alternatives for the system to choose from under different environmental states. Due to the different energy requirements of different mechanisms and the various response times involved, the selection of an optimum strategy in terms of enhanced persistence will depend on the set of available mechanisms, as well as on the pattern of environmental fluctuations or variability. Considering these relations, the following modeling strategies could be adopted:

1. The relation of any temperature dependency on the environmental temperature range, such that temperature dependency (e.g., in terms of a temperature coefficient) increases with increasing distance from the average temperature range.

2. The relation of temperature dependency on the temperature history of the system, such that temperature dependency will be related to the prevailing temperature regime of a previous time interval; in addition, the time course of temperature changes can be considered. This could be achieved by specification of some kind of reference temperature, defined as a weighted average of preceding environmental temperatures. This relation to the time element in temperature input can be seen in the context of the concept of environmental tracking as a major adaptive strategy. Assuming a somewhat bell-shaped temperature relation of a given process, specifying an optimum temperature or temperature range, this optimum temperature will not be a constant value but will vary according to the prevailing environmental temperature; in other words, it will track this temperature pattern. This strategy is, of course, based on the assumption that the time lag in the adaptation process is negligible in relation to the time course of the temperature changes; the system could otherwise easily get out of phase, always lagging behind the temperature regime. The second implicit assumption for the effectiveness of such environmental tracking as an adaptational strategy is that rapid short-term changes are small as compared to the long-term trends (e.g., daily variations are generally fewer than the seasonal fluctuations), which is essentially true for many aquatic systems. In situations where this

might not be the case, for example, in the tropics or very shallow lakes or lagoons, different strategies of adaption have to be adopted.

EFFECTS OF LIGHT ON PRIMARY PRODUCTION

Let us now consider the effect of light on primary production. This is not only the key process in energy transfer in biotic systems, but has also attracted model builders for many years. Two different types of processes are involved: enzymatic processes and photochemical processes. Rates of enzymatic processes depend on the concentration of active enzymes and on temperature as outlined above. The rates of the photochemical processes depend on pigment concentration and irradiance. Photosynthesis is now determined by the rates of both processes, and the main consequence of adaptation can be seen in the matching of the two processes under various environmental conditions (Steemann Nielsen, 1975).

Significant variability in light response patterns over short time spans is a widely recognized fact. Numerous observations have been made on the phenomenon of light acclimation, and extensive laboratory and field experimentation has been devoted to the problem (e.g., Steemann Nielsen, 1975, Hameedi, 1977, Kremer and Nixon, 1978). Physiological adaptation to irradiance is basically attributed to two different mechanisms, i.e., changes in the pigment concentration (adaptation of the photochemical process, *Chlorella*-type), and/or changes in the enzyme concentrations (adaptation of the enzymatic part of the process, *Cyclotella*-type). The two adaptation types are not, however, sharply separated; transition types occur but are represented by different approaches to include adaptation phenomena in the description of the light-photosynthesis relation, as will be shown below.

Now, why and how should one include this phenomenon in a model? The effect of light acclimation in phytoplankton will, for example, be of significance in a model that simulates short-term changes in daily radiation which fall into meteorological patterns. Such patterns, in this case representing cloud cover, can be simulated using stochastic methods for daily variations and are, for example, calibrated to the monthly averages of cloud cover throughout the year. An example of such an application is given in the Kremer and Nixon (1978) model of Narraganset Bay. Depth and time integrations of light-photosynthesis relations under given conditons of vertical mixing would also require an accounting of adaptation.

To treat the phenomenon on a mechanistic, microscale level would require one to account for the chlorophyll quota of the cells (in the case of the *Chlorella*-type) in some kind of internal pool model, comparable to the internal pool representations of the nutrients recommended by many authors, e.g., Grenney (1973), Davies et al. (1978), or Dugdale (1977). Such an approach is rather elaborate and, in most cases, the parameters for environmental dependency of cell quota of chlorophyll and chlorophyll/productivity relations are known only semi-quantitatively. Chlorophyll : carbon ratios are known to vary over an order of magnitude from approximately 20 to 200 (Steele and Baird, 1961). Assimilation numbers, i.e., mg C per mg Chl. a per hour under light and nutrient saturation levels, are compiled in Platt and Subba Rao (1975), and temporal variations for a given coastal area are reported in Platt (1969, 1975); these were found to range from 0.1 to 20 mg C per mg Chl. a per hour. Data from the northeast Pacific Ocean are given in Hameedi (1977). Assimilation numbers range from 0.85 to 5.5 mg C $(\text{mg Chl. a} \cdot \text{h})^{-1}$; the corresponding I_{opt} values are given with 2.7 to 6.1 mW cm^{-2}.

A more holistic and convenient alternative can be deduced from the work of Steemann Nielsen et al. (1962). The basic assumption is that optimum light for growth I_{opt} or light saturation level, tracks the previous light history to which the cell has been exposed. This leaves the causal relations (involving the chain of light history-chlorophyll quota-productivity/light) aside, using only the relation light history-productivity/light. This corresponds to the above mentioned *Chlorella*-type of adaptation, which is related to the photochemical part of photosynthesis. This mechanism seems to be primarily characteristic of green algae (Steemann Nielsen, 1975).

