



International Biological Program
Analysis of Ecosystems
Eastern Deciduous Forest Biome
Memo Report 71-19

LAKE GEORGE MODELING PHILOSOPHY

By

Richard A. Park
and
John W. Wilkinson

Department of Geology
and
School of Management

With Contributions From:

W. A. Wallace
J. A. Bloomfield
J. S. Fisher
I. K. Hwang
Samuel Katz
R. C. Kohberger
J. P. Weyant

FWI Report No. 71-5

October 1971
Rensselaer Polytechnic Institute
Troy, New York

US-IBP E.D.F.B. Memo Report 71-19

Lake George Modeling Philosophy

This memo report contains information of a preliminary nature prepared primarily for internal use in the US-IBP Eastern Deciduous Forest Biome program. This information is not for use prior to publication unless permission is obtained in writing from the authors.

The phytoplankton model has been changed significantly since this report was first written; the updated version of the model is described in Memo Report 71-117, which will be sent as soon as it is available from the printer.

This report supersedes Memo Report 70-2; therefore that report is no longer being distributed.

NOTE: Research supported by the Eastern Deciduous Forest Biome, U.S.- International Biological Program, funded by the National Science Foundation under Interagency Agreement AG-199, 40-193-69, with the Atomic Energy Commission - Oak Ridge National Laboratory.

TABLE OF CONTENTS

ABSTRACT	i
INTRODUCTION	1
CONCEPTUAL MODELS	2
DATA COLLECTION AND ANALYSIS	5
Sampling	5
Data Management	10
Statistical Analysis	14
FUNCTIONAL MODELS	16
Mathematical Models	17
Phytoplankton	18
Herbivorous Zooplankton	20
Predatory Zooplankton	21
Nutrients	22
Programming	24
Driving Variables	25
Preliminary Experimentation	26
EVALUATION	28
HETEROGENEITY ANALYSIS	33
SIMULATION	40
FORECASTING	43
APPLICATION TO WATER MANAGEMENT	44
MACROMODELS	46
OPTIMIZATION	48
SUMMARY	51
ACKNOWLEDGEMENTS	52
REFERENCES	53
APPENDICES	55
A. Phytoplankton Model	55
B. Herbivorous Zooplankton Model	57
C. Predatory Zooplankton Model	58
D. Nutrient Model	59

TABLE OF ILLUSTRATIONS

Figure 1	- Flowchart of the Modeling Strategy at Lake George	3
Figure 2	- Conceptual Model of Aquatic Decomposition	4
Figure 3	- Comprehensive Ecosystem Conceptual Model	6
Figure 4	- Comprehensive Conceptual Model Transfer Matrix	7
Figure 5	- Map of Sample Stations	8
Figure 6	- Graphical Comparison of Read/Test and File-Scan Retrieval Methods	13
Figure 7	- Data Management System Flowchart	15
Figure 8	- Water Temperature Profile, Experimental and Predicted. Prediction Equation: $T_m = 10.24 - 5.96 * \cos(2t/365) - 7.65 * \sin(2t/365)$	27
Figure 9	- Simulated Phytoplankton Concentration	29
Figure 10	- Zooplankton Concentration	30
Figure 11	- <u>Cyclotella</u> Trend Surface Map, 1st Order Surface	36
Figure 12	- <u>Synedra</u> Trend Surface Map, 3rd Order Surface	37
Figure 13	- Diatom Biotope Dendrogram, Obtained by Q-Mode Cluster Analysis, Using Sorenson's Coefficient	38
Figure 14	- Diatom Q-Mode Ordination Map, Using Sorenson's Coefficient; the Directions of Increase of Two Environmental Factors, Nutrient Enrichment and Water Depth are Shown	39
Figure 15	- Diatom Biotope Heterogeneity Map	41
Figure 16	- Hypothetical Discriminant Function Analysis of Water Quality Data	45
Figure 17	- A Model for Population-Recreational Quality Interactions of a Fresh Water Site	47
Figure 18	- Environmental Control: A Conceptual Model	49

ABSTRACT

Modeling of the Lake George ecosystem utilizes a progression of models, each representing a particular level of abstraction and complexity. Conceptual models graphically depict the relationships of the ecosystem components and processes which are of interest, thus defining the scope of the data collection and analysis. Efficient data management assures accessibility of data to all site investigators. Functional models based on literature and data from ongoing studies, and including phytoplankton, herbivorous and predatory zooplankton, and nutrient models, are programmed for both time-sharing and batch-mode processing. These models are refined on a continuing basis in order to achieve content, construct, concurrent, and predictive validity. By utilizing lake basin heterogeneity, as determined from quantitative analysis of diatom death assemblages and inspection of land-use and vegetation data, it is possible to simulate various portions of the lake as separate point models; this permits rigorous concurrent and predictive validation. When sufficiently valid models are available they can be used to forecast the general ecologic consequences of management decisions; specific macromodels can be used to examine specific environmental problems. Mathematical programming models can determine optimal management plans for processes such as sewage collection and treatment. Analyses of interactions between environmental management models and ecosystem models can lead to more realistic water quality standards.

INTRODUCTION

The objectives of the International Biological Program Analysis of Ecosystems effort are 1) to understand better the dynamics of ecosystems through integrative research, and 2) to be able to predict the consequences of Man's impact on those ecosystems. The achievement of both these objectives is made possible by means of systems modeling.

Research at Lake George has at its focal point the development of ecosystem models. By requiring that all projects contribute to the overall model, it is possible to ensure a truly integrative research effort. Each investigator proceeds on his own within the guidelines dictated by the modeling objectives; these separate studies lead to the development of submodels which are in turn combined into the overall ecosystem model. This modular approach permits the investigators to function in semi-autonomous fashion while contributing to the general effort.

Because the research objectives transcend individual projects, all investigators are involved to a certain extent in the production of routine data which are synthesized by the modeling group. On the other hand, most investigators wish to pursue details that are not necessary in a general ecosystem model. This is consistent with the modeling objectives in that several different levels of ecosystem models are being developed, each yielding insight into ecosystem dynamics and each capable of predicting certain ecosystem responses.

The systems analytical approach used at Lake George is nothing more than formalized scientific methodology, as has been pointed out by other authors (Dale, 1970). However, the formalization of this methodology is important because of the complexity of the study and the multiplicity of research effort involving numerous investigators from various disciplines. The ecosystem analysis follows a logical sequence of models, each representing a different level of abstraction of the "real world" (Fig. 1).

CONCEPTUAL MODELS

This study has utilized conceptual models, which are graphical representations of the ecosystem, in the initial modeling phase. These have been developed by the modeling team in close cooperation with the other Lake George investigators. They have been useful in defining the scope of the overall program in that they have served to identify those ecosystem components which need to be measured and the processes which need to be studied more intensively.

The decomposition conceptual model (Fig. 2) is an example of a first-level model, the development of which lead to a clearer definition of the research objectives for that particular subsystem. Not only did it indicate a need for a functional subdivision of micro-organisms rather than the taxonomic subdivision followed by most microbiologists, but it also identified a number of transfer paths that would have to be studied before a realistic mathematical formulation could be attempted.

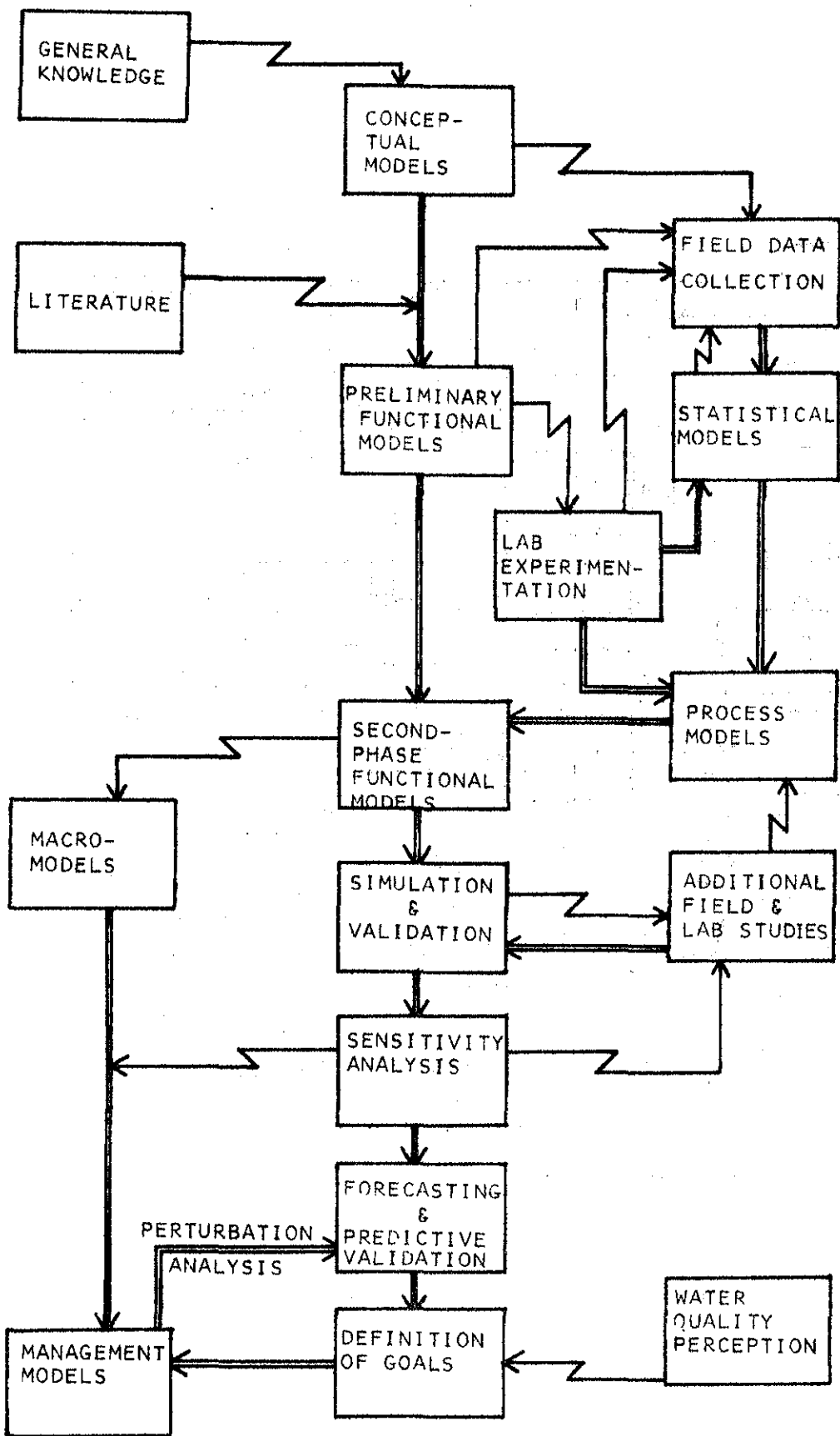


FIGURE 1 - FLOWCHART OF THE MODELING STRATEGY AT LAKE GEORGE.

