ESTIMATING MODEL PREDICTION ACCURACY: A STOCHASTIC APPROACH TO ECOSYSTEM MODELING

Kurt Fedra

November 1980
WP-80-168

INTERNATIONAL INSTITUTE FOR APPLIED SYSTEMS ANALYSIS
A-2361 Laxenburg, Austria

PREFACE

In recent years there has been a considerable interest in the development of models for river and lake ecological systems. Much of this interest has been directed towards the development of progressively larger and more complex simulation models. In contrast, relatively little attention has been devoted to the problems of model uncertainty and errors in the field data, of inadequate numbers of field data, of uncertainty in the relationships between the important system variables, and of uncertainty in the model parameter estimates. IIASA's Resources and Environment Area's Task on "models for Environmental Quality Control and Management" addresses problems such as these. They are important methodological problems in the modelling of poorly-defined environmental systems, which is a principal theme of the Task. This paper examines how the uncertainties of the model calibration exercise affect the confidence that can be placed in predictions of future behavior obtained from the model (se also Working Papers WP-79-27, Wp-79-63, WP-79-100, WP-80-87).

A second principal theme of the Task on Environmental Quality Control and Management is a case study of eutrophication management in two Austrian lake systems. This paper is also a contribution to that case study.

ACKNOWLEDGEMENTS

The research described in this paper was carried out within the frame of the "Austrian Lake Ecosystems Case Study", supported by the research grant N.3905 of the "Fonds zur Förderung der wissenschaftlichen Forschung, Austria."

The author feels indebted to his colleagues G.van Straten and M.B.Beck for their valuable contributions during numerous discussions and to A.John for her linguistic help.

This paper was presented at the Second International Conference on the State-of-the-Art in Ecological Modelling, held at Liege, Belgium, April 1980.

ABSTRACT

Ecosystems are, as a rule, characterised by a large behavioral repertoire showing a high degree of structural variability and complex control mechanisms such as adaptation and self-organisation. Our quantitative understanding of ecosystems behavior is generally poor, and field data are notoriously scarce, scattered, and noisy. This is most pronounced on a high level of aggregation where considerable sampling errors are involved. Also, no well established and generally accepted ecological theory exists, so that an operational ecosystem model consists of many more arbitrary, simplifying assumptions (more often than not implicitly hidden in process descriptions) than properties measurable in the field. Consequently, predictions of future systems behavior under changed conditions -- a most desirable tool for environmental management -- cannot be precise and unique in a deterministic sense. Rather, it is essential to estimate the levels of model reliability and the effects of various sources of uncertainty on model prediction accuracy. A concept of allowable ranges for model data-input and expected model response, explicitly including uncertainty in the numerical methods, is proposed. Straightforward Monte Carlo simulation techniques are used, and the approach is exemplified on a lake ecosystem eutrophication problem. The method attempts to predict future systems states in terms of probability distributions, and explores the relations of prediction accuracy to data uncertainty and systems variability, the time horizon of the prediction, and finally the degree of extrapolation in state- and input-space relative to the empirical range of systems behavior. The analysis of almost 100,000 model runs also allows some conclusions on model sensitivity, and some desirable model properties in light of prediction accuracy are identified.

1. INTRODUCTION

Let me consider a mathematical model of an ecological system from a very pragmatic point of view, namely as a means to an end, which I will (rather narrowly) take to be the prediction of the system's response to changing conditions. "Conditions" stands for everything which is outside the system as defined by the model and is generally identified with the imports (material inputs) and forcings which drive and control the systems performance. But it could also comprise any factor likely to alter the systems behavior, which in a given model might be represented by a certain coefficient or parameter; from the pragmatic point of view I would like to adopt, there is no difference between an input or a coefficient: both are numbers one has to specify to run the numerical model.

The model, which is the model structure (which qualitatively describes the relations within the system or between its elements, and the relations of the system to its environment, the above "conditions") and a set of coefficients which quantifies the structural relations, is taken to represent the real world system. That means, that for a given set of environmental conditions or inputs, the model should reproduce the behavior of the system observed under these conditions. These conditions and the associated behavior of the system are the data we have, available (if at all) in the form of samples in time and space, of certain variables or properties of the system. The separation of the data into input conditions and behavior is of course only meaningful in terms of the model one uses, and depends entirely on the definition of the (model) system. Also, the selection of those properties one samples, to describe the system and its environment, depends basically on some (intuitive) concept of the system.

Rarely will the data one might have about a specific ecosystem allow one to derive the model structure, if one has in mind what is generally called a physical or mechanistic model, which also claims to have an explanatory value: each term in the model should have some physical meaning, and in principle should be measurable or experimentally accessible. However, environmental sciences provide us with a vast body of information, which (although scattered and sometimes even contradictory) allows the conjecture of a model structure for a given system, with only minimal specific data. Using such a priori information of course makes it necessary to test the conjectured model structure; however, as this involves a high number of additional assumptions which are all more or less interdependent, this is very difficult to achieve in a scientific way. The basic problem might be that the field data one generally has, do not directly represent the elements and processes conjectured in the model, or, the other way round, that most models do not describe what has been measured.

Typically, the data describing a certain ecosystem and its environment will consist of a time-series of point measurements with a certain spatial distribution. However, the measurements rarely have been done on exactly the objects or properties which are represented in the model, let alone their time- and space-resolution. Most of the measurements can only be taken as an approximation of what is conceptually used in the model, as for example "available nutrients" approximated by e.g. orthophosphate or nitrate. Often some (constant stoichiometric) conversion has to be made, e.g. if chlorophyll measurements are to be used to estimate algae biomass in terms of say phosphorus, or if productivity (in terms of nutrient uptake) is measured by C^{14} techniques. Another major controversial point is the problem of aggregation and averaging. This applies to spatial distributions as well as to variability in time (within the model time step), and also to functional heterogeneity within lumped compartment a as for example "primary producers". In each case certain assumptions have to be made when model output is to be compared with field data: generally these are the assumptions of homogeneity, and linearity or additivity. Being aware of these problems, one would have to take a sufficient amount of measurements and determine their sample statistics (which, in fact again depend on some conjectures of the system and the parent distributions of the variables). Ideally, one would have to directly measure on the appropriate level of aggregation. However, any practitioner in the field knows about the practical, logistic problems of a statistically sound measurement design, especially for large and diverse ecosystems. And many of the compartments used in ecosystems modeling are more easily drawn in a flow chart, than measured.

In practice, strictly appropriate information does not exist, and we are left with scarce and scattered unsynoptic data on the wrong variables. Generally, the analyst ignores that, makes the above assumptions (more often than not unconsciously) and proceeds with some calibration of the model, using what data he has. The input conditions (represented by the inputs and forcings) measured in the same insufficient way as the behavior of the system are assumed to be exactly known, and the estimated "best" parameter vector is then used for predictions of the systems response to changes in the input conditions. Admittedly, this critique is somewhat biased, and without doubt there exist many approaches to account for the above problems (e.g. Lewis and Nir 1978, Di Toro and van Straten 1979, Fedra 1979b, Fedra in press, Fedra et al. in press).