Using the simple Steele (1962) equation for light-dependent growth of phytoplankton (Fig. 7), we have

$$G = G_{max} \cdot \frac{I}{I_{opt}} \exp\left(1 - \frac{I}{I_{opt}}\right) , \qquad (2.1)$$

where G represents particulate production, i.e., gross production minus respiration minus excretion of dissolved organic compounds, and G_{max} is the maximum growth at light saturation level I_{opt}. The parameter I_{opt} is made a variable by defining

$$I_{opt}(t) = a \cdot I'(t-1) + b \cdot I'(t-2) + c \cdot I'(t-3) \; , \qquad (2.2)$$

where I'(n) is the mean daily irradiance at day n, and a,b, and c are constants for weighting the average of I' over the preceding three days. Values of 0.7, 0.2, and 0.1 are used by Kremer and Nixon (1978) to approximate the observations of Steemann Nielsen et al. (1962).

A different approach is discussed by Platt et al. (1977). Again, the parameter G_{max} is made a variable, based on the Steele equation (2.1); we may write

$$\frac{\partial G}{\partial I} = \frac{G_{max}}{I_{opt}} \exp\left(1 - \frac{I}{I_{opt}}\right) - G_{max} \frac{I}{I^2_{opt}} \exp\left(1 - \frac{I}{I_{opt}}\right) \qquad (2.3)$$

and

$$\lim_{I \to 0} \frac{G}{I} = e \cdot \frac{G_{max}}{I_{opt}} \; . \qquad (2.4)$$

Let us now assume that, for low light intensities (where the photochemical part of the total photosynthesis process is governing, i.e., limiting), the initial slope of the G vs. I curve depends only on pigment concentration (Chlorophyll a), with a proportionality of, say, α (Fig. 7), where

$$\frac{\partial G}{\partial I} = \alpha (\text{Chl. a}) \quad . \qquad (2.5)$$

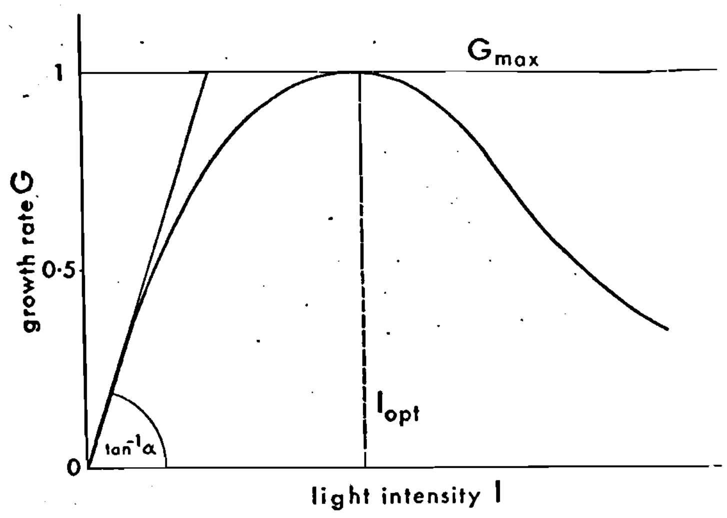

Figure 7. Photosynthesis-light response after Steele (1962). G_{max} is frequently called the assimilation number; α gives the slope of the photochemically determined part of the curve.

Now let β be the ratio of carbon to chlorophyll, such that

$$\beta = \frac{B}{(\mathrm{Chl.}\ a)} \quad . \qquad (2.6)$$

By substituting Eq. (2.5) in Eq. (2.4), and using Eq. (2.6) for Chl. a, we get

$$e \ \frac{G_{max}}{I_{opt}} = \frac{\alpha}{\beta}\ B \qquad (2.7)$$

or, rewritten for I_{opt} and dividing by biomass B,

$$I_{opt} = \frac{\beta}{\alpha} \cdot e \cdot G^{B}_{max} \quad . \qquad (2.8)$$

Now, many observations on the depth distribution of photosynthesis in widely differing water types have shown remarkable similarities (Vollenweider, 1970); the depth distribution reaches a maximum at a depth where the available light is about 50% of its mean surface value. Based on these observations, Steele (1962) made the following formal assumption:

$$I_{opt} = \frac{I_o}{2} \quad , \tag{2.9}$$

where I_o denotes the mean subsurface irradiance. Substituting Eq. (2.9) for I_{opt} in Eq. (2.8) gives

$$G^B_{max} = \frac{\alpha I_o}{2\ e\beta} \quad . \tag{2.11}$$

This is simply the hypothesis that the assimilation number or maximum growth rate per unit pigment is proportional to the mean subsurface irradiance. As mentioned above, the response time for this adaptation falls within the range of a few days; one should, therefore, make G^B_{max} an empirical function of the mean light intensity of the preceding days or light history of the system. As compared to the first approach, this example would represent the *Cyclotella*-type of adaptation, related to the enzymatic processes in photosynthesis. The *Cyclotella*-type seems to primarily characteristic of diatoms (Jørgensen, 1964, 1969).

From the modeling point of view, this is basically the same approach as discussed in the first example, but applied to another parameter. It must be said for both approaches that these formulations would allow adaptation to unreasonably high or low light levels, so that upper and lower boundary conditions have to be included for actual modeling purposes. However, Steemann Nielsen (1975) states in his monography on marine photosynthesis:

> ...the different populations of algae found throughout the year are adapted to just the light conditions found during the last one or two days. No delay in adaptation takes place.