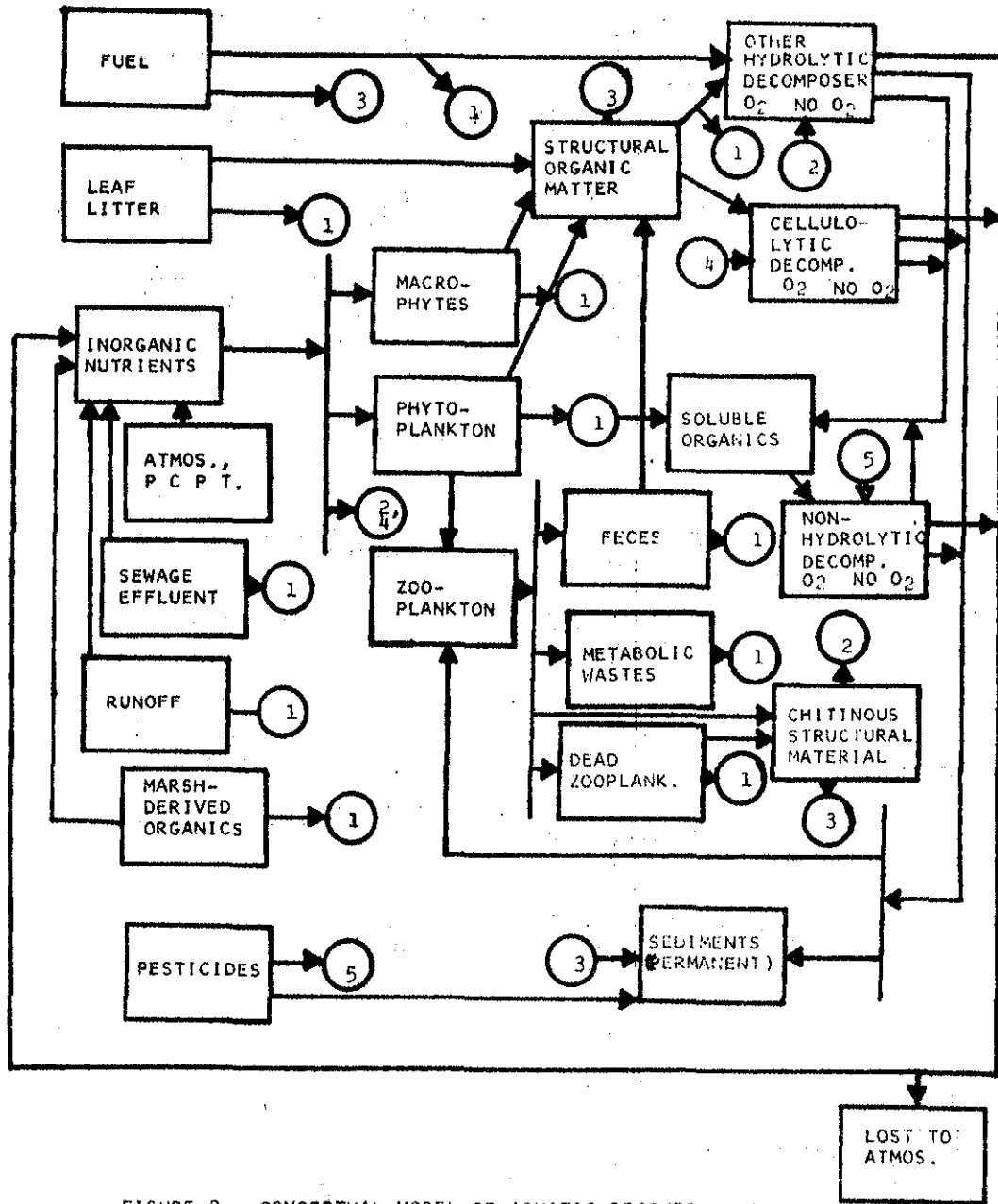


FIGURE 2 - CONCEPTUAL MODEL OF AQUATIC DECOMPOSITION

A comprehensive Lake George ecosystem conceptual model (Fig. 3) was developed in cooperation with all Lake George investigators. This has served as a framework for the individual studies, with each investigator contributing his prior knowledge and current data for several of the compartments. Those compartments which are not currently being studied, but which add significantly to the ecosystem dynamics as shown by the conceptual model, are the objects of new proposals. Figure 3 cannot show all transfer paths among the compartments so a transfer matrix indicating all important transfer paths (Fig. 4) was prepared. In a comprehensive mathematical model each of these paths will be represented by an equation or family of equations.

DATA COLLECTION AND ANALYSIS

Sampling

In the Lake George study, as in most biologic studies, the initial sampling design was dictated primarily by an intuitive feel for the system, tempered by a consideration of personnel and budgetary limitations. It was realized from the start that the lake could not be completely described; therefore, the decision was made to study intensively three stations located in different parts of the lake (Fig. 5). It was assumed that the lake is heterogeneous and that varying land-use patterns result in varying levels of water quality and biologic productivity. The lake is long (32 miles) and narrow (3 miles maximum width), with most people living at the south end and the outlet being at the north end (Fig. 5). Thus, the sampling stations were located at

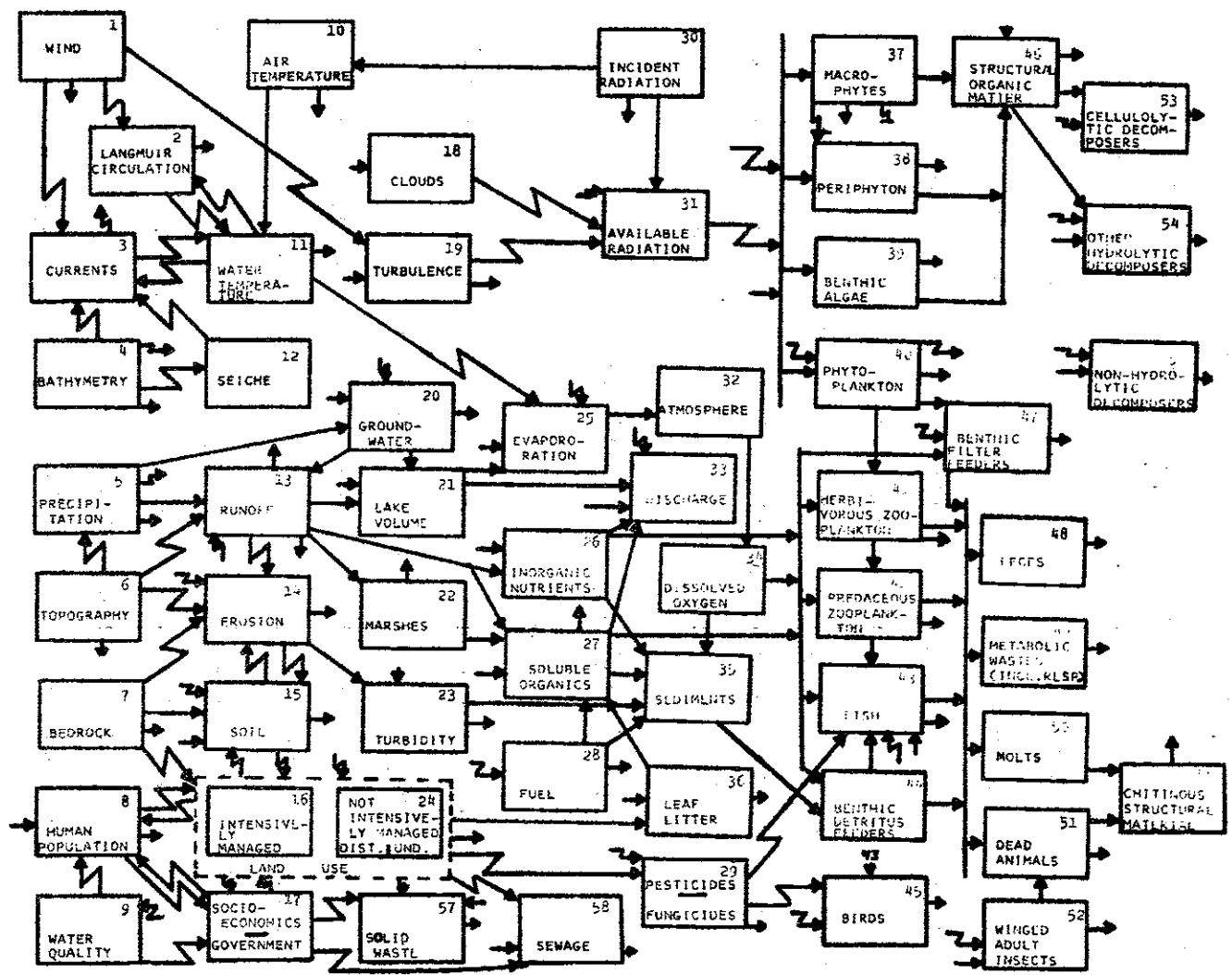


Figure 3 --- Comprehensive ecosystem conceptual model.

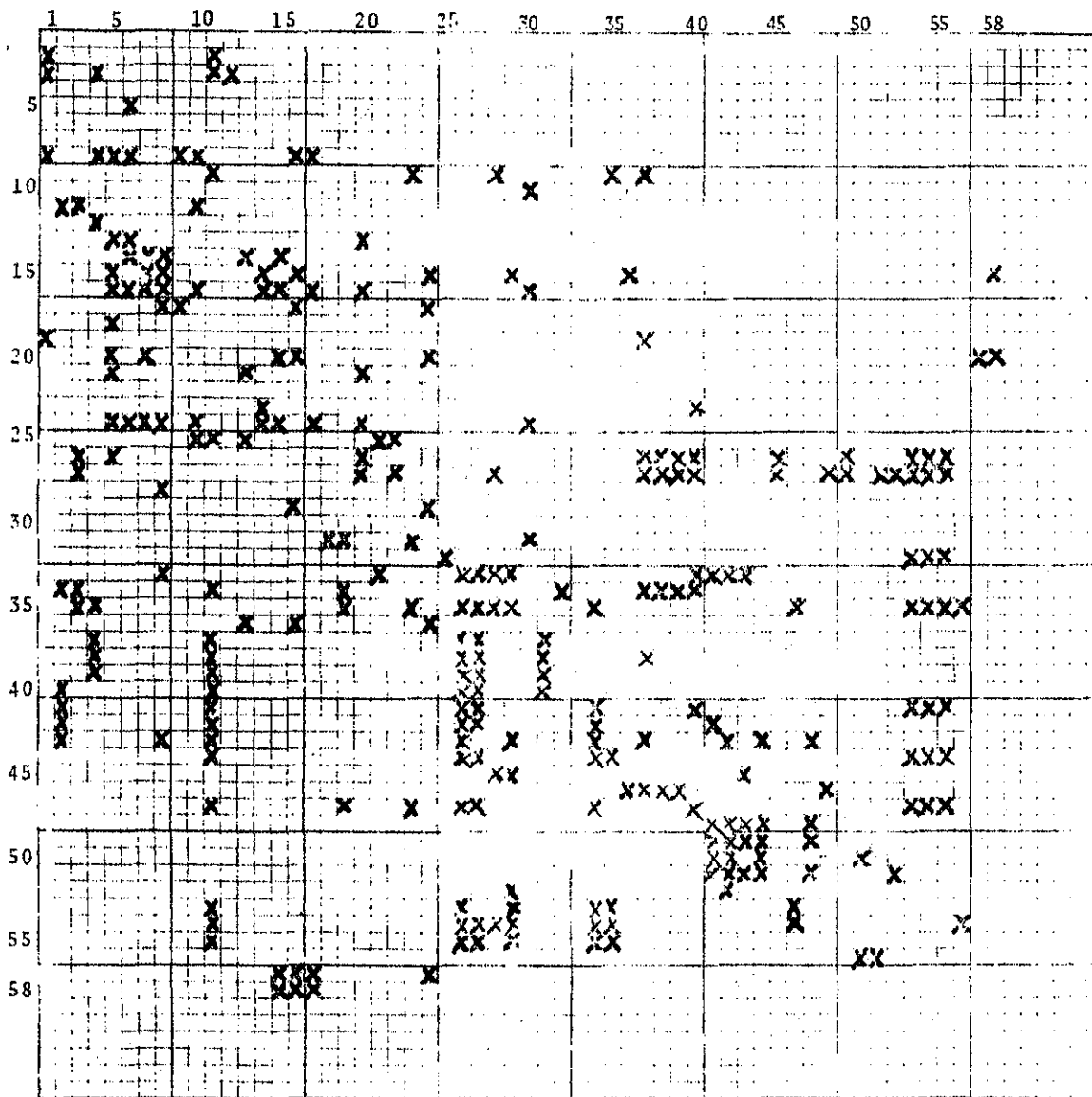


Figure 4
Comprehensive Conceptual Model Transfer Matrix.