If one recognises that the information we have about an ecosystem is fuzzy, then the model also has to be fuzzy. This seems to be the case already for a descriptive use of a model, and obviously when we attempt to predict, a further element of uncertainty is introduced, as our knowledge about the future input conditions for the system can at best be of a statistical nature. Even if some kind of control and management is to be simulated, there is no such thing as a complete control for a natural ecological system. The importance of the fuzzy nature of ecological processes for control and management is increasingly emphasised on different levels of complexity (Clark et al. 1979, Beck et al.1979).

Returning to the pragmatic point of view suggested above, the problems raised can obviously not be solved by assuming them away; uncritical confidence in numerical methods based on unproven (and often unprovable) assumptions can hardly result in reliable predictions. Obviously, all the limitations and insufficiencies have to be considered, and uncertainty, fuzziness, and unknown variability have to be explicit parts of a forecasting exercise. As uncertainty seems to be an inevitable integrated element of prediction (and this holds true not only for ecosystems modeling), it has to be accounted for. Estimates of prediction accuracy or error propagation in a model based forecast should be an essential part of the prediction itself, if only to make obvious the limits of predictability.

2. THE APPROACH

The basic attempt in the proposed approach is to avoid arbitrariness and unwarranted assumptions as much as possible, and wherever this seems to be impossible, at least to make them explicit and explore their effects on prediction. The approach tries to explicitly include data uncertainty as well as systems variability. It does not attempt to estimate a unique best set of model parameters (assuming the input conditions and the reference behavior for the calibration procedure to be exactly known), but looks for an ensemble of acceptable solutions to the calibration problem, explicitly allowing for the uncertainty in input conditions and observed behavior. This ensemble of model inputs (comprising parameters as well as input conditions and initial states) is used for predictions, where only one or a few conditions are changed. This of course results in an ensemble of answers, which allows a probabilistic (in a somewhat subjective sense) interpretation of the forecasts.

2.1 The concept of allowable ranges

Reconsidering the meaning of field data in terms of the systems elements and properties conjectured in the model, we obviously have only some rather uncertain estimates of the values we are looking for, namely the numerical values describing the input conditions, the model parameters, and finally the expected ("observed" in the field) behavior of the model. Clearly, forcing the model output trajectories through the measurement points by means of a highly sophisticated calibration scheme might produce quite meaningless answers, especially as the data for the input conditions will have to be assumed as being known exactly. Rather, one might try to deduce, from the available information, plausible ranges within which each of the numbers we have to specify has to be. The specification of these allowable ranges can of course take advantage of data from the literature, and certainly all the available data might be appropriately lumped or pooled. Being aware of the fact that ecosystems might have a rather large behavioral repertoire, it is very important, for the explicit purpose of prediction, to capture all of that repertoire in estimating the model parameters. Since we cannot exclude the possibility of any of the systems behavioral features occurring in the future, we have to account for them in the way we predict.

Allowable ranges are specified for the model parameters as well as for the input describing data, which together form the model input data (the set of numbers one has to put into the model to run it). The more data there are available, the narrower the ranges can be - if there are almost no data available, one can at least define some limits of physical or biological plausibility (e.g. an extinction coefficient cannot be smaller than that of clear water, or a daily growth rate for phytoplankton should hardly exceed a value of ten). Generally, the wider a range is specified, the more likely the true value (whatever that may be) will lie within it, but the less useful this information will be. One obviously has to compromise between arbitrariness and meaninglessness in many cases, which should throw some light on the usefulness of a formal model or analysis in such a case.

2.2 The concept of response-space

The kind of information one needs for the specification of the input data (parameters and input conditions) is largely determined by the structure of the model. The comparison of model output with the observations on the system behavior are much more flexible. Again ranges are used, but these ranges can be defined for various measures of different kinds: besides the more straightforward range within a given variable has to be at a given point in the period simulated, relational and integrated measures might be used as well. Total yearly primary production, or the minimum relative increase of phytoplankton biomass, the maximum allowable peak value, average trophic efficiency of a biological compartment and many more similar conditions can be specified in terms of ranges. Generally, not only state values but also process rates and flows as well as their sums or integrals over certain periods and various relations between such measures can be used to define the expected model reponse; the selection of appropriate measures depends largely on the kind of information available about the system. Considering each of these measures as one dimension of a hyperspace, the model response clearly has to be within the region defined by the ranges (Fig.1). The description of the systems behavior is thus conceptualized as a region in n-dimensional hyperspace, where -- given a high number of observations on the systems behavior over a comparatively long period of time -- probability density might be an additional dimension.

Ecological systems, most pronounced in temperate zones, perform periodic fluctuations within a seasonal cycle. For many systems, cyclic stability with regard to certain features can therefore be an important condition to meet, unless an obvious trend was observed. In the absence of such a trend, however, the input conditions can be assumed to be of a cyclic stable nature, and pooled to derive the estimates for the above ensemble. Consequently, observations on systems properties in comparable periods of different years can also be pooled, and the resulting behavior definition envelops the systems behavior in a certain period. This envelope includes not only the variability due to measurement or sampling errors, but also the variability of the system including the input conditions in this period, as the assumed cyclic stability is of course no perfect one. Again, if the resulting definition is broad to the extent of meaninglessness, this would suggest that an important determining element which was not constant or cyclicallly stable during the period of observations failed to be recognised, or simply, that the available data are insufficient to describe the system precisely enough for a formal analysis.

2.3 The concept of probabilistic behavior

Given the allowable ranges for the input data (again a region in a hyperspace) and the behavior definition, the ensemble of input data combinations or models (model structure plus input data) is sought, which produces the expected response in accordance with the behavior definition. The numerical method to do so is a straightforward application of Monte Carlo techniques. A random sample from the input data space is taken, used for a run of the simulation model, and the resulting model response is then classified according to the behavior definitions. If all the definition constraints are fulfilled, the input data set is saved, and the process repeated until a sufficient number of data sets has been found. This can, for example, be tested by some appropriate statistics of the data sets themselves, and the search is stopped, whenever the distributions and correlation structure of the behavior giving data sets are more or less unchanged by additional data sets.

The resulting ensemble of data sets and model responses represents (for a given system in a certain period, conceptualized in a given model, described by a given data set, and all the additional a priori information one might have) the "best available knowledge". Each of the single "answers to the calibration problem" is an equally valid description of the system. The variability in the ensemble of data sets and model responses reflects the uncertainty associated with the conceptualization, the observations, and finally the variability of the system itself. As stated above, too large a variability should make one cautious to proceed with a formal analysis; rather, more information about the system should be sought.