Light adaptation in terms of a variable chlorophyll biomass ratio in phytoplankton may cause complication of primary production and phytoplankton representation by treating the pigment as an additional variable. On the other hand, if chlorophyll is used to describe the phytoplankton instead of energy content, carbon, nitrogen or phosphorus, then the time-varying stoichiometry has to be accounted for in various other processes such as grazing or nutrient cycling. Therefore, it might be more appropriate (although phytoplankton measurements are very often in terms of chlorophyll) to relate primary production to another convenient biomass measure and account for the time-varying light dependency of the process by making the I_{opt} value in a more or less bell-shaped light dependency curve, and the G^B_{max} value a function of the preceding days light level. Light adaptation by means of a time-lagged relation of chlorophyll content and assimilation number to light input (again, an example of environmental tracking) will be accompanied by another constituent mechanism in case of multi-species plankton communities. A multi-species phytoplankton community (in fact, all natural phytoplankton communities are multi-specific), is characterized by inherent functional dissimilarities of the component species (in our example, different light optima), which leads to differential success under variable environmental conditions and thus again to a pattern of environmental tracking. The same implicit assumptions that were made explicit for the temperature adaptation must be considered for the light adaptation: the general (seasonal) pattern must prevail over short-term stochastic (meteorological) fluctuations. The importance of this relation for the effectiveness of adaptation strategy will be discussed further in a modelling example in the section on adaptation at the community level.

NUTRIENT KINETICS

A similar series of arguments related to the concept of environmental tracking can be given for a refined formulation of the nutrient uptake and related growth in phytoplankton. The Michaelis-Menten expression is commonly used to describe the nutrient uptake kinetics (Fig. 8):

$$V = V_{max} \cdot \frac{S}{K_s + S} , \tag{3.1}$$

where V is the specific uptake rate normalized to cell content of a nutrient with a concentration S.

$$V = \frac{1}{S} \cdot \frac{dS}{dt} \tag{3.2}$$

and K_s, the Michaelis constant, is given by

$$K_S = V_{max}\frac{S}{V} - S \quad , \qquad V_{KS} = \frac{V_{max}}{2} \tag{3.3}$$

Eq. (3.1) is generally assumed to describe the cell's nutrient transport process; in steady-state conditons, this would be equivalent to growth rates. Evidence that the uptake of various compounds such as nitrate and ammonium, phosphate, silicate, etc., can be described adequately by Michaelis-Menten equations, has been gathered with various methods and different species as well as mixed, natural populations. However, this model is only accurate under conditons of exclusively temporary low nutrient concentrations, which in nature occur only in more eutrophic regions.

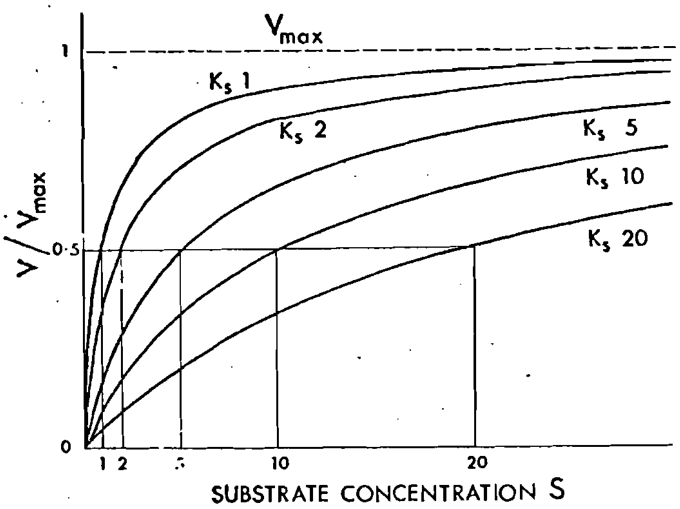

Figure 8. Relative nutrient uptake V/V_{max} as a function of a substrate concentration according to (4.1) for different values of K_s.

Although Monod (1942) used Eq. (3.1) to describe substrate/growth relations in carbon-limited bacteria, the application of the equation to growth rates under transient conditions has proven inadequate: experiments of numerous authors (see Dugdale, 1977), variously working with nitrate, phosphate, silicate and vitamin B_{12} indicated disagreement with Eq. (3.1) when V is interpreted as a growth rate. The reason for the disagreement is the adaptation of the cells to low nutrient concentrations, or the decreased amount of limiting nutrients contained in the cells under nutrient-limited conditions.