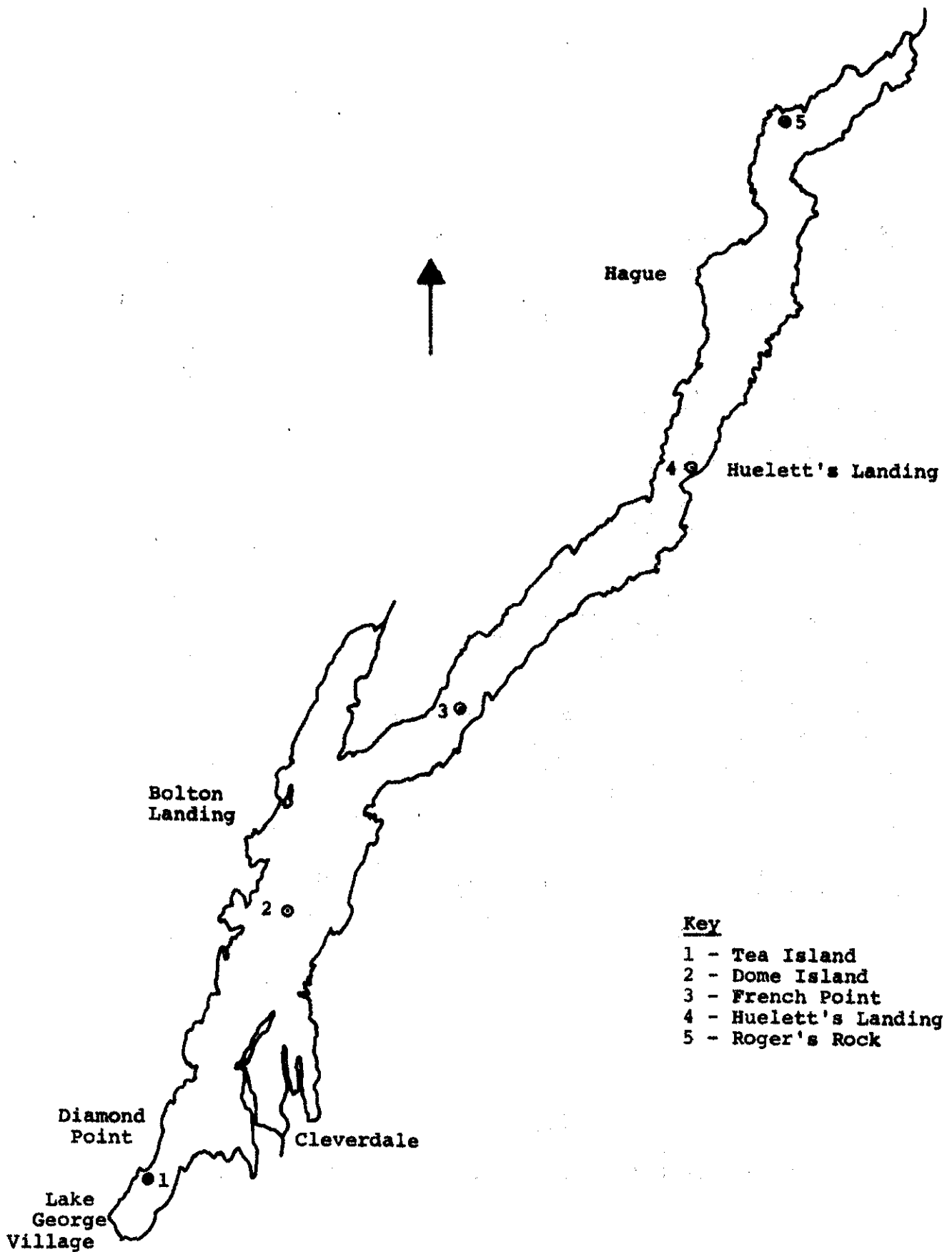


Figure 5 - Map of Sample Stations.

approximately equal intervals from south to north.

During the first field season sampling cruises involving all the Lake George site personnel were conducted as often as the samples could be analyzed with the available laboratory facilities and technicians; this amounted to every two weeks during the summer of 1970. Three replicate sets of samples were taken at each station. In addition, 24-hour cruises were occasionally made to determine diurnal variations.

Prior to intensive field studies in 1971, the modeling group hosted a sampling workshop for all principal investigators. Based on the general discussion and with a proper regard for statistical inferences, several changes were made in the sampling program. Because of low within-group variance the replication was reduced, thereby making it possible to add two additional stations, one in the vicinity of Huletts Landing and one in deep water off Dome Island, both areas of the lake that apparently represent different combinations of environmental factors (see "Heterogeneity Analysis"). Seasonal variations were found to be such that it was possible to increase the sampling period to three weeks. This permitted the addition of a more intensive sampling program along two transects representing a relatively undisturbed large bay (Northwest Bay) and an area of cultural eutrophication (north from Lake George Village). All these data contribute to the development of process models by the individual investigators; they also constitute the basis for subsequent model validation over a wide range of environments.

The modeling group also obtained useful data from sources outside the International Biological Program. These data have been processed and put into the data base so that they too can be used in model development and evaluation. The data sets include the land-use (LUNR) data on a square kilometer grid, obtained from the New York State Office of Planning Services; the 1970 census data; Lake George water-quality perception data, based on questionnaires returned by all types of recreationists, cottage and homeowners, hotel and motel owners, marina owners, and owners of other types of commercial establishments; water chemistry and diatom frequency data; and diatom death assemblage and core data.

Data Management

In order to make full use of the data, they must be easily accessible to all site investigators. Lake George is a part of the IBP Eastern Deciduous Forest Biome and has access to the information system located at Biome headquarters at Oak Ridge National Laboratory. Data sets are currently being prepared for storage on that system. However, it was recognized that the Lake George site should also have the flexibility and fast turn-around time afforded by an on-site system. For that reason a data management system has been developed specifically for the Lake George data. The system uses Rensselaer's IBM 360 model 50 with 512K processor storage, 1 Meg hierarchy support and a full battery of peripherals.

The first step in the system development was to survey available packages. Because the target computer was the 360/50, SHARE and IBM's Program Information Department systems were

evaluated. However, these systems were of such size, generality, and speed that it would be impractical to use them for the Lake George data. The decision was made to develop a custom system.

File structure and format were considered next. Despite the dissimilar types of data, all had the same basic identifications consisting of collection date, station number, and depth. Moreover, discussions with principal investigators indicated that data retrieval only need be based on these identifications. Therefore, the retrieval routines could search the locations of the identification fields without regard to the data arrangement. For this reason the format of each type of file was based on whatever seemed most natural for the given data, the only restrictions being the fixed locations of the identifications.

First choice of programming languages for the overall program was PL/I. This was quickly ruled out because of PL/I's slow execution speed and lack of interfaceability with other programming languages. A more satisfactory arrangement seemed to be a FORTRAN IV main frame with 360 ASSEMBLER routines handling the files and those functions that are better suited to ASSEMBLER than FORTRAN.

The usual method of locating specific data from files is the read/test approach. However, for the Lake George data, the retrieval system needed only to locate records fitting exact patterns. The read/test algorithm seemed a waste of CPU time because of the file-scan special feature hardwired into 2314 and some 2311 disk drives. This method is unsupported by IBM and had to be developed for the Lake George data base;

however, with file-scan the input/output channel locates and retrieves the data while the CPU is freed for other jobs (Fig. 6) so it was felt the savings in CPU time more than justified its development. The file-scan access method became the heart of both data retrieval and file updating systems, with FORTRAN routines inputting user control cards and evolving the required pattern. File updating is accomplished by using the retrieval algorithm in reverse: file-scanning is further exploited to add, delete and modify data records.

The layout of the program cards was designed so as to minimize errors in keypunching of commands by reducing format restrictions. To a certain extent the cards are free-form and unordered so problems of right-justified integers, implied decimal points and card order were virtually eliminated. Several conversion routines had to be developed in order to achieve this; they were found to be at least as fast if not faster than the conversion modules in FORTRAN's input/output package.