The available information, however, is of a statistic or probabilistic nature (although in a rather subjective sense). Each of the model responses in the behavior class might be understood as a sample from the overall response space of the model, which is taken to represent the behavior space of the system. From the frequency distributions of the variables considered, some conclusion on the probability density distribution of the behavior space could be drawn. The behavior space is characterised by the probability distributions along the individual axes as well as by the cross-correlation structure. The concept of the behavior space is readily extendable for the predictions. Changing any of the input data to represent some change in external or internal conditions, will result in an ensemble of predictions which could be interpreted in the same probabilistic way. The probability density of the predicted response will again allow an estimation of the relative accuracy of the forecasts, especially if they are extended for a long time relative to the observation period (Fig. 2). Trivial projections in terms of the questions posed might mainly be taken as a warning that the limits of predictability (on the basis of the information utilised) are reached.

3. AN EXAMPLE OF APPLICATION

The approach outlined above has been applied to the test case (among others) of a lake ecosystem. Recent concern about the eutrophication of the lake as well as the installation of sewage diversion and treatment plants suggested a formal analysis of the relation of the lake's water quality to the nutrient loading. The basic problem was the prediction of future water quality (in terms of several variables such as primary production, algae biomass, or nutrient concentrations) as related to different phosphorus loading, resulting from different potential control options. Characteristically, the data set available was not sufficient for a detailed, spatially disaggregated description of the system.

3.1 Ecosystem and simulation model

The lake system used for this analysis is the Attersee, a deep (171m, average depth 84 m), large (3.9 109 m3, 46 km2 surface area), oligotrophic lake in Austria, with an average theoretical retention time of seven to eight years. A detailed description of the physical and limnological features of the lake can be found in the "Attersee"-reports of the former OECD lake eutrophication project and the ongoing Austrian Eutrophication Program, Projekt Salzkammergutseen (Attersee 1976, 1977, Müller 1979). The available data made it possible to estimate ranges for the phosphorus loadings, the in-lake concentrations of phosphorus, algae biomass dynamics, primary production, and finally phosphorus export. Average hydraulic loading, light/temperature patterns over the year and thermocline depths could also be estimated from a four year data set. The resulting estimates in terms of model input data for the model described below are given in Fedra (1979b). Generally, the ranges for most of the estimates were in the order of +/- 50% of the mean values.

Rather than developing one more simulation model for the above purpose, an available model which included the main features under study (Imboden and Gächter 1978) was modified for the approach described. The model, which dynmically simulates particulate phosphorus (algae) and dissolved phosphorus (limiting nutrient) for a stratified lake with variable thermocline depth, uses Monod kinetics, self-shading of algae, a first order loss term directly coupled to remineralization, and sedimentation. The model includes hydraulic loading, inflow and outflow of phosphorus, and estimates primary production per unit lake area, using a time varying production rate coefficient (integrating the effects of light and temperature). A completely mixed epilimnion is assumed, whereas hypolimnion concentrations are computed as functions of depth, using eddy diffusivity, which is also used to describe exchange processes through the thermocline. To facilitate the use of the model in the Monte Carlo framework, auxiliary parameters had to be defined to describe the time varying production rate coefficient (by means of a sine function, specifying minimum, maximum, and the time of the maximum) as well as the depth of the thermocline, using a linear interpolation between starting-time/depth and end-time/depth. Altogether, 22 input-data, including the auxiliary coefficients and the initial conditions have to be specified for the model.

The behavior definition uses ten constraint conditions describing a region in a 7-dimensional response space for the model: the constraints are defined for yearly primary production, algae biomass peak (maximum and timing), relative increase of algae, orthophosphate maximum during the mixed period, yearly phosphorus output, and finally cyclic stability of total phosphorus (maximum relative difference between beginning and end of the simulation year).

3.2 Exploring the model response

From 22-dimensional regions in input-data space (each defined by a set of ranges) altogether 23000 samples were drawn and used for model runs. The model response space corresponding to the gross (unstructured, disregarding any correlations between the input-data) input-data space was plotted on planes of two response variables used in the behavior definition (Fig. 1). The figure contrasts the response from a rather broad definiton with a (although quite arbitrary) narrow one, which could simulate "increasing knowledge" about the system. In any case, the independent selection of input values from ranges with an assumed rectangular probability density function, resulted in only a small percentage of "successful" behavior-runs (between 0.5% to about 10%, depending on the definitions used). As expected, the set of input-data for the behavior group shows a marked correlation structure. Rather than the individual absolute value for a single coefficient, the combination of values determined the model behavior. Extreme values for a given coefficient can well be balanced by smaller changes in several other coefficients to result in the same response-region. These findings should throw some light on attempts at rigid deterministic calibrations with reference data and input conditions assumed to be certain.

Figure 3 shows an ensemble of behavior-runs ("stochastic mean" with a minimum/maximum envelope) resulting from the standard definition set; the plots for the state variables particulate phosphorus and phosphate are found to envelope the comparable 5-year data set from the lake. However, it should be stressed again that the comparison of field data with the model output is somewhat dubious: whereas "particulate phosphorus" in the model includes only living algae's phosphorus (actually assuming a constant proportion of phosphorus in the photosynthesizing biomass), the field measurements do not discriminate living algae and everything else containing phosphorus that would be retained on the filters used in the chemical analysis (e.g. zooplankton and all kind of organic detritus). The same is true for the "phosphate", which in terms of the model represents all "directly utilizable for photosynthesis" phosphorus, which is clearly neither $P\text{-}PO_4$ nor soluble phosphorus.

3.3 Extrapolating into the future

Predictions of future systems response to changes in the phosphorus loading conditions were made by subsets of the behavior-giving input-data ensemble, where the loading determining coefficients were changed by a certain factor. This "relative" change not only accounts for the uncertainty in the inputs, but also preserves the correlation structure of the behavior generating ensemble of input-data sets. Input changes representing increases of 50% and 100% (to simulate the effect of no control actions but increasing nutrient release in the catchment area) and reductions to 75%, 50% and 25% of the current (1975-1978) empirical range of loading were simulated for a ten year period. Some examples of these scenarios, again showing the stochastic mean with a minimum/maximum envelope are given in Figure 4.

To estimate prediction accuracy as related to the changes in the phosphorus loading (the degree of extrapolation in input space), and as related to simulation time (the extrapolation in time), the coefficient of variation vs extrapolation was plotted. Figure 5 shows one example for the model output variable yearly primary production. The plot shows an increase of prediction uncertainty with time, stabilizing when a new equilibrium is reached after a transient period following the change in the phosphorus loading. The plot also indicates an increase of uncertainty with the amount of change in the input conditions, showing a minimum of the coefficient of variation in the empirical range. Summarizing, prediction uncertainty (measured as the coefficient of variation of the Monte Carlo ensembles) increases with the extrapolation in time as well as in input space. Being related to the initial variability in the descriptive empirical case, there is an obvious (and intuitively to be expected) relation of prediction reliability or non-triviality to these three magnitudes: input variability (incorporating data uncertainty and systems variability in time), degree of extrapolation in the controlling inputs, and the degree of extrapolation in time. Obviously, the more precise the original knowledge about the system is, the larger the extrapolation in the controlling conditions and in time can be, before the limits of predictability are reached; or, the larger a change is to be simulated, the better the knowledge about the system has to be.