Now let V' be the absolute rate of uptake or transport, with units of mass taken up per unit population per time unit as compared to V, the nutrient specific uptake rate with dimension time^{-1}. At steady state, where $V = \mu$ (μ being the specific growth rate of the Monod formulation),

$$V = \frac{V'}{Q} \quad , \tag{3.4}$$

where Q is the amount of limiting nutrient per unit population, the cell quota. The relation of growth rate to cell quota Q is again described by a Monod-type hyperbola (Caperon and Meyer, 1972):

$$\mu = \frac{\mu_{max}(Q - Q_o)}{K_Q + (Q - Q_o)} \quad , \tag{3.5}$$

where Q_o indicates the threshold level where growth is reduced to zero, and K_Q is again the half saturation constant. Droop (1968) proposed a simpler expression:

$$\mu = \frac{\mu_{max}(Q - K_Q)}{Q} \quad , \tag{3.6}$$

which is equivalent to Eq. (3.5) for the case $K_Q = Q_o$. Plots of μQ (which is uptake of mass per unit population per unit time) versus Q, the cell quota, result in a straight line (Droop, 1973). Rearranging Eq. (3.6) to

$$\mu Q = \mu_{max}(Q - K_Q) \tag{3.7}$$

for growth, and using Eq. (3.1) for uptake, and including (3.4), we have

$$V' = V'_{max} \frac{S}{K_S + S} \quad . \tag{3.8}$$

For steady state conditions,

$$V' = \mu Q \quad , \tag{3.9}$$

we get

$$\mu Q = V'_{max} \frac{S}{K_S + S} \quad , \tag{3.10}$$

and, consequently,

$$\mu = \frac{V'_{max}}{Q} \cdot \frac{S}{K_S + S} \tag{3.11}$$

V'_{max}/Q is a nutrient specific maximum uptake rate. Let V'_{max}/Q be ρ. By inserting ρ into Eq. (3.11), i.e.,

$$\mu = \rho \cdot \frac{S}{K_S + S} \quad , \tag{3.12}$$

we end up with a hyperbola of the original Monod formulation type, but including the variable ρ, which is inversely proportional to cell quota Q. Nutrient scarcity, resulting in a descreased Q, will increase ρ. This represents the cell's adaptive ability to grow under low nutrient conditions, simply because less of the limiting nutrient would be used to produce the next cell.

In this process of adaptation to low nutrient concentrations, there is again a strong historical element in the cell quota Q, as it depends heavily on the nutrient regime of the preceding days. Winter et al. (1975), proposed the following model, using a time lag t_1:

$$\mu(t) = \frac{\mu_{max}(t) S(t - t_1)}{K_S(t) + S(t - t_1)} \quad , \tag{3.13}$$

where t_1 was again approximately three days (as in the light acclimation model) for their calculations for Puget Sound. This is, in fact, a semi-empirical and simple representation of the phenomenon discussed above. One might as well, as was shown in the previous section for light, use a weighted average of the nutrient concentration S over the preceding days instead of the representation in (3.13).

Again, this simple representation, excluding cell quota, is given as an example of environmental tracking. It must be pointed out, however, that a more causal and mechanistic model, including cell quota, would require a rather elaborate model with internal nutrient pools. As a consequence of the uncoupling of nutrient uptake and growth in such a model, one would not only be able to represent the adaptations to low nutrient levels, but also the phenomenon of nutrient luxury uptake and the related time-lagged overshoot in production in a highly dynamic nutrient regime, which may be critical in algae blooms. Again, the selection of either of the alternatives, or even a much simpler representation with less biological validity, as can be found in many ecosystem models, depends mainly on the purpose of the model.

As the effects of luxury uptake of nutrients, which applies primarily to phosphorous, can only result in time delays or shifting effects of production related to the external nutrient regime, it becomes obvious that the inclusion of this phenomenon--by uncoupling nutrient uptake and growth in internal pool models as outlined above--in a simulation model of an aquatic ecosystem should depend on the relevant time scale, which in turn depends on the modeling purpose. If the main interest is in the establishment of more long-term budgets, and consequently larger time steps are used, the result of additional sophistication and complication of an internal pool model will probably turn out to be unnecessary, in terms of the problem envisaged. If, on the other hand, one wants to predict the dynamics of the plankton, rather than the yearly averages of production in relation to nutrient loading, the uncoupling of growth and nutrient uptake has to be included as a major element of the short-term dynamics of aquatic primary production under transient nutrient concentrations (Nyholm, 1977, Rhee, in press, Loogman et al., in press).

With regard to nutrient kinetics, one of the major problems still far from being completely solved is the question of interaction of different nutrients and nutrient competition. Elbächter (1977) demonstrated that there are significant differences in the nutrient specific growth between unialgal and multi-species experiments. This was primarily ascribed to nutrient competition. The various uptake rates and half-saturation constants for different nutrients in different species, as frequently reported in the literature, will cause changes in the biomass relations in multi-species communities, subsequent to changes in the ratio of these nutrients. In this context, luxury consumption of nutrients must be considered, as it can significantly affect growth limitations in mixed populations (Droop, 1974,1975).

Interaction between limiting and non-limiting nutrients will be of special interest under a highly dynamic nutrient regime with variable ratios of the nutrients. Two basic theories of multiple-nutrient limitation are represented in ecosystem modeling approaches: the first is that there is a multiplicative effect, represented by

$$\frac{\mu}{\mu_{max}} = 1 - \frac{K_{QA}}{Q_A} \quad 1 - \frac{K_{QB}}{Q_B} \quad \cdots\cdot \quad , \text{etc.} \qquad (3.13)$$

The second alternative corresponds to Liebig's law of the minimum, which predicts independence from all but one, i.e., the "truly limiting" factor:

$$\frac{\mu}{\mu_{max}} = 1 - \frac{K_{QA}}{Q_A} \quad \text{or} \quad \frac{\mu}{\mu_{max}} = 1 - \frac{K_{QB}}{Q_B} \quad . \qquad (3.15)$$

A series of experiments by Droop (1974), using phosphorus and vitamin B_{12}, substantiated the latter hypothesis. However, very little experimental data are available, rendering final and general statements difficult.