To complete the utility of the system, routines that perform transformations and calculations upon the retrieved data have been included. At present the system contains transformation routines to calculate finite birth and instantaneous birth and death rates and rates of photosynthesis. New routines are currently being developed. In situations where a specific routine would be too large to include in the program, the power of the 360 operating system comes into play and data can be passed back and forth between job tasks or modules can be overlaid. One further facility of the program

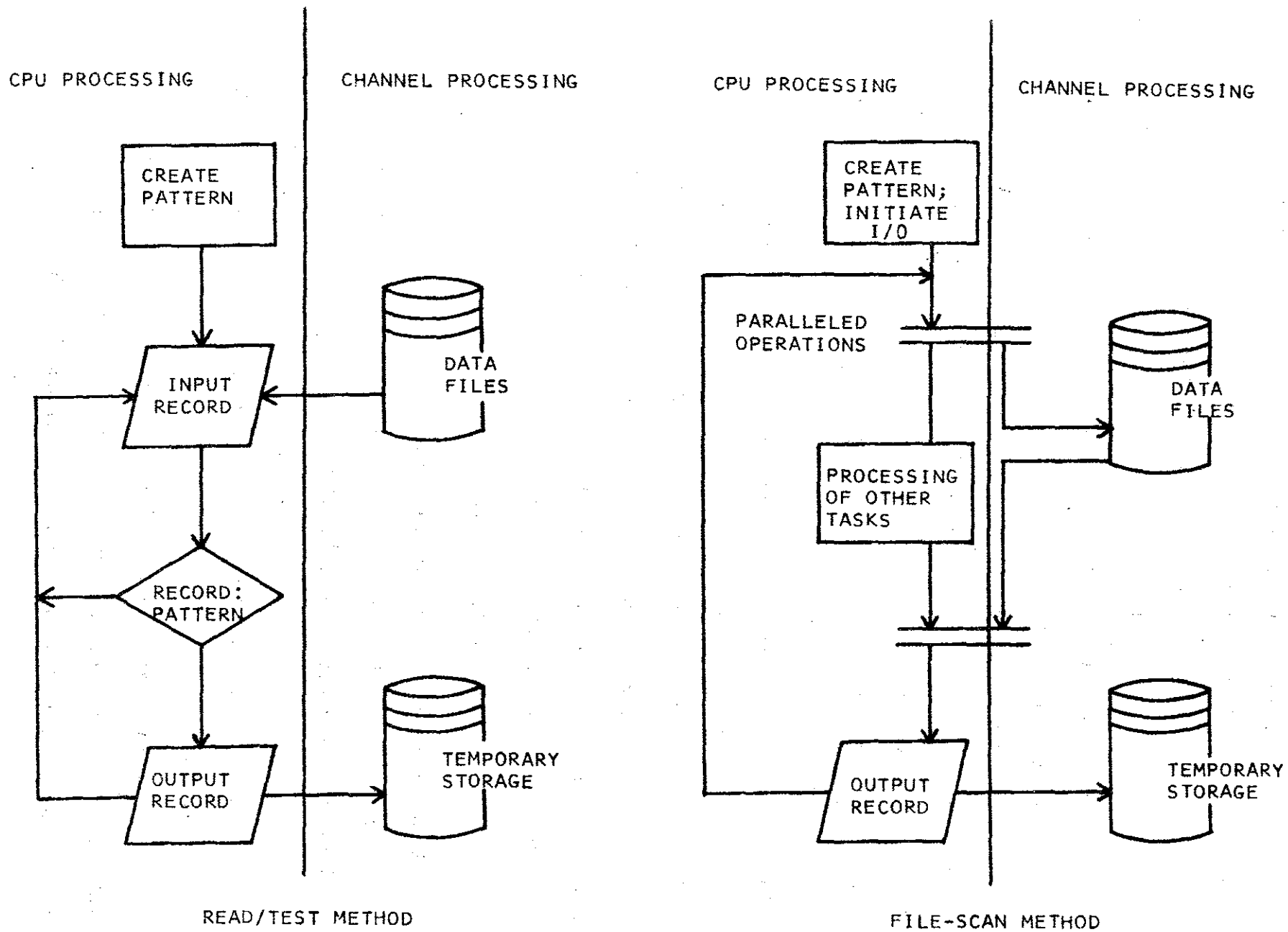


FIGURE 6 - GRAPHICAL COMPARISON OF READ/TEST AND FILE-SCAN RETRIEVAL METHODS.

is that it allows the user to supply his own routines that are not already a part of the system. The program will call the routines and let them do whatever processing is desired using the data files and the program subroutines. The system was designed to be very flexible in order to meet new demands.

A cursory look at the system is given in the accompanying flowchart (Fig. 7). Not included for readability are informatory and diagnostic messages from each module to the printed output file. The coordinating routine accepts control cards and decides what functions are to be called. The update and retrieval subroutines each use the control cards to set up patterns for which the file-scan routine is to search. This routine either retrieves or updates records. Retrieved records are moved to temporary data sets and optionally punched and/or listed. The transformation coordinator calls the required subroutines to carry out desired calculations on the data previously retrieved. In addition, user-supplied routines are granted the full power of the system.

Statistical Analysis

Members of the modeling team have served as internal consultants on problems of data processing. At first this was done on a demand basis; however, it was found that investigators oftentimes did not take full advantage of the service, so a policy of periodic review of analytical procedures was instituted.

Code sheets have been designed to aid in the transfer of field observations to machine-processible form. Key punch formats have been devised to give maximum flexibility with a

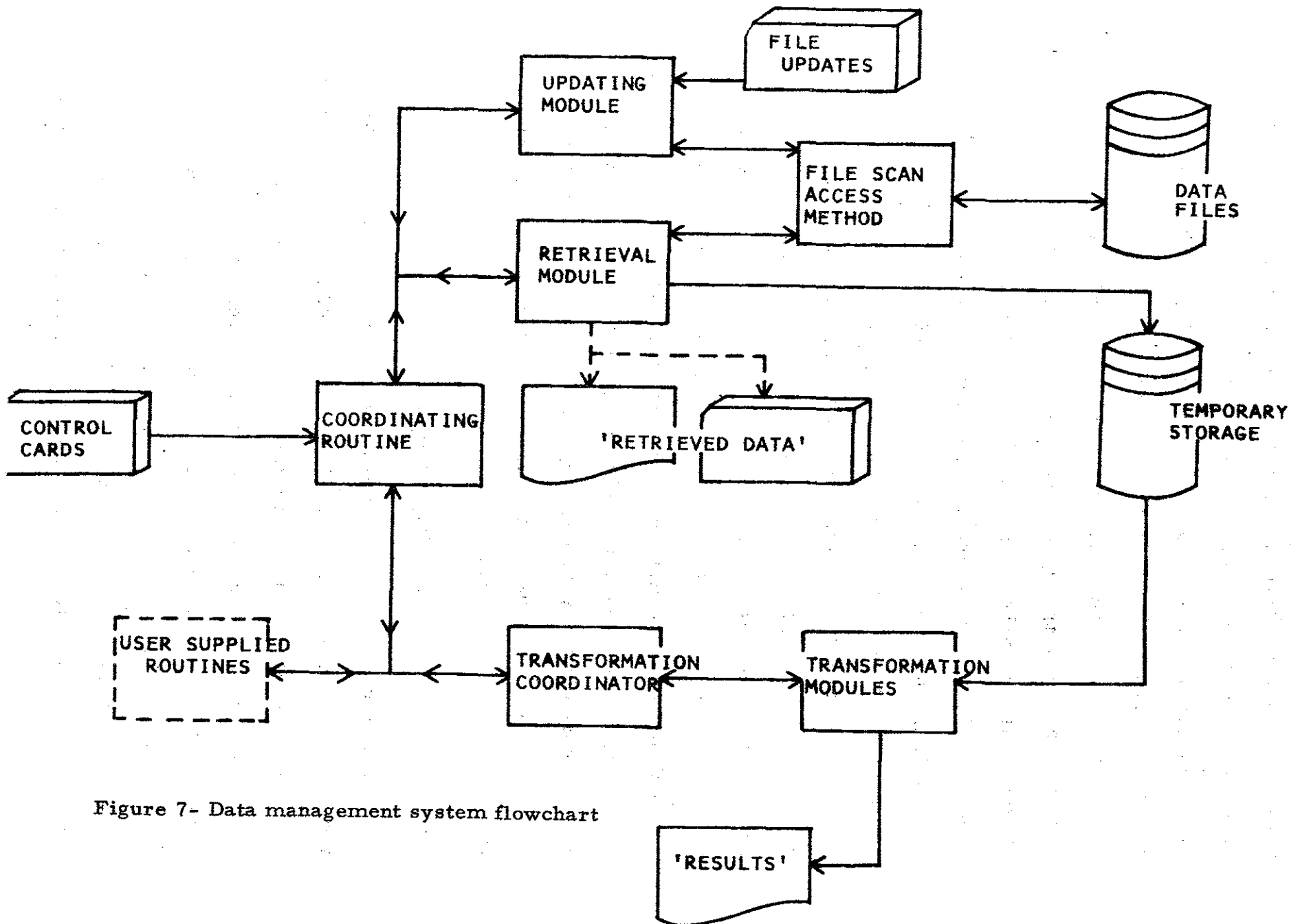


Figure 7- Data management system flowchart

minimum chance of keypunch error. And transformations have been programmed to enable the reduction of meaningful data from complex laboratory and field analytical procedures (such as photosynthetic rate based on ^{14}C uptake).

The modeling team includes professional statisticians; and, while the sampling design has been dictated primarily by substantive rather than statistical considerations (see "Sampling"), every effort is made for efficiency in statistical inference at the data analysis stage. In addition to internal consulting, the team has gradually built up a library of both specialized and packaged programs; these are supported on a continuing basis so that all Lake George data can be processed efficiently. They include a program to calculate average daily stream discharge, cluster analysis and ordination programs and trend surface and double Fourier programs, as well as the following packages (all of which are in the Rensselaer system through the efforts of the modeling group): BMD, MPS (mathematical programming system), SSP, SPSS, OMNITAB, and SYMAP.

FUNCTIONAL MODELS

No scientific study should ignore previous work; this should be evident in the development of models as well as in the formulation of the study and the collection of data. With this in mind, the Lake George modeling group has spent considerable time developing models based on the literature and the intuition of the other Lake George investigators while the initial data were being collected (Fig. 1). Thus, now that data are available, they are being used to test and

modify models based on current ecologic theory, without wasting valuable time duplicating prior studies. Each model can be thought of as a hypothesis to be evaluated and changed accordingly; in this way the modeling proceeds efficiently in a manner consistent with good scientific methodology.

The objective of this phase of the research is to develop realistic models that incorporate terms representing actual biologic, chemical and physical processes. Such models are called functional models because they represent the functions of the ecosystem, rather than just the observed effects. They are preferable to empirical models in that

- 1) they lead to a better understanding of the ecosystem, and
- 2) they permit predictive modeling beyond the range of the data available from the current study.

Mathematical Models

The mathematical formulation of the functional models is probably the single most important step in the modeling procedure. The terms that contribute to the formulation are representative of biologic, physical and chemical processes; they may constitute separate process models, or, for expediency, they may be empirical models. However, in this study an attempt has been made to avoid empirical, or "black-box", models whenever possible. In addition, the number of exogenous variables has been kept to a minimum in order to facilitate the generality and predictive capability of the models.

Development of the biologic models began with the classical Riley model (Riley, Stommel, and Bumpus, 1949; Riley, 1963; Park and Wilkinson, 1970). However, more advanced models developed by another group (Di Toro, O'Connor, and Thomann, 1970) were then adopted and have served as the basis for further research.

Phytoplankton.

This model (see Appendix A for equation and notations) contains terms for the source and sinks of phytoplankton biomass. The source term is identified as photosynthetic growth rate, G_p , and the sink terms are rates of respiration, R_p , loss to predation by herbivorous zooplankton, L_{hzg} , and sinking, S_p , respectively. When the source exceeds the sink there will be a net increase in the phytoplankton population. When the reverse is true, the phytoplankton population will start to decrease. However, the population can never be negative.

The interaction between phosphate and ammonia limitations as well as other environmental driving variables, such as temperature and incident solar radiation, which influence phytoplankton growth have been considered. However, the problem of individual species and their associated nutrient and environmental requirements is not addressed. Instead the population is characterized as a whole by a measurement of the biomass of phytoplankton present. The effect of nutrient concentration on the growth rate of phytoplankton is assumed to follow Michaelis-Menten kinetics with respect to the important nutrients (Dugdale, 1967; Epply, Rogers and McCarthy, 1969; MacIsaac and Dugdale, 1969). A straightforward approach

has been used to formulate the growth rate reduction due to limitation of more than one nutrient (Di Toro, O'Connor and Thomann, 1970). For the case of two limiting nutrients, phosphate, N_p , and ammonia, N_a , with Michaelis-Menten constants, K_{mnp} , and K_{mna} , respectively, the functional expression for the photosynthetic rate is shown in Eq. (1.1). Ammonia was included after regression analysis indicated a high correlation between ammonia and diatom concentrations.