A different representation of prediction accuracy was shown in figure 2 (where prediction refers to the mean estimate, and accuracy is measured in terms of confidence intervals). The probability distributions fitted for the response variable frequency distributions can be read in the above terms. These probability distributions are not primarily to be understood as the probabilities of certain systems states in the future -- they are rather representations of prediction uncertainty, or the propagation of the initial uncertainty and variability in the available information. However, being aware that the predictions are biased by the (unrepresented) model-error (e.g. O'Neill and Gardner 1979), the probability distributions for future states might also be interpreted in the usual way.

4. DISSCUSION

The above analysis and the generalizing conclusions to be drawn are certainly biased with regard to the model used and, to a lesser extent, with regard to the data set used. The arbitrary selection of any model for a given system seems to be unavoidable in light of the meager data available; the model order and structure cannot be derived from the available data, and one has to use a priori information about the system to be described. However, the thus conjectured model might well turn out to be inadequate, and changes in the model structure will become necessary. One indication of inadequate model structure -- in terms of the above approach -- would be, if no behavior-giving combinations of input-data can be found in the specified region; or if the distributions of the single input data within the ranges sampled suggest a high number of possible solutions outside the specified "plausible" bounds. If a combination of unrealistic inputs still results in a realistic behavior of the model, one might also question the validity of the model structure. This of course requires that the expected behavior is defined in a sufficiently detailed way.

The variability in the prediction results directly from the variability in the ensemble of input-data used. And the variability of the input-data stems from two basic sources, both reflected in the ranges used for the initial input-data space to be sampled, and in the ranges describing the empirical systems behavior: data (measurement) uncertainty and systems variability. By including systems variability (through the use of several year's data), future variability in the conditions driving and controlling the system are somewhat accounted for (under the assumption that a representative part of the systems behavioral repertoire has been captured in the observation period). This should also account for another basic problem of the "naive extrapolation" approach: systems containing biotic elements are known to adapt to changes in their driving conditions, their structure and parameters (in terms of a model description) are state- and input- dependent (cf. Fedra 1979a, Straskraba 1976, 1979).

The above analysis indicated, that for a model with 22 input-data (which, at least for ecological models is a rather low figure) or "degrees of freedom" in the estimation procedure, behavior-giving values can be found all over the ranges (independently) sampled. On the other hand, only a small percentage of the possible combinations resulted in a satisfactory model response. As a consequence, the ranges for the search should be constrained as much as possible, for reasons of effiency as well as to avoid "unrealistic" input-data combinations (where the unrealistic value in any of the parameters or inputs will be "balanced" by some changes in all the other values) in the behavior ensemble. This of course requires, that all the parameters used in the model are physically interpretable and can be measured or at least estimated from field measurements or experiments. The same holds true for the state variables of the model and measures derived: only if they are measured (or are at least measurable), can their allowable values be reasonably constrained in the definition of the systems' behavior. Including unmeasured (and unconstrained) state variables will result in behavior runs (in terms of the constrained measures), where the uncertainty is all transferred to this unconstrained "leak" in the behavior definition. The ability of even a simple model to balance its (constrained) response in terms of some variables by (unconstrained) changes in others, requires that all model behavior (and, of course, output), should be interpretable in physical (measurable in the field) terms. Also, the above approach raises some doubt whether models by including more and more detail (requiring more and more state variables and parameters, and consequently more data for the "calibration") become more realistic. Obviously, increasing model complexity without increasing the available data for constraining input-data ranges as well as allowable response ranges, just adds degrees of freedom for the calibration or estimation procedure. Undoubtedly such models can be very useful, especially in more qualitative "hypothesis testing" approaches. But their value for prediction might well be questioned.

Uncertainty in ecological modeling seems to be an inevitable element in the method as well as in the object of study, which is most obvious when one tries to predict the future. The analysis of model uncertainty and its "inverse", prediction accuracy, is certainly at an early stage of development (cf. O'Neill and Gardner 1979). However, being aware of model, and especially prediction uncertainty and the thus obvious limits of predictability, might well help to avoid a naive trust in numerical models. Analysis of the various sources of model uncertainty and their relations and interdependencies will be necessary to improve model applicability. And the least impact from model error analysis on model application should be a critical re-evaluation of the questions that can reasonably be answered by means of numerical models.

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Strǎskraba,M. 1979 Natural control mechanisms in models of aquatic ecosystems. Ecol.Model. 6: 305-321. Figure 1: Response-space projections on output-variable planes, indicating the expected (empirical) ranges of behavior; standard input-data space definition (left) and symmetrically reduced sub-region (right).

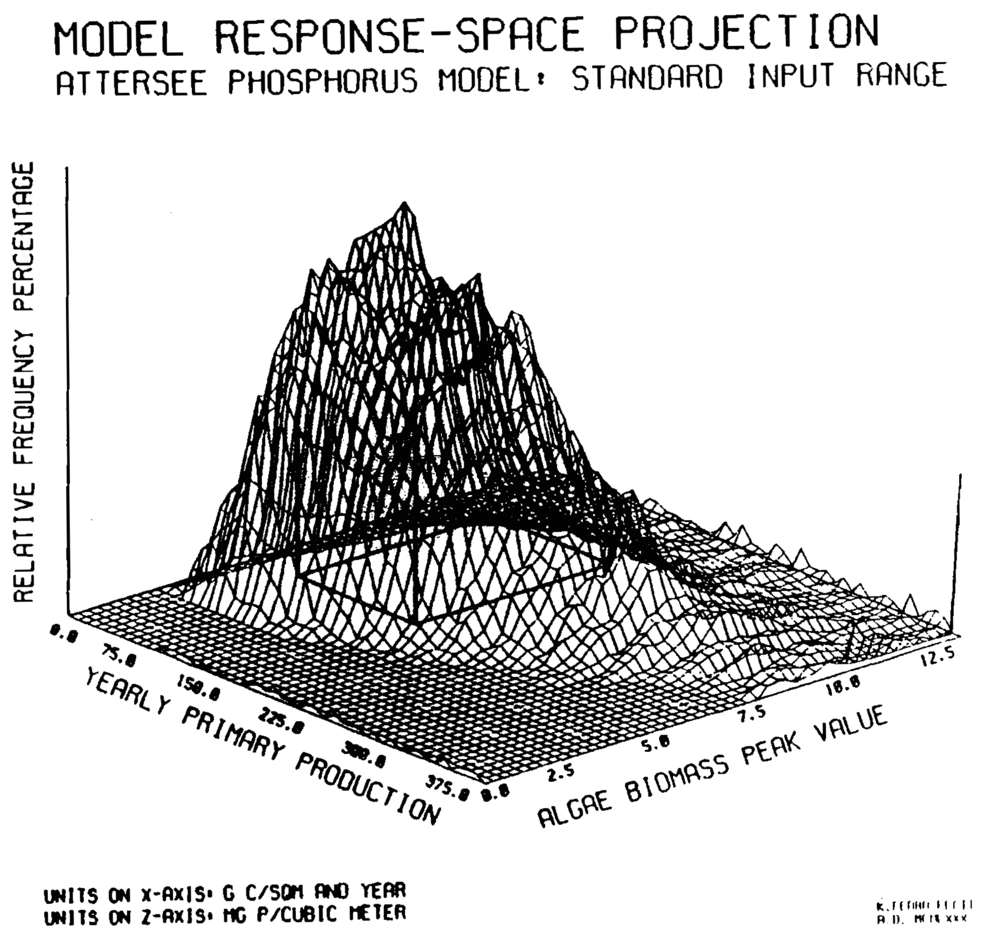

Figure 1a. Response-space projections on output-variable planes, indicating the expected (empirical) ranges of behavior; standard input-data space definition.