The effect of temperature on nutrient uptake, at least in marine phytoplankton, was described with a simple exponential relationship with a Q_{10} of about 1.8-1.9 (Dugdale, 1976).

Packard et al. (1971) used the following expression to describe effects of temperature on nutrient uptake:

$$V_{max} = \mu_{max} \frac{\delta}{R} \; \frac{1}{T_{opt}} - \frac{1}{T_t} \quad , \tag{3.16}$$

where V_{max} represents the maximum uptake rate in (3.1), normalized to cell quota Q; T_{opt} denotes the optimum value of the ambient temeprature T_t for growth, R is the universal gas constant, and δ represents the slope of μ vs. 1/T.

Finally, there is a tight coupling between light and nutrient uptake, based on the fact that the light-produced ATP drives at least nitrate and ammonium uptake systems (Falkowski, 1975, Falkowski and Stone, 1975). Experiments of Davies (1976) and Harrison et al. (1976) also indicate that V_{max} is a function of light level and varies directly with it.

To summarize from the ecosystems modeling point of view, nutrient uptake and related growth in phytoplankton is one of the key processes in any aquatic ecosystems model. The selection of the necessary degree of detail depends again on the underlying modeling purpose. However, recent experience has shown that for a more realistic representation of short-term dynamics under a fluctuating nutrient regime, the uncoupling of growth and nutrient uptake is necessary. This uncoupling and the use of internal pool models allows one to consider both the effects of adaptation to low nutrient levels and the phenomenon of luxury uptake. As a compromise, one might consider a simplified approach using a time-lagged dependency of growth to external nutrient concentration. Such a representation will be based on the concept of environmental tracking as a major adaptive strategy. A similar result could be obtained by relating the K_m values (or nutrient affinity) to the available nutrients (Loogman et al., in press). Whenever nutrient interaction and multiple nutrient limitation has to be taken into account, a switch pattern for nutrient limitation seems to be preferable over any combined effect.

ADAPTATION ON THE COMMUNITY LEVEL

The above examples of some first attempts to include representations of adaptation phenomena in the formulation of biological processes within the frame of ecosystems models, can be partially interpreted as adaptation at the population level, representing a single species which, for simplicity, will be assumed to be functionally homogeneous, as well as at the community level, which is for a lumped group, composed of numerous functionally dissimilar species. However, the representation of adaptation at the community level has to account for a two-fold effect, i.e. the "physiological" one within the species as discussed above, and a second, superimposed, "ecological" one, which results from changes in the structure and composition of the community under variable environmental conditions. Such changes in the structure and composition must be considered as a major adaptive strategy at the community level.

Again, the same underlying mechanisms as mentioned above can be identified: adaptability is based on a latent repertoire of different potential behaviors, which is realized through changes in the composition of the functionally slightly different components, namely, the species. The parallels to, for example, the set of different enzymes at the organism level are most obvious. The appropriate behavior is adopted by rather simple means, i.e., the differential success of the functionally different component species under different environmental conditions. The basic machinery of the set of component species is always available and is tuned by quantitative changes in the species composition according to the respective environmental conditions. The functional dissimilarity or diversity is therefore a basic prerequisit of community adaptability, but must be such that it allows the single species to persist, even under the most unfavorable conditions to be encountered.

Due to the continuous adjustment of community features by enhanced dominance of the "best" adapted, environmental tracking is again a basic strategy. Its effectiveness is not only dependent on the scope of the alternative behaviors or community compositions and structures, but also on the patterns of environmental variability.

The effect of community adaptation is reflected, for example, in the varying compositions of the spring, summer, and winter plankton in most aquatic systems. Another example might be species successions under conditions of increasing eutrophication. Both examples emphasize the role of competitive species interaction in community adaptation. The problem of model representation can be handled, therefore, in two ways. Treating at least the major component species separately, so that changes in the community structure are explicitly represented, would be the mechanistic approach; however, a sufficient amount of physiological information on the component species must be available, which is rarely the case in most studies. Following the above line of reasoning, the alternative would be to allow for adaptational adjustments of the parameter values describing the total community; these parameters have to be made time-variable and relate to the course and pattern of determining state and input variables with a certain time lag. This corresponds to the basic arguments in the previous sections; only the physical interpretation of the underlying phenomena is slightly different at the community level.

Community adaptation simultaneously reacts to all relevant environmental properties such as light, temperature, nutrients, etc. This simultaneous influence of numerous variables and the stochastic variability of these environmental features are important conditions for the maintenance of diversity in natural communities. Under constant environmental conditions and under the influence of only one governing variable, a single species would be selected after some time; the less adapted groups would not be able to compete. However, as a given species may exhibit varying degrees of adaptability with regard to various environmental variables and different sets of environmental conditions, disadvantages in one aspect or instant of time might be balanced in another aspect or at another time. Functional dissimilarity and stochastic environmental variability are therefore important for the persistence of communities and ecosystems as such.