Respiration is the reverse process of photosynthesis and is also temperature dependent (Riley, Stommel and Bumpus, 1949). In the process of respiration the phytoplankton oxidize their organic carbon into carbon dioxide and thus cause the decrease in phytoplankton biomass. A constant respiration coefficient is assumed in Eq. (1.2).

The calculation of filtering rate is not a simple matter. The filtering rate varies with temperature, phytoplankton concentration, and phytoplankton cell sizes (Conover, 1966; Burns, 1969). It is also species dependent. However, to investigate the phytoplankton and zooplankton population as a whole by a biomass measurement, the species dependence and individual characteristics may be neglected. Thus, a linear relationship in (1.3) is assumed to exist between the rate of loss of phytoplankton due to predation and the concentration of herbivorous zooplankton. The grazing rate here is assumed to be a constant.

Phytoplankton loss to sediments is a complex process, as is transport away from the model point or profile. For simplicity in the present study, a constant sinking coefficient is assumed in (1.4). However, terms are being developed for

vertical and horizontal mass transport resulting from both concentration and thermal gradients (see Bella, 1970 for a somewhat simplistic model). These will permit prediction of the concentration of biomass as a function of depth for various values of empirical constants associated with current distribution, vertical mixing, and thermal regime. For example, the thermal regime of the lake, as seen in a series of monthly profiles, is represented by empirical constants to describe the convective patterns and the diffusion processes. The empirical constants change with time, with typical seasonal variations, leading to time variations in the predicted concentrations and their depth dependence.

In developing this model, various simplifying assumptions have been made primarily on the basis of an intuitive assessment of the important features of the systems being studied. However, the model is believed to be adequate for this stage in the iterative modeling process.

Herbivorous Zooplankton.

The investigation of zooplankton population dynamics is complicated by the fact that zooplankters may be herbivorous, carnivorous or omnivorous. In order to simplify the investigation, the system is divided into two parts, herbivorous and predatory zooplankton. The omnivorous zooplankters are considered as either herbivorous or predatory, but not both.

The same types of terms which pertained to the phytoplankton model are also applied to the herbivorous zooplankton model which is presently being used (Appendix B). The growth rate equation is given in (2.1). Note the biomass conversion

factor, a_{hzp} , which relates the filtered biomass of phytoplankton to the herbivorous zooplankton biomass. This factor is also called the assimilation efficiency and is the ratio of phytoplankton organic carbon utilized to herbivorous zooplankton organic carbon produced (Conover, 1966). For convenience, Michaelis-Menten kinetics are used to represent the grazing of phytoplankton by herbivorous zooplankton, even though it is known that the process does not satisfy the Michaelis-Menten assumptions. Research currently in progress should permit the formulation of a more satisfactory grazing process model, which will then be incorporated into the functional model. The Michaelis-Menten constant, K_{mp} , is highly species dependent. A rough estimate was obtained from the range of the values reported in the literature.

The sink terms are approximately the same as they were in the phytoplankton submodel. A constant loss rate due to mortality is assumed for simplicity. This constant probably will need to be replaced by a mortality process model in order to achieve a robust, realistic functional model.

Predatory Zooplankton.

The framework of this model (Appendix C) is almost a photocopy of that used in the herbivorous zooplankton submodel. Further simplification is achieved for the time being by assuming a constant rate of loss due to predation and natural mortality combined. The value of this constant can be obtained either empirically or numerically. In order to attain a realistic model, it will probably be necessary to model separate species. This is feasible with information and data that are now accumulating.

Nutrients.

This model (Appendix D) is still in the formulation stage; as of now it is merely a framework which incorporates appropriate terms from the trophic-level (or food chain) models discussed above.

The model has six source and two sink terms. The primary interaction between the nutrient system and the phytoplankton system is the nutrient sink due to assimilation by phytoplankton growth. A secondary interaction among the nutrient systems, the decomposer systems, and the food-chain systems is the excretion of nutrients by zooplankton and higher level animal species and the release of nutrients in an organic form by the death of phytoplankton, zooplankton and higher level animals (Park and Wilkinson, 1970; Di Toro, O'Connor and Thomann, 1970).

The nutrient addition due to man-made inputs, such as wastewater from industrial and municipal discharges, sewage, boating, pesticides, littering, and agricultural runoffs, is considered as an external controllable variable which influences the nutrient system. Separate submodels are currently being developed for municipally-treated sewage and leach-field treated sewage. The nutrient addition due to natural input, such as precipitation, leaf litter, groundwater, etc., is also considered, but as an external uncontrollable variable to the system. This will be represented by empirical models based on stream chemistry, forest cover, and hydrology.

The nutrients released by the death of phytoplankton are

in an organic form and thus a biomass conversion factor, a_{np} , is needed in Eq. (4.3). The same argument is used in Eq. (4.5) where two biomass conversion factors, a_{nzh} (ratio of nutrient to herbivorous zooplankton biomass) and a_{nzp} (ratio of nutrient to predatory zooplankton biomass) are included.

The release rate of nutrients by zooplankton excretion consists of two parts, excretion by herbivores and excretion by carnivores. The rate of nutrient excretion is the difference between the rate grazed and the rate metabolized. For example, in the herbivorous zooplankton system, the rate of phytoplankton grazed is $a_{np} * f_{rg} * Z_h * P$, and the rate of metabolization is $a_{np} * G_{hz} * Z_h$ (the equation of G_{hz} is shown in (2.1)). Thus, the intended excretion rate is the difference. The rate of total nutrient excretion by zooplankton is shown in (4.4). The input rate by the excretion of higher food-chain elements is simply assumed as a constant. In addition, a constant rate is also assigned to the loss to sediments.

The nutrient depletion due to the assimilation by phytoplankton forms a major sink to the nutrient system if the phytoplankton population is large. The rate can be obtained by multiplying the product of the growth rate of phytoplankton and the phytoplankton concentration by a proper biomass conversion factor.

Programming

With completion of the mathematical formulations, the functional models are expressed in computer logic in order to facilitate evaluation and experimentation. The Lake George modeling group uses both time-sharing and batch-mode operations. Time-sharing is advantageous during the developmental stages because it gives almost instantaneous turn-around. The terminal can be used as a "scratch pad", with the programmer entering statements and having them compiled immediately (this varies with the system - some systems compile the entire program). Serious programming errors can be detected at once; errors in logic can often be detected as soon as enough statements are compiled to enable testing of the algorithm. Time-sharing also greatly facilitates interactive simulation, giving the investigator the capability of changing parameters, altering the driving variables, and terminating execution at will.

Batch processing is preferable in the later stages of modeling when integrative multicomponent models are being used and, especially, when large-scale evaluation runs are being performed with large data sets or numerous iterations. Batch processing has much faster execution time and, oftentimes, has to be used for such long runs. It is also more efficient for runs generating large amounts of output (although some high-speed remote devices with cathode ray tube units may still service this need on a time-sharing basis). At the present time the Lake George group is converting some of its models to batch processing.

At many computer installations the choice of suitable programming languages is restricted to FORTRAN. The Lake George group uses the Rensselaer IBM 360/50 with large core storage and has access to both FORTRAN and PL/I, as well as specialized simulation languages. PL/I has been used for most modeling at the site because of its flexibility of logic, extensive library of functions, and full character set. Its use precludes routine program sharing with other sites; however, PL/I can be translated to FORTRAN fairly readily, with loss of some of the original efficiency of execution. At the present time, IBM Conversational Programming System (CPS) PL/I is used for time-sharing applications, and both PL/I and FORTRAN IV have been used for batch processing. The specialized simulation languages have been rejected because of lack of generality, lack of support, and lack of universality.

Driving Variables

In order to experiment with the functional models once they are programmed, it is necessary to have values for the exogenous or driving variables. These are used as input for the program. Historic data can be used for purposes of preliminary testing; however, the use of large data sets greatly increases the execution time of the program and is impractical for time-sharing. As an alternative, short routines have been written to generate values for the driving variables. These same types of routines can be used for model experimentation involving future time, as in forecasting.

The derivation of the temperature equation serves as an example. The available data indicate that water temperature has a fairly stable seasonal pattern. Therefore, it has been possible to develop a prediction equation. For purposes of evaluating the phytoplankton-herbivorous zooplankton model, values at a depth of 6 m (the photosynthetic maximum depth) were used. The prediction equation (1.6) was obtained by harmonic regression analysis of 1969-70 data. This equation gives an approximate representation of temperature as a driving variable and is adequate for the entire year (Fig. 8).

The minimum of the curve occurs at about February 24 (0.6°C), and the maximum at August 24 (19.88°C). The prediction curve peaks too soon and its values are too low. The empirical data exhibit a sharp increase to the maximum and a sharp decline from the maximum. This tendency is especially apparent in 1969. While behavior at the maximum is steeply sloped, around the minimum the empirical data are much shallower. These tendencies were only partially accounted for in the regression model. On the whole, however, the model is good enough for use as a driving variable in the initial verification.

Preliminary Experimentation

The combined phytoplankton-herbivorous zooplankton model has been evaluated for the fall period because most of the experimental data, both water chemistry and primary production, were readily available for this period. Now that more data are available, the verification will be updated and expanded to a yearly period.