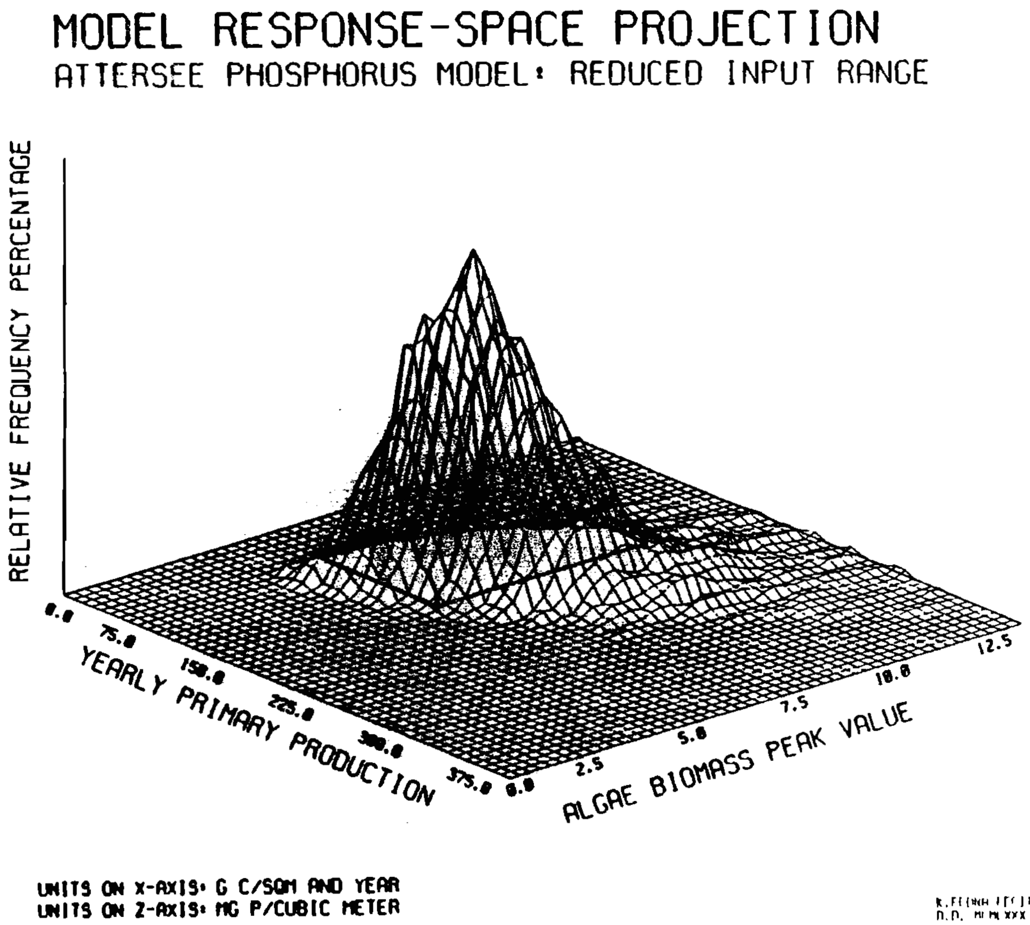

Figure 1b. Response-space projections on output-variable planes, indicating the expected (empirical) ranges of behavior; symmetrically reduced sub-region.