From the modeling point of view, the problem lies in the determination of parameters and description of processes for such heterogeneous biotic compartments in a variable environment. Let us consider the following example: given a multi-species community with component species of various sizes, where large organisms have relative advantages under low temperature conditions, and small organisms have relative advantages under high temperature conditions, what will be the average size of organisms found in such a community as the result of adaptive optimization under variable temperature conditions? Several strategies for such adaptive optimization can be thought of and their relative success will depend on various systems properties such as the range of size groups, response times for changes in the community composition, and the temperature input pattern. To gain some insight into the relation of these factors, a simple modeling exercise was carried out, using primarily a traditional representation of the photosynthesis/light relation in a hypothetical phytoplankton community under different patterns of a light regime.

Consider a community of n species with the relative abundance of a single species or fraction of the total community biomass (more generally, species importance; see Fedra, 1977) of k_i; the community average for any parameter $\overline{P}_c$ can be estimated by the weighted average

$$\overline{P}_c = \sum_{i=1}^{n} k_i P_i \quad , \qquad \sum_{1}^{n} k_i = 1 \quad , \tag{4.1}$$

where P_i denotes the respective paramter value for a single species. The averaged community parameter values are thus functions of the species composition of a lumped compartment, whereby species composition will alter under variable environmental conditions. However, such a weighted average is only a reliable estimate for the community value in the case of linear relations between the ecological process considered and the species parameters. Referring to Eq. (2.4), the relative growth rate G_i^B of a species within the community depends on $G^B_{max}i$ and $I_{opt}i$ of the species. By assuming in a rough first approximation that all

$G^B_{max}i$ of the component species are approximately equal (so that the component species differ only in one parameter value, i.e., $I_{opt}i$), and introducing

$$I^*_i = \frac{I}{I_{opt}i} \tag{4.2}$$

and

$$k^*_i = k_i \cdot G^B_{max}c \quad , \tag{4.3}$$

the relative growth of a given component species will be described by

$$G_i = k^*_i \cdot I^*_i \exp(1 - I^*_i) \quad . \tag{4.4}$$

Now, as the fraction of a single species will depend on its relative success within the community

$$k_i(t) \propto (G_i(t - 1)) \quad , \tag{4.5}$$

where l denotes a time lag in the order of magnitude of generation time, and the relative increase in G_i becomes larger the closer I^*_i is to unity, the community average of I_{opt} will approach I' whenever I is constant for more than the minimum time lag for adaptation process.

A simple model was constructed to simulate the dynamics of a multi-species community of algae in an annual cycle. A spatially dimensionless approach, considering one point in a completely mixed body of water only, was chosen for simplicity. An array of ten to twenty species with initially assigned fractions of total community biomass was used, differing only in their I_{opt} parameter values (according to the assumptions above);
the community dynamics (determined as the sum of the single species dynamics in terms of relative success within the community total) were calculated according to Eq. (4.4) with a time step of one day. Referring to Eq. (4.1), the community estimate of I_{opt} is a function of the component species parameter values

and fractions; relative biomass increase of the component species was accordingly normalized to total community biomass, which was kept constant at 100%, so that any linear loss term could be neglected. For comparison, the community I_{opt} value was estimated using the community productivity (determined by the sum of the component species contributions). Total community productivity was determined for the simulation time using this community parameter as well as the initial time-invariant estimate of (4.1). A comparison of these two values allowed an estimate of the relative error introduced with a time-invariant estimate of community I_{opt} as compared to a time-varying parameter value.

Following the above concept of environmental tracking and its relation to environmental predictability, the model was run with different patterns of light input: for the yearly cycle of input, a sinus pattern with superimposed random variability was used:

$$\mathrm{LIGHTM} = \mathrm{SIN}\ (\mathrm{TIME}) \cdot (3.14159/182.5) \cdot 10 + 10 \quad , \tag{4.6}$$

$$\mathrm{LIGHT} = \mathrm{LIGHTM} \pm \mathrm{LIGHTM} \cdot \mathrm{VAR}/100 \cdot \mathrm{RANF} \quad , \tag{4.7}$$

where LIGHTM gives the long-term mean of the light input (with an overall yearly mean of 10.0); LIGHT is the actual input value for the simulation, TIME is simulation time in days, VAR is a user-defined range for the stochastic variability in percent (0-100% in order to avoid negative light values), and RANF denotes a pseudo-random number generating algorithm, using a ten digit seed, which allows reproducible sequences of random numbers ($0 < \mathrm{RANF} < 1$). The sign in Eq. (4.7) is determined by a similar random algorithm.

The changes in the community estimate of I_{opt} observed in the simulations were a result of community adaptation through changing composition, governed by the light input. Physiological adaptation in the single species was not taken into account in these first runs.

Model output (for an example, see Fig. 9) includes a graphic representation of the time series of the component species fractions, the light input (long-term mean and daily value), community productivity and an estimate using a time-invariant I_{opt} value, derived from the initial community composition, the two estimates of community I_{opt} (one representing the light-limited, the other light-inhibited state of the community), as well as Simpson and Shannon's diversity indices. In addition, basic statistics are given for these variables.