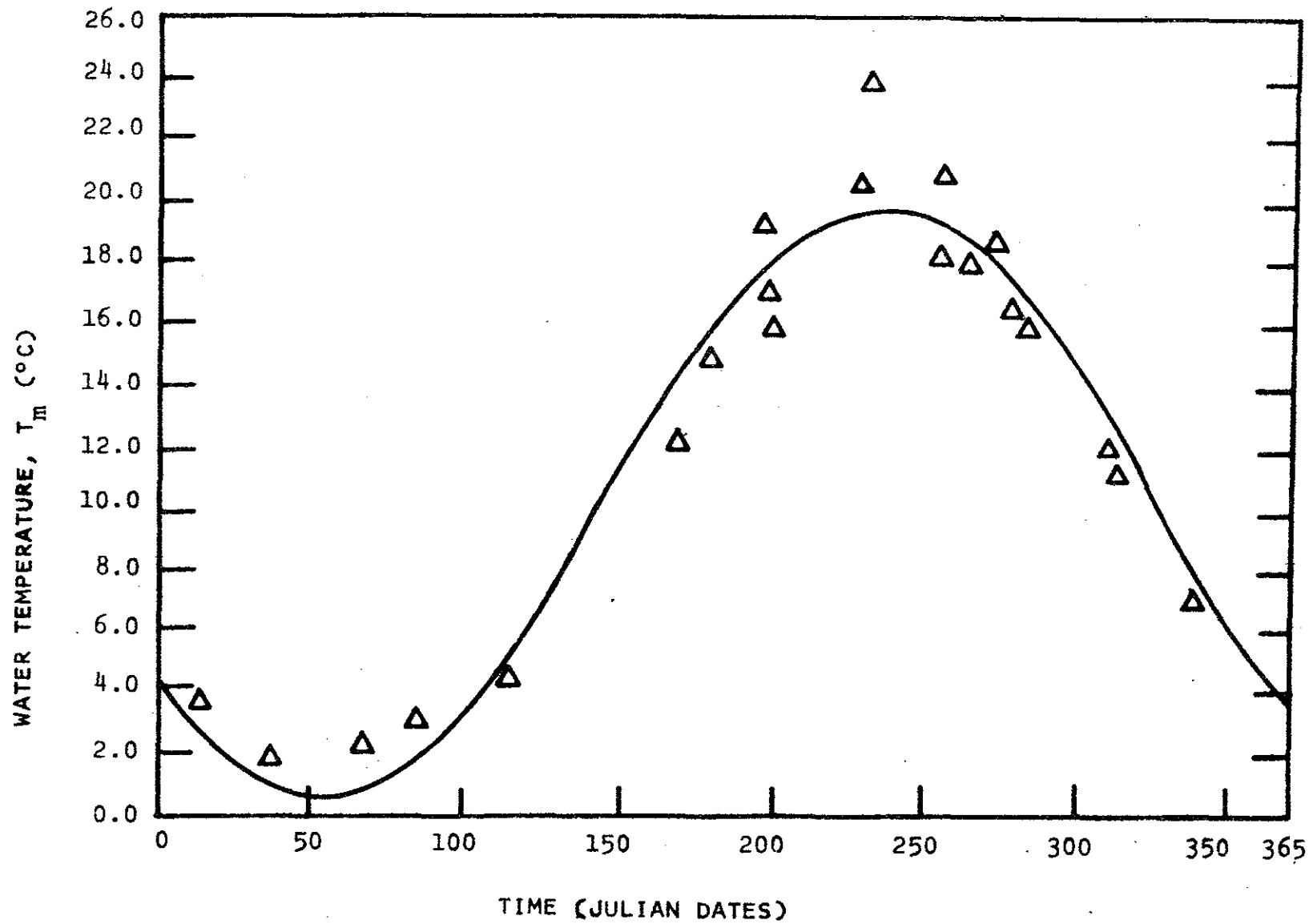


FIGURE 8 - WATER TEMPERATURE PROFILE, EXPERIMENTAL AND PREDICTED.

In the verification of the phytoplankton-zooplankton functional model which incorporates Eqs. (1) and (2), the zooplankton submodel has been simplified slightly (rates of loss due to predation by carnivores and mortality were combined as one term). The simplification was made to facilitate experimentation.

The Runge-Kutta Method of numerical integration was used to obtain a solution for the model. Numerical values used for this verification are presented in Table 1. Part of these values were obtained from site investigators and part from literature. Numerical results are shown in Table 2 and Figs. 9 and 10.

It can be seen in Table 2 that temperature, T_m , shows a steady decrease from 19.365° to 12.560°C in fifty-six days. Phosphate, N_p , Ammonia, N_a , and incident solar radiation I_o , behave randomly like the experimental data presented. The inclusion of ammonia as an additional limiting nutrient seems to provide much better results in both phytoplankton concentration, P , and herbivorous zooplankton concentration, Z , than the previous runs where only phosphate was considered. When the model results are compared with available data, the only significant conclusion is that both phytoplankton and zooplankton populations have a downward tendency during the fall period. The verification will be extended now that additional data are available; in the future, rigorous testing criteria will be developed to facilitate formal validation.

EVALUATION

Model evaluation is an extremely important part of the

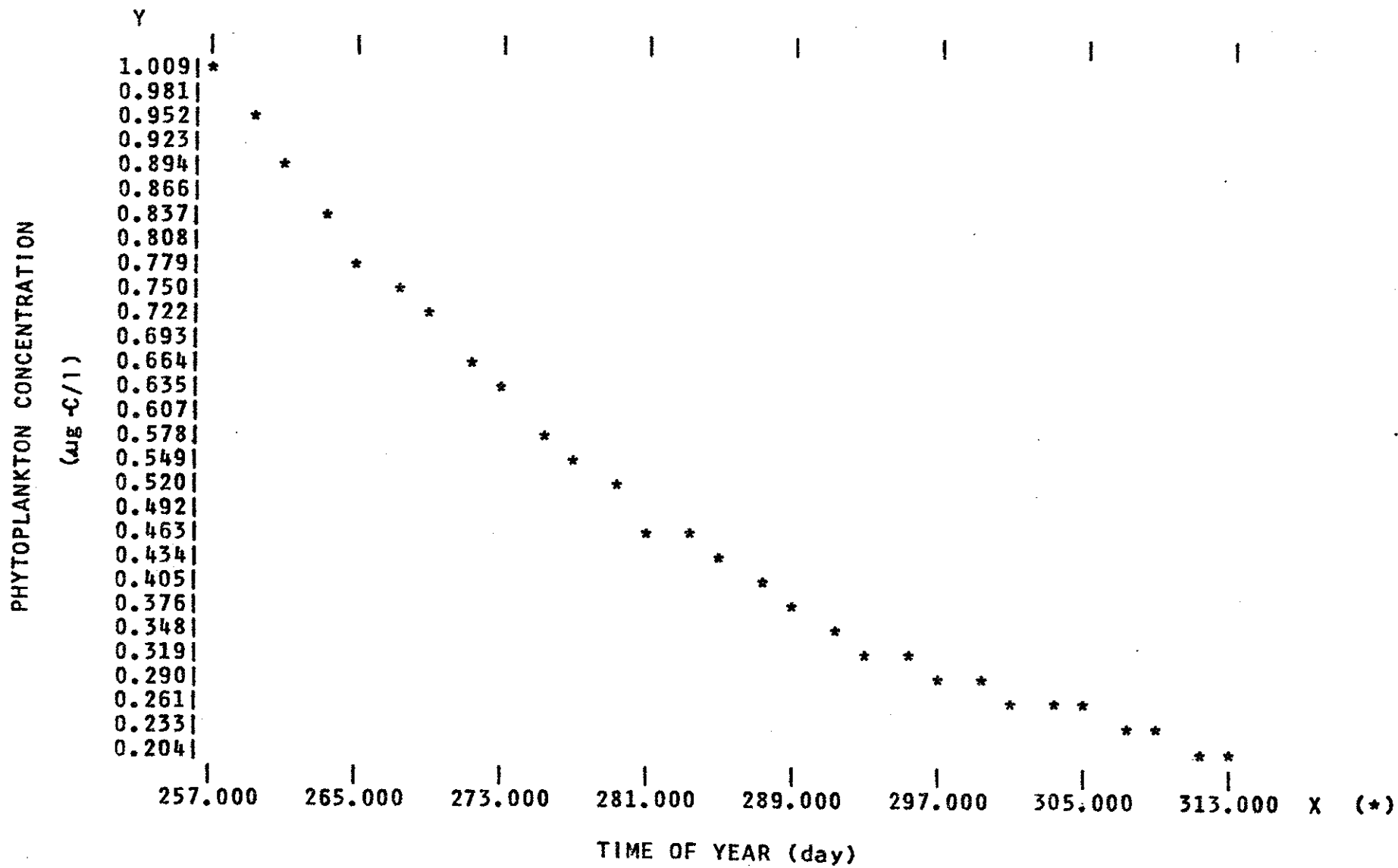
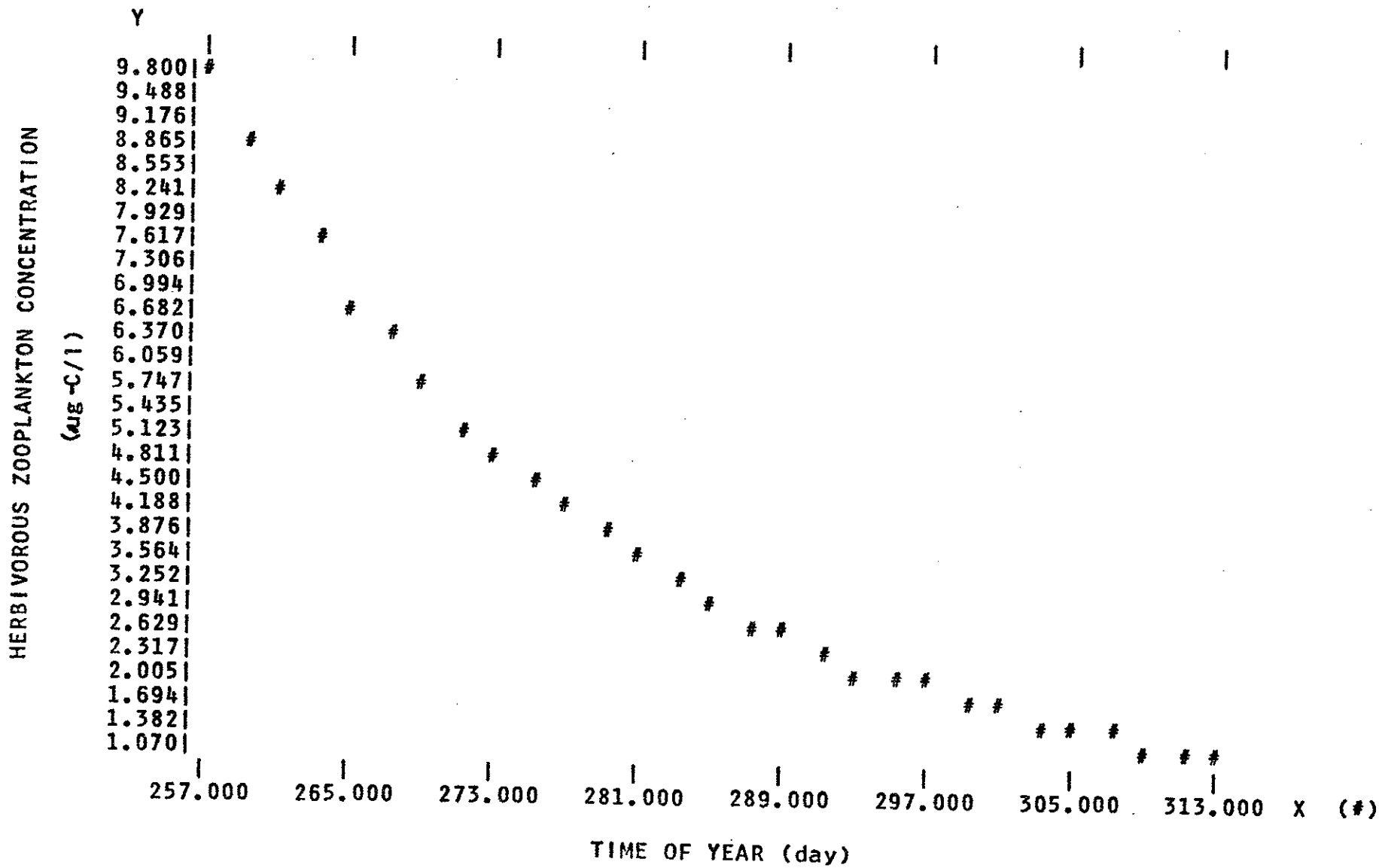


FIGURE 0 - SIMULATED PHYTOPLANKTON CONCENTRATION



modeling process; without some degree of confidence in the model's results, the entire process has been just an exercise. Unfortunately, ecosystem model evaluation has received scant attention in the literature. For this reason the Lake George group has assumed the task of developing criteria for the evaluation procedure.