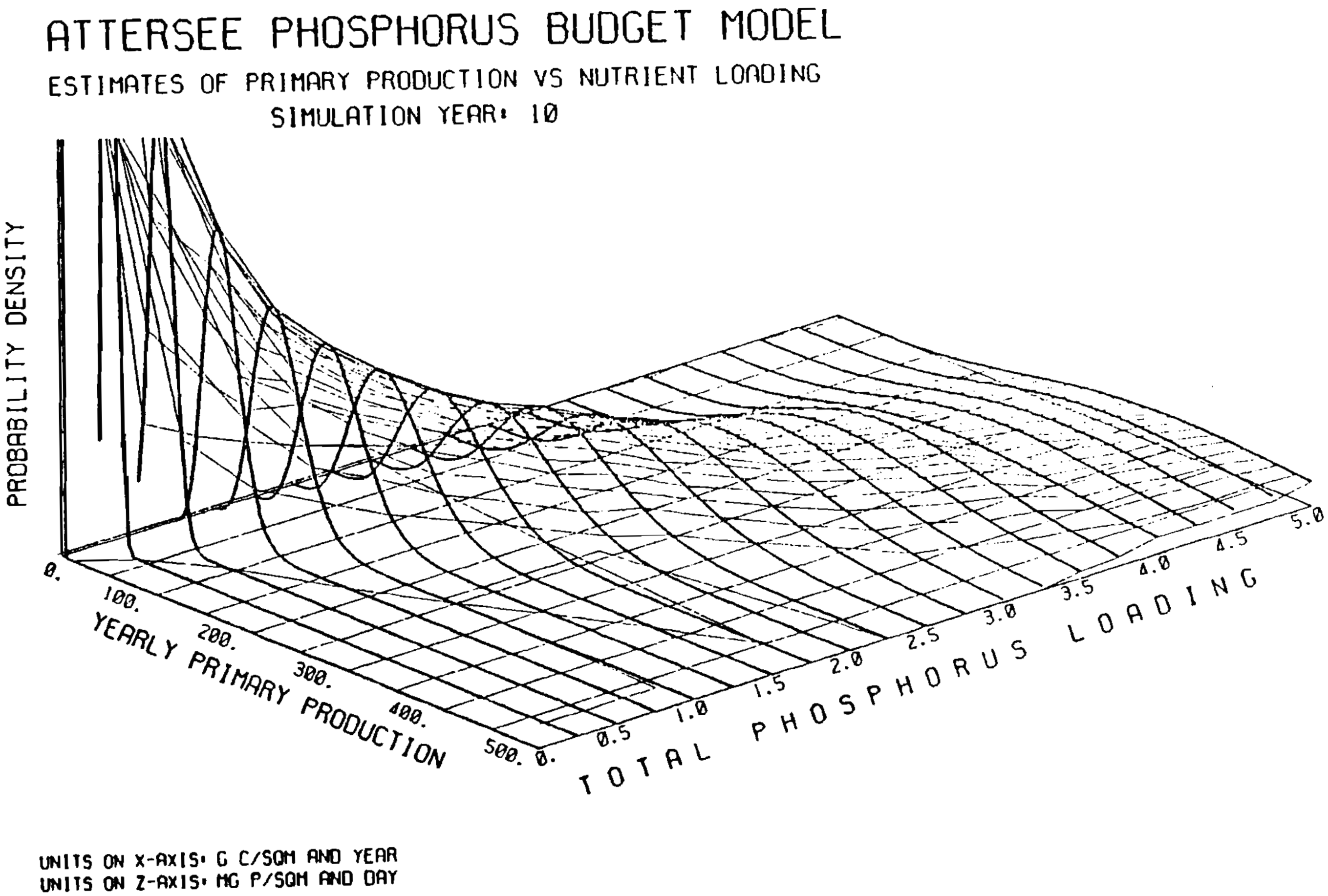

Figure 2. Probability distributions for yearly primary production at various levels of phosphorus loading. Equilibrium values after 10 simulation years. Note the large ranges in the high loading classes; empirical loading is estimated around 1 mg P m^{-2} day^{-1}.

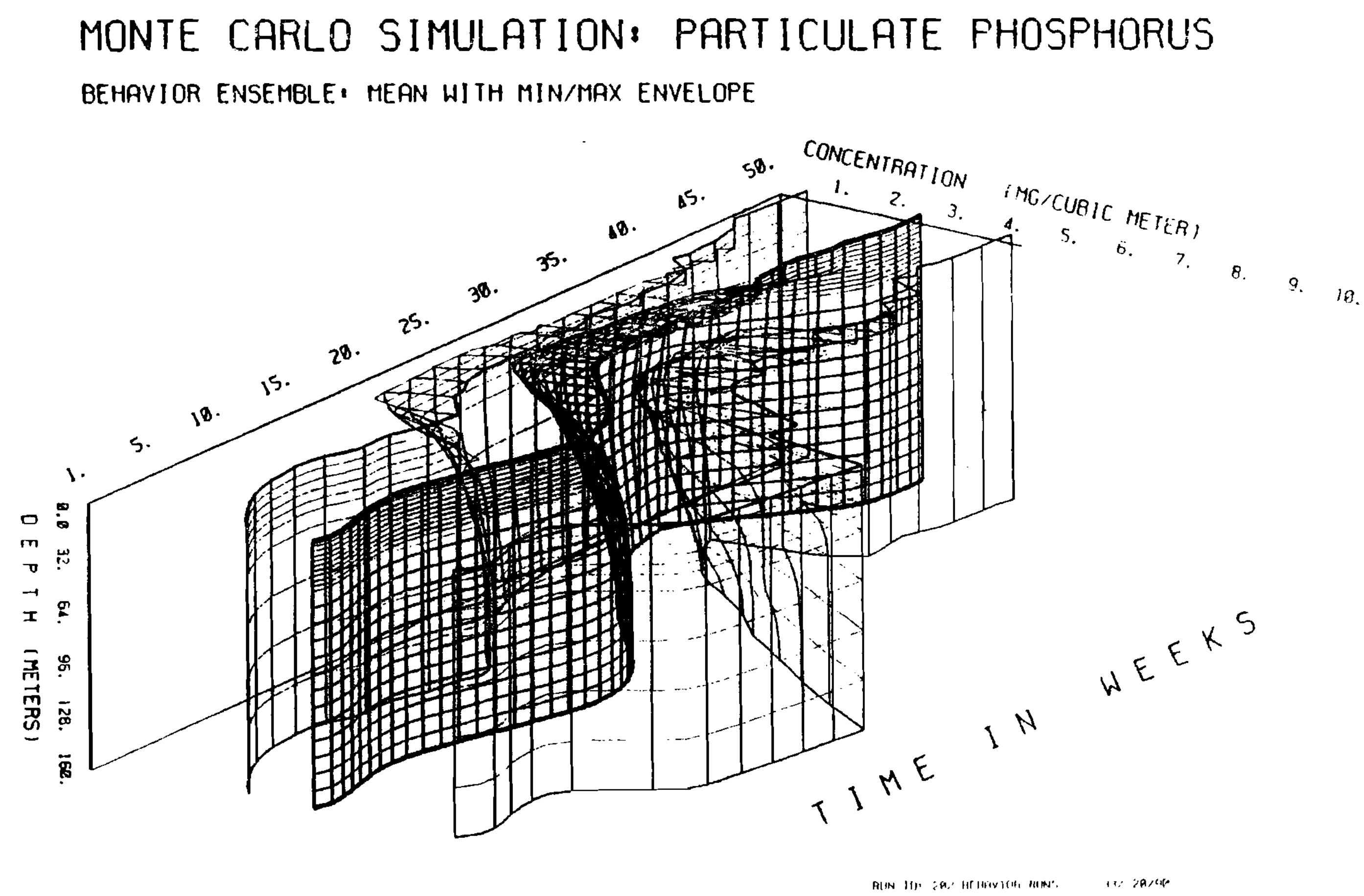

Figure 3a. Monte Carlo ensemble (arithmetic mean with minimum/maximum envelope) of "behavior" runs compared with Figure 3b.