For the first series of simulations, the specified I_{opt} values of the component species varied around the annual mean of light input with a range corresponding to literature data for different species and groups of algae. Initial fractions of the component species were either equal or based on long-term runs of the model for 10 years.

Some general conclusions about the model behavior were obtained:

1. No steady-state community composition could be established under the simple model assumptions. Long-term simulations of up to 10 years showed an increasingly pronounced dominance of the species with their I_{opt} values close to the long-term mean of light input, which was also indicated by the decrease of the diversity indices. Random variability in the light input did not significantly influence this pattern. However, initial fractions and parameter value specifications greatly influenced the "stability" of the community composition.

2. The governing community I_{opt} paramter was found to be time-varying as expected, tracking the light input pattern with a certain time lag of the order of magnitude of several days; time lag and accuracy of tracking were again related to the initial conditions.

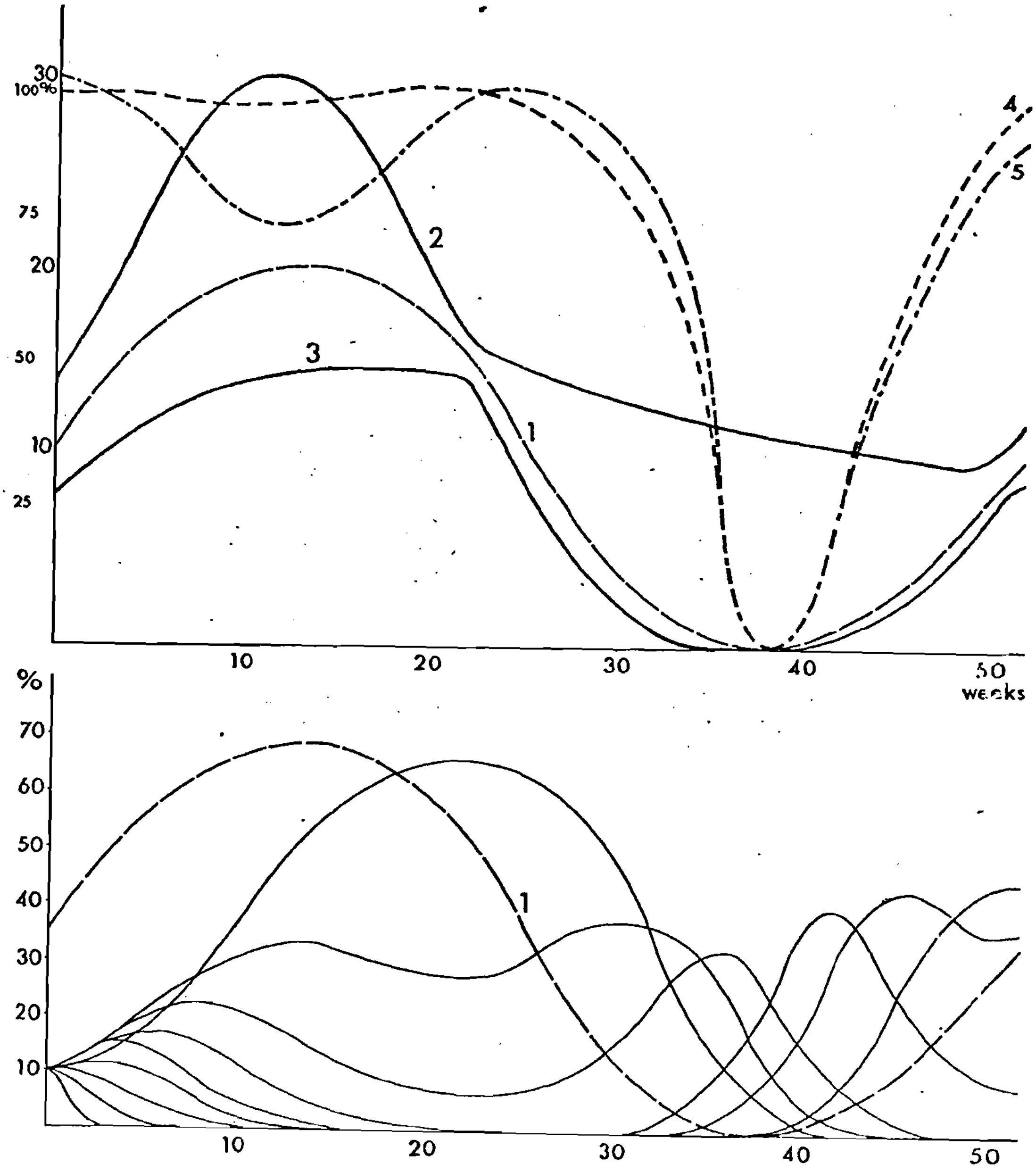

Figure 9. Community adaptation model output. Curve 1: light input, arbitrary units, yearly mean: 10.0. Curves 2,3: upper (light limited state) and lower (light inhibited state) value of community I_{opt}, arbitrary units. Curves 4,5: community productivity as percentage of maximum value, 4: with time-varying community I_{opt}, 5: with constant value of 10.5. Lower solid curves: component species(10), percentage of total community. Initial values: 10% each, I_{opt} values from 6 - 15.