The problem of testing the validity of a simulation model is similar to establishing the "truth" of a hypothesis. The testing process involves specifying a set of criteria which differentiate between that hypothesis which is "true" and that which is "not true"; then the criteria are applied to the model since the simulation is, in essence, a set of hypotheses. However, the very nature of simulation, in particular ecosystem modeling, is so inherently complex that a totally consummated validity test is practically non-existent. Yet, one must be confident that the simulation is not fallacious; therefore, the following concepts, originally developed in the validation of psychological tests and later re-defined for general use (Baisuck and Wallace, 1970), are being used in the Lake George ecosystem modeling activity.

Content validation consists of a qualitative verification that the model contains necessary system components and that the variables are expressed in forms compatible with the modeling objectives. It is important that this be a conscious part of the evaluation, especially in a large-scale multi-disciplinary study, because objectives quite often change during the initial conceptualization and data collection phases. In the general Lake George ecosystem model content validity implies inclusion of all process models, with appropriate variables,

consistent with trophic-level modeling of an oligotrophic lake.

Construct validation is the statistical or subjective evaluation of empirical relationships that were included in the model on the basis of observed effects, without knowledge of the actual underlying processes. In the Lake George model the determination of construct validity involves regression equations and coefficients that were necessitated by unknown functional relationships or by the need to simplify the ecosystem complexity. Because model development is a continuous process, it is important that the construct validity be re-evaluated as additional data become available.

Concurrent validation measures the congruence of simulated output with past and present (historic) data. This constitutes the principal justification for simulation studies (as used in the sense of this paper - see "Simulation"). Unfortunately, many investigators seem to regard this as the only formal evaluation procedure, and even then the techniques are not well established. The concurrent validity of the phytoplankton-zooplankton model is presently being determined on the basis of data from the 1970 and 1971 field seasons.

Predictive validation measures the accuracy with which the model predicts future states. This entails a dynamic, interactive evaluation whereby predicted results are compared with observed results as they occur in the real world. Model parameters are updated as necessary, so that in a changing ecosystem the environmental factor space is gradually enlarged beyond the original bounds which were known at the time the

model was first developed. Inherent in this validation concept is the idea that the model will be modified over a period of time in order to achieve better predictive capability.

The determination of how well a model predicts ecosystem behavior necessarily involves complex procedures, and a clear-cut strategy is not available at this time. Several areas of investigation have been proposed. A time series and spectral analysis of the computer model's output appears to have great promise as a predictive comparison device (Fishman and Kiviat, 1967). Other proposed methods are the Turing test and Theil's Inequality Coefficient. In using the Turing test, experienced researchers are given sets of real and simulated values to determine if they can tell the difference. This form has been used at least once in the validation of a simulation model (Van Horn, 1971). Theil's Coefficient (U) is either 0, perfect prediction, or 1, very bad prediction, where
$$U^2 = \frac{\sum_i (P_i - A_i)^2}{\sum_j A_j^2}$$
 with P = predicted value, A = actual value (Naylor and Finger, 1967).

These techniques are currently under investigation as validation tools. At the present time it is too early to determine what the final suggested procedure will be.

HETEROGENEITY ANALYSIS

One of the outstanding advantages of constructing ecosystem models at Lake George is that the models can be tested under a variety of conditions within the one contiguous body of water. Thus, factors which are of little concern

are minimized; and important factors, such as the effects of land-use and pollution loads can be examined more easily. However, it is necessary to determine the lake heterogeneity objectively in order to take full advantage of this capability.

The approach at Lake George has been an empirical one, utilizing diatom death assemblages in the bottom sediments as environmental indicators. Diatom death assemblages offer several advantages in a preliminary examination of lake heterogeneity. The siliceous frustules are quite durable, and a sample of the flocculent layer of sediment may represent an integration of the life assemblages over a period of two or three years. Therefore, a single sample at a particular station can give a better estimate of long-term water quality than a series of chemical and biologic samples taken from the water column. In addition, the samples can be taken quite easily and analyzed at a later date, thereby enabling the investigator to take numerous samples over the area of the lake.

In this study over 150 sediment samples taken on a systematic grid over the lake at 1-mile intervals parallel to the axis of the lake and at 1/2-mile intervals across the lake indicate a significant amount of heterogeneity of the diatom assemblages. This heterogeneity compares fairly closely with differences in human population density around the lake, and, to a lesser degree, with differences in bathymetry and biologic factors such as lakeside marshes and rooted aquatic plants.

These preliminary findings are based on extensive quantitative analyses. Slides were made from each sediment sample and were counted by integral scans at a magnification of 1000X until 300 to 500 diatom valves were identified to genus. The data were then analyzed for ecologic trends and patterns.

First, trend surface analysis, a form of polynomial regression analysis, was used to spot regional and local trends of each genus over the lake area. The genus Cyclotella showed a relative increase in abundance from south to north (Fig. 11); and the genus Synedra showed a relative decrease in abundance from south to north (Fig. 12); other genera had similar regional trends. These trends coincide with a decrease in human population density from south to north and seem to reflect a change in nutrient enrichment of the lake.

Cluster analysis was used to classify genera into groups (biofacies) with similar distributions and samples into groups (biotopes) with similar diatom compositions (Fig.13). The biotopes correspond quite well with observed lake environments. One biotope contained all samples off-shore from areas of dense human habitation (Lake George Village, Cleverdale, Bolton and Huletts Landing); another biotope included samples from deep-water areas of the sparsely populated north basin.

Ordination was used to examine the gradational relationships among both samples and biotopes. The ordination model (Fig. 14) indicated that nutrient enrichment and depth of