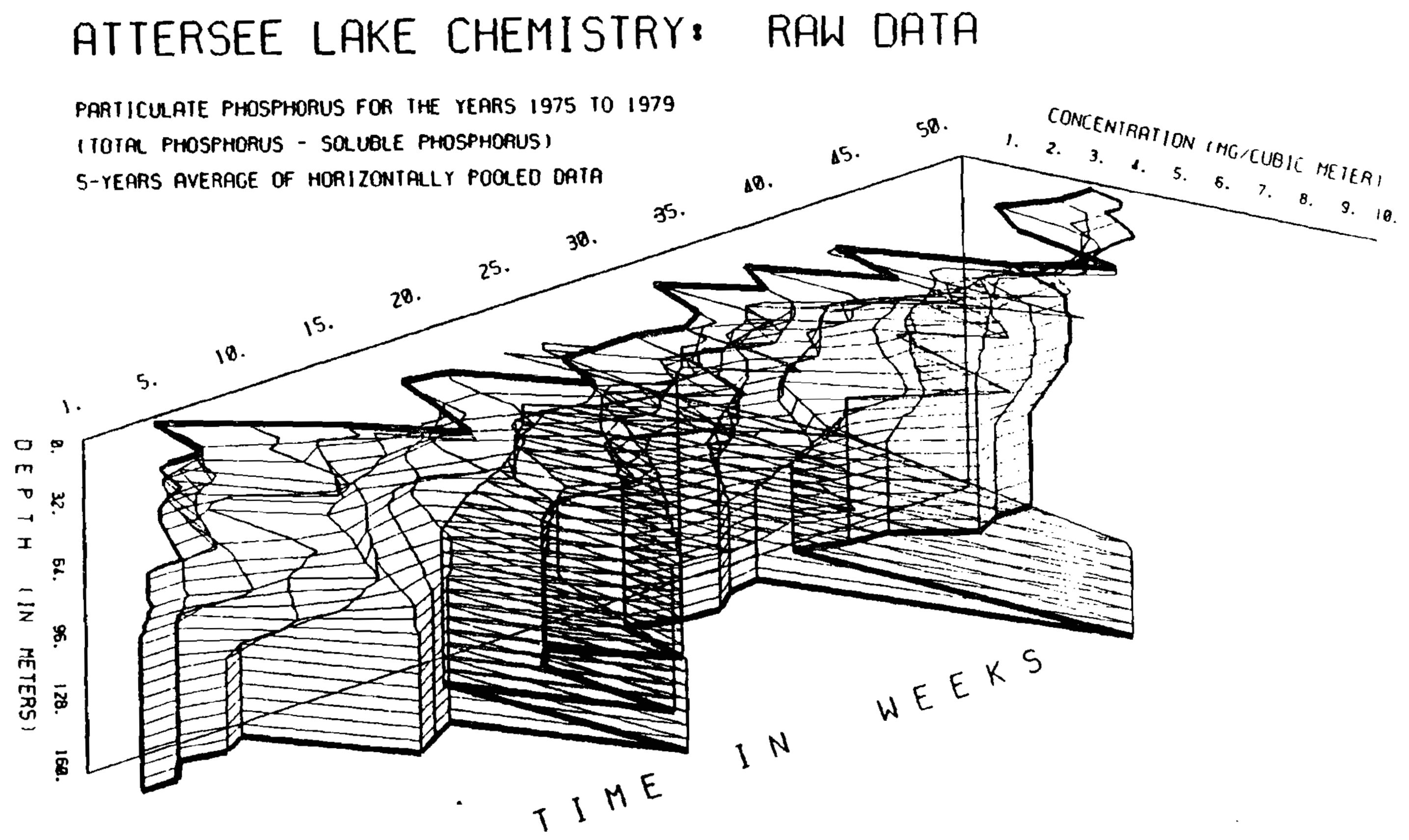

Figure 3b. Field data set averaged for a five-year period (raw data courtesy of F. Neuhuber).

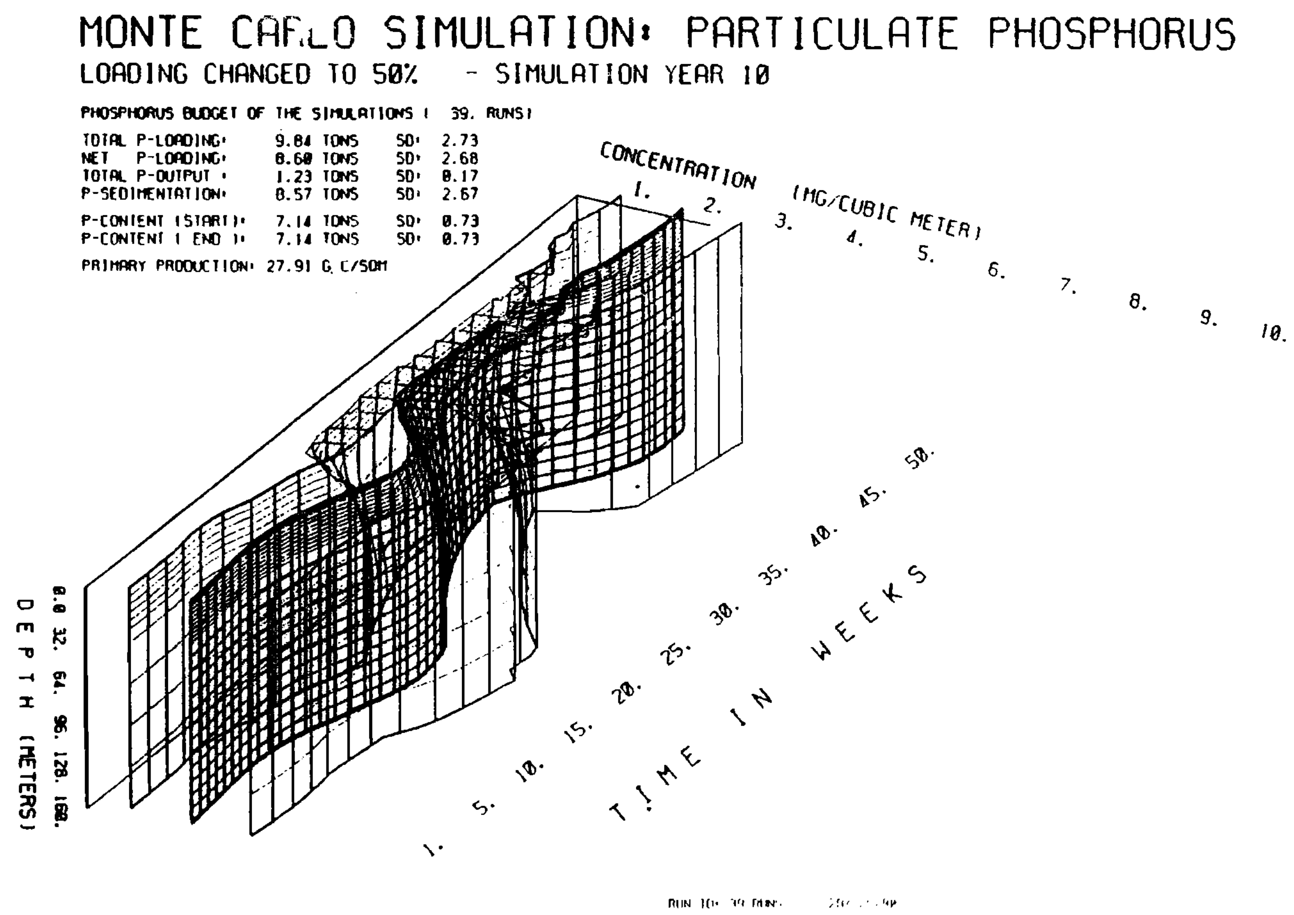

Figure 4a Monte Carlo ensembles (arithmetic mean with minimum/maximum envelope) for phosphorus loading conditions changed to 50%.