3. Actual community productivity was underestimated with the constant community I_{opt} for about 3-5% for yearly budgets, as compared to the adapting parameter; however, during certain periods of the year, the observed differences amounted to more than 20%, increasing with input variability. Initial conditions did not significantly influence this relation for symmetric distributions of the species parameters around the input mean.
4. Both diversity indices were found to be time-varying, showing smooth polymodal oscillations throughout the year, and representing the species' succession patterns with different degrees of evenness.

To summarize the results of the model runs, the importance of community adaptation for the description of functionally non-homogeneous biotic compartments has been documented for this simple model, and a pattern of environmental tracking simulated. The significance of the adaptation process was found to be more pronounced in the short-term dynamics within the annual cycle as compared to yearly budgets. However, a substantial influence of the initial conditions must be noted, at least for the quantitative aspects, whereas a general pattern could be observed in any case. No doubt, a much more detailed analysis, using actual field data and more realistic boundary conditions, will have to be made for a quantitative assessment of the phenomenon.

As a general conclusion, the inclusion of adaptation in the representation of biological processes is proposed to increase biological realism in ecosystem models. For adapting lumped multi-species compartments, the time-lagged coupling of any "optimum" parameter to the respective input variable is suggested. This modeling strategy should allow for increased biological realism without necessitating an increase in the number of variables and thus the dimensionality and complexity of a model.

Even if the parameters governing the tracking are not yet exactly known in many cases, any shift of parameter values in the right direction will at least improve the reliability of the model predictions, not only with regard to seasonal or short-term fluctuations in input or state variables, but especially under conditions of considerably changed inputs or new regions in state space. However, with regard to the parameters governing the tracking, it seems likely that they shown only comparatively small variability as a consequence of the mechanisms involved and the small range of frequencies with which they are evolutionarily designed to cope.

CONCLUDING REMARKS

Considering the state-of-the-art of modeling biological processes and relations within the frame of mathematical ecosystem models, it seems obvious that no satisfactory level of objectivity has yet been reached. Taking rational models (p. 5) as one goal, it is clear that the major part of the work is still to be done. This will include an increase in the experimental data bases, where the systems approach has to be kept in mind for the design of experiments and data collection, as well as the search not only for even more refinements in traditional formulations but--much more promising--for new theoretical approaches.

The previous sections were meant to discuss only a few aspects of modeling biological processes in the aquatic environment, using a few selected examples. However, some directions of major interest can be identified.

The use of time-varying parameters in the representation of complex biological processes can be seen as a first approach towards more biologically realistic formulations. Constant steady-state parameters have to be reconsidered as regards their dependency on various system variables under transient-state conditions. In addition to these often straightforward relationships, the role of internal control of biological systems, subsumed under adaptation and self-organization, must be emphasized. Theoretical as well as experimental work will be necessary to identify the basic components and goals of internal control, as well as the general strategies and mechanisms applied. The complexity of functional and structural adaptation in diverse natural biotic systems will, for conceptual as well as technical reasons, necessitate the identification of appropriate macrovariables and holistic features of ecosystems, together with the development of an appropriate general ecosystem theory on a holistic level. The inclusion of stochastic variability in model representations might be a first step in this direction.

There is little doubt that a thorough understanding of the basic functional relations in our environment is of a crucial and continuously growing importance. Scientific responsibility asks, therefore, for a solid and rational basis for any predictions, if ecological modeling is meant to be more than complicated curve fitting, computerized intuition, or at best, educated guesswork.

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APPENDIX "A"

LIST OF SYMBOLS

B	biomass
Chl.a	Chlorophyll a
E	activation energy
F	input variable
F_o	long-term average of input variable
F_u,F_l	upper and lower boundary of input range for adaptation
G	growth, production
G_G	gross production
G_{max}	maximum rate of primary production
$\bar{G}$	daily sum of primary production
G^B	primary production normalized to biomass
I	incident radiation
I'	daily mean of incident radiation
I_o	sub-surface irradiance
I_{opt}	light saturation level for photosynthesis
K	reaction rate
K_s	Michaelis constant (substrate specific)
K_Q	Michaelis constant (cell quota specific)
LF	light/nutrient factor
M	metabolic rate
Q	cell content of a nutrient (cell quota)
Q_o	threshold level of nutrient in the cell
Q_A,Q_B	cell quota of nutrient A,B
Q_{10}	temperature coefficient
$\bar{P}_c$	community parameter estimate
R	universal gas constant

R_T	rate reduction factor due to temperature
S	substrate (nutrient) concentration
T	temperature
T_u, T_l	upper and lower lethal temperature for photosynthesis
T_{opt}	optimum temperature for photosynthesis
T_{min}, T_{max}	temperature limits for adaptation
TF	temperature factor
V	specific nutrient uptake rate
V'	absolute uptake (transport) rate
V_{max}	maximum uptake rate
a,b,c,g,h,n,	constants
f	photoperiod (fraction of day)
k_i	importance value fraction of i-th species
t	time
α	initial slope of G vs I curve
β	carbon to chlorophyll ratio
γ	temperature constant
δ	slope of μ vs 1/T
ε	extinction coefficient
θ	temperature coefficient
μ	specific growth rate in terms of nutrient uptake
ρ	nutrient specific (1/Q) maximum uptake rate
τ_1, τ_2	components of temperature factor TF