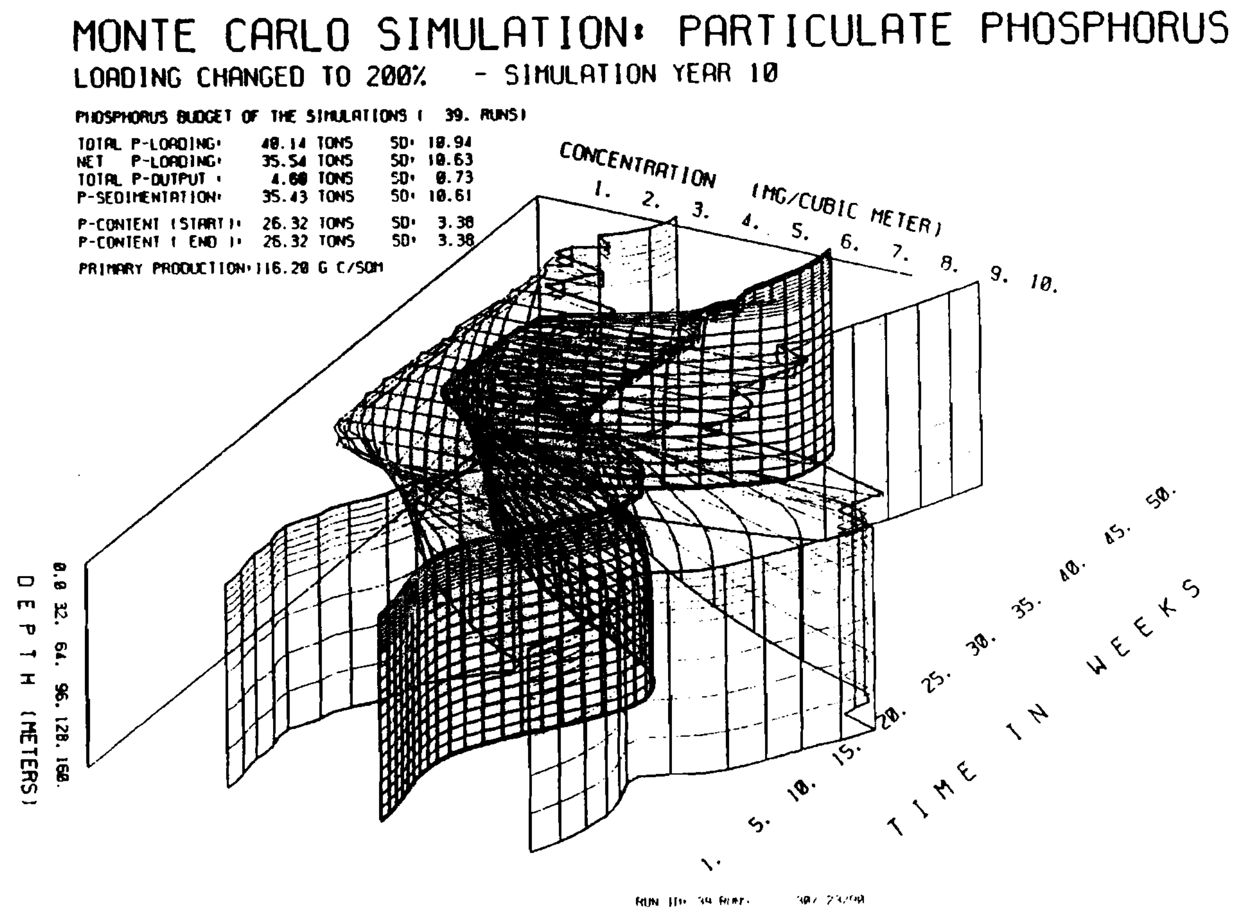

Figure 4b. Monte Carlo ensembles (arithmetic mean with minimum/maximum envelope) for phosphorus loading conditions changed to 200% of the empirical loading.

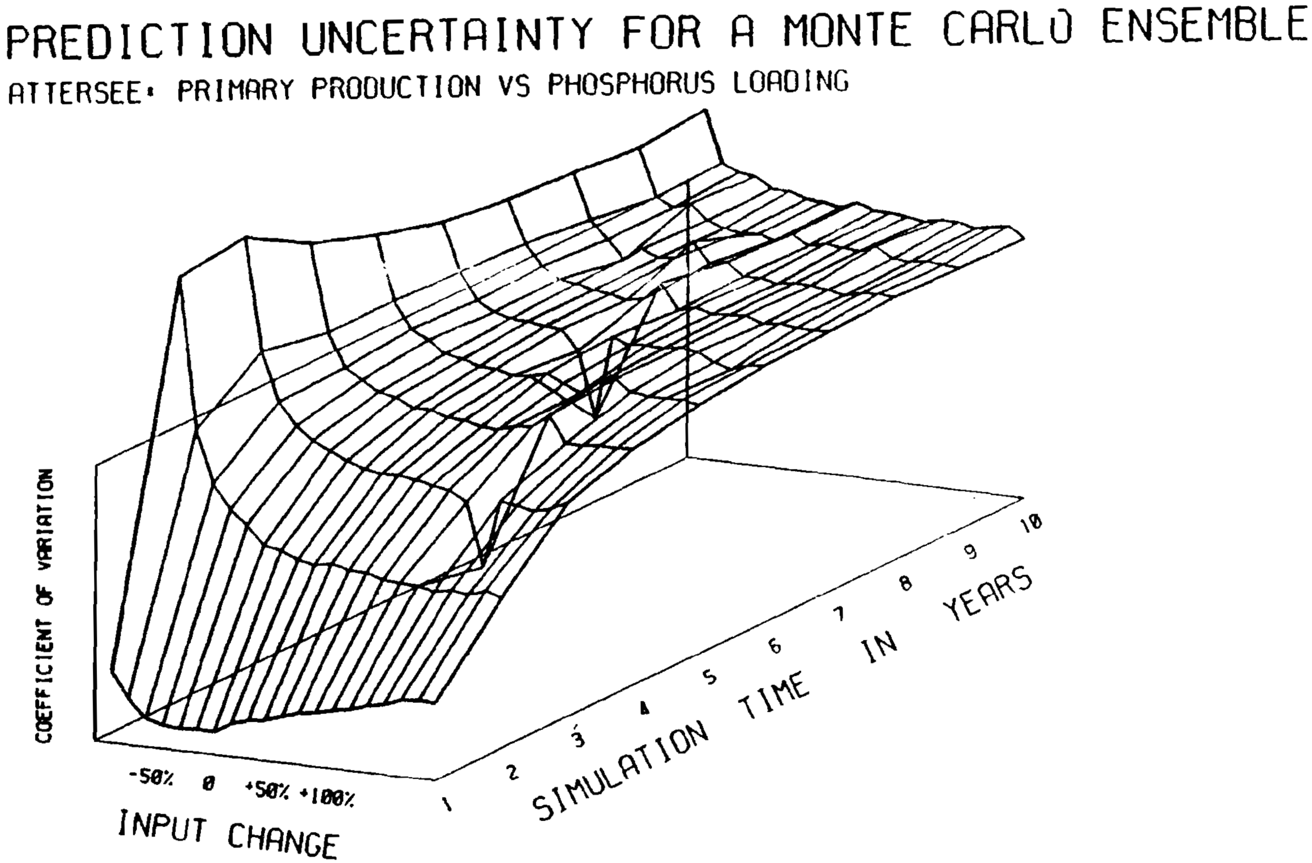

Figure 5. Coefficient of variation for selected response variables vs. simulation time and input extrapolation.