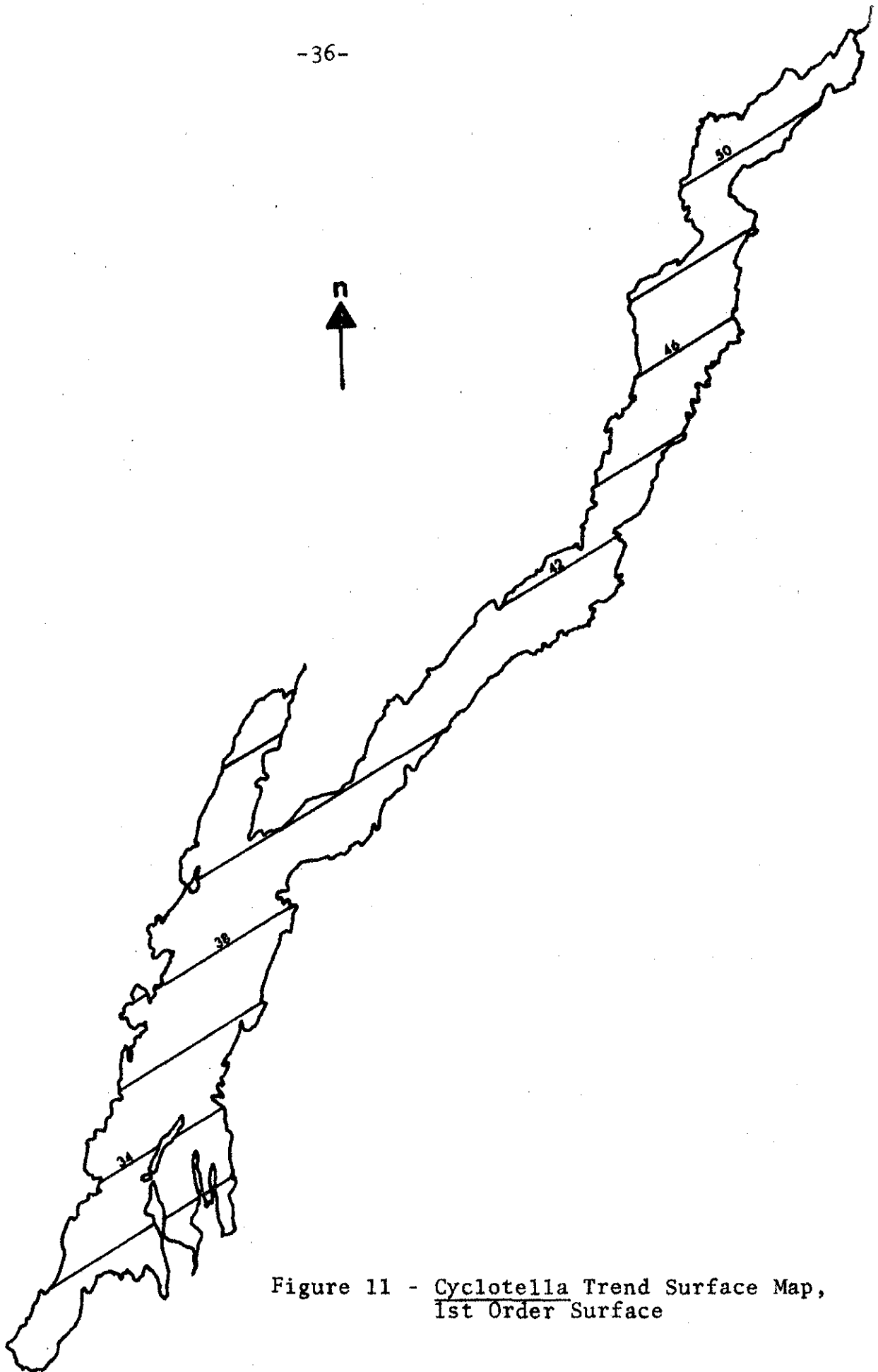


Figure 11 - Cyclotella Trend Surface Map,
1st Order Surface

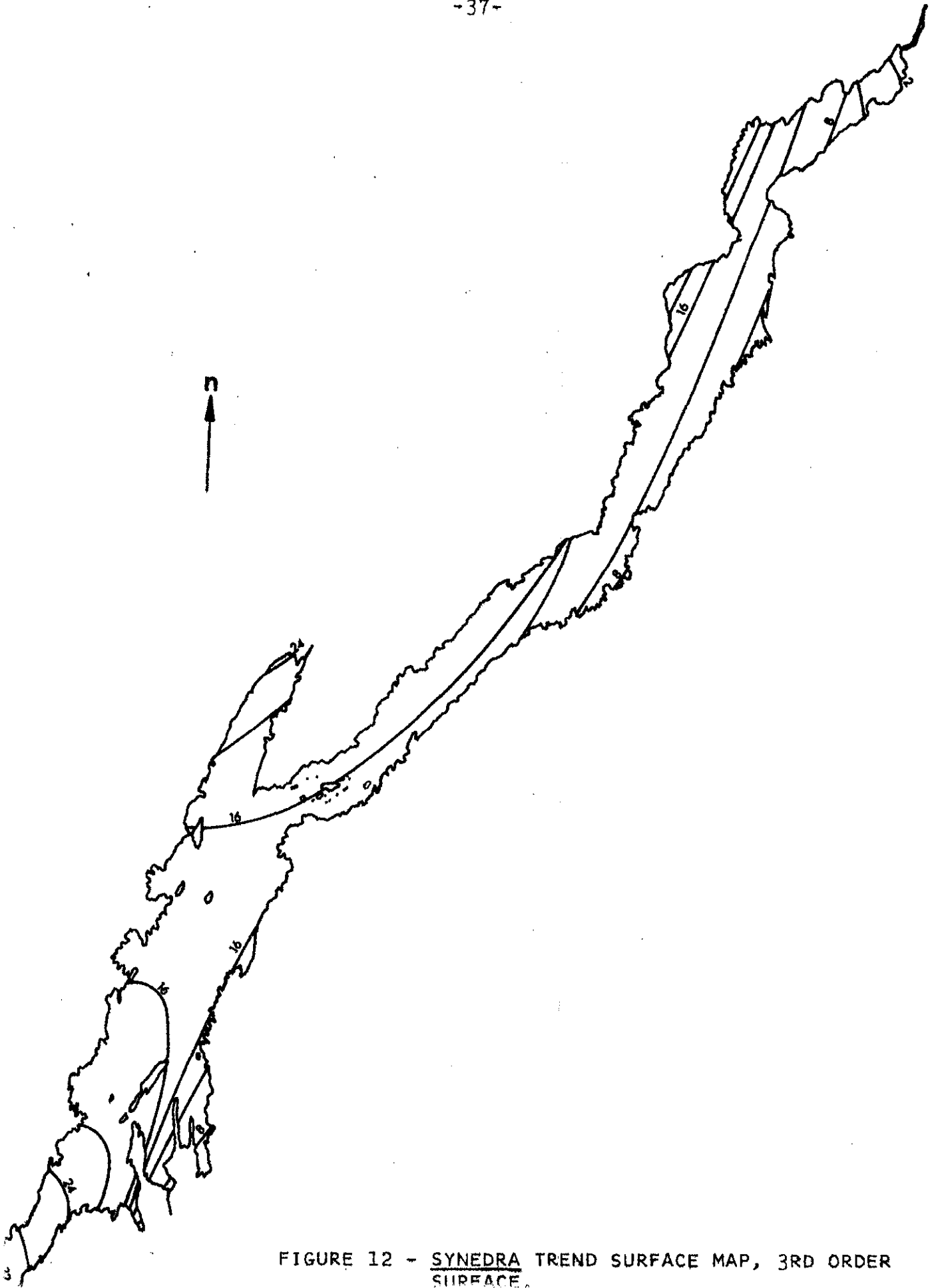


FIGURE 12 - SYNEDRA TREND SURFACE MAP, 3RD ORDER SURFACE.

Percent Similarity
100 75 50

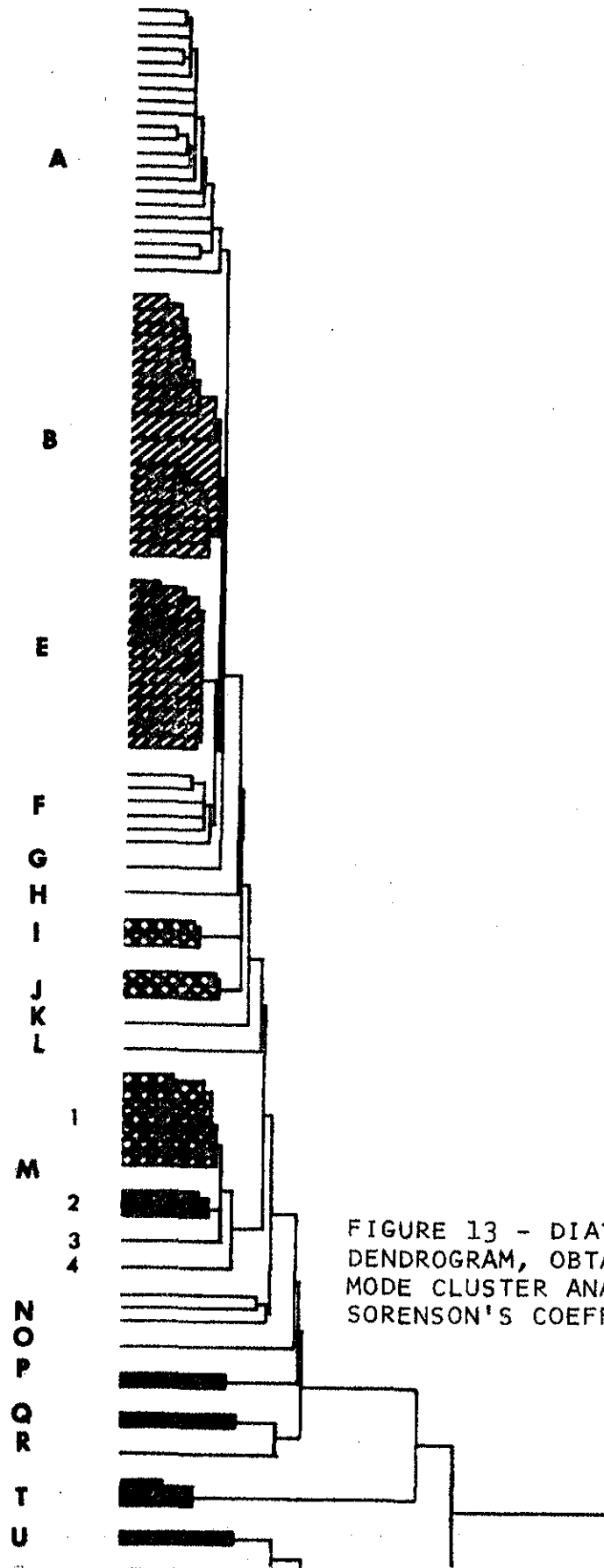


FIGURE 13 - DIATOM BIOTOPE DENDROGRAM, OBTAINED BY Q-MODE CLUSTER ANALYSIS, USING SORENSON'S COEFFICIENT.

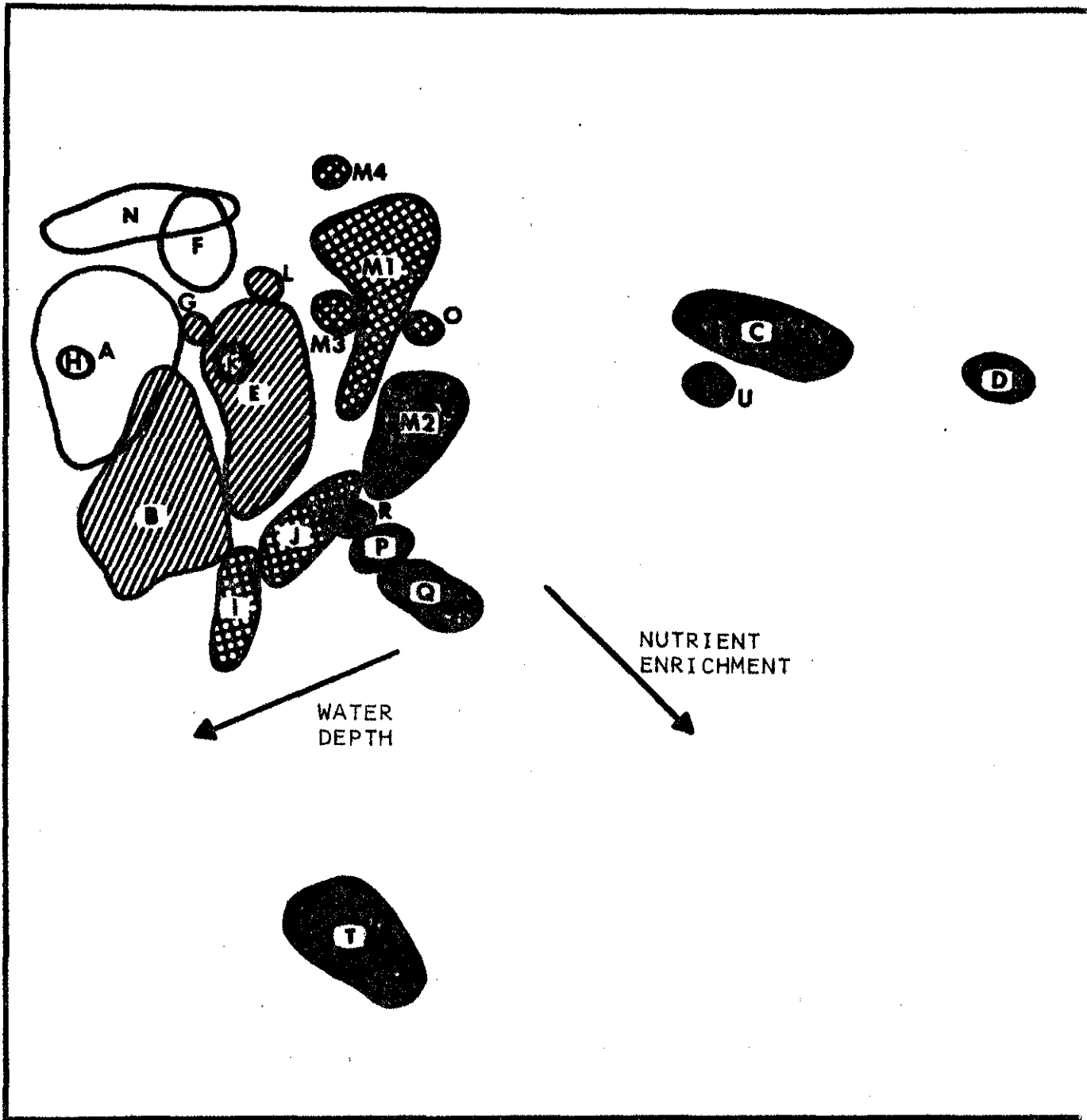


FIGURE 14 - DIATOM Q-MODE ORDINATION MAP, USING SORENSON'S COEFFICIENT. THE DIRECTIONS OF INCREASE OF TWO ENVIRONMENTAL FACTORS, NUTRIENT ENRICHMENT AND WATER DEPTH ARE SHOWN.

water were the two most apparent environmental factors affecting the distributions of the diatoms. By observing their positions in the model, it was possible to assign "nutrient enrichment values" to the biotopes; and this information was then plotted on the map (Fig. 15). The darker the pattern, the greater the indicated nutrient enrichment (and concomitant biologic productivity).

Analysis of variance of the biotopes indicates that the biotopes are significantly different from each other. At the present time the spatial distribution of the biotopes is being investigated. By noting the biotic gradients between adjacent areas and by analyzing the entropy or relative mixing of adjacent biotopes based on their constituent biofacies (established by R-mode cluster analysis), it is possible to divide the lake into relatively homogeneous segments for purposes of overall simulation and validation.

SIMULATION

The integration of the biologic and abiotic (including hydrologic and mixing) models into a complex model driven by a few key exogenous variables will permit extensive symbolic experimentation in the Lake George basin. Following the terminology of some of the other IBP modeling groups, "simulation" is used to refer to experimentation with historic data - that is, experimentation mimicing environmental effects already observed within the confines of the ongoing study. This leads to a determination of the concurrent validity of the model. The research is just reaching this phase of the modeling (see Fig. 1) at this time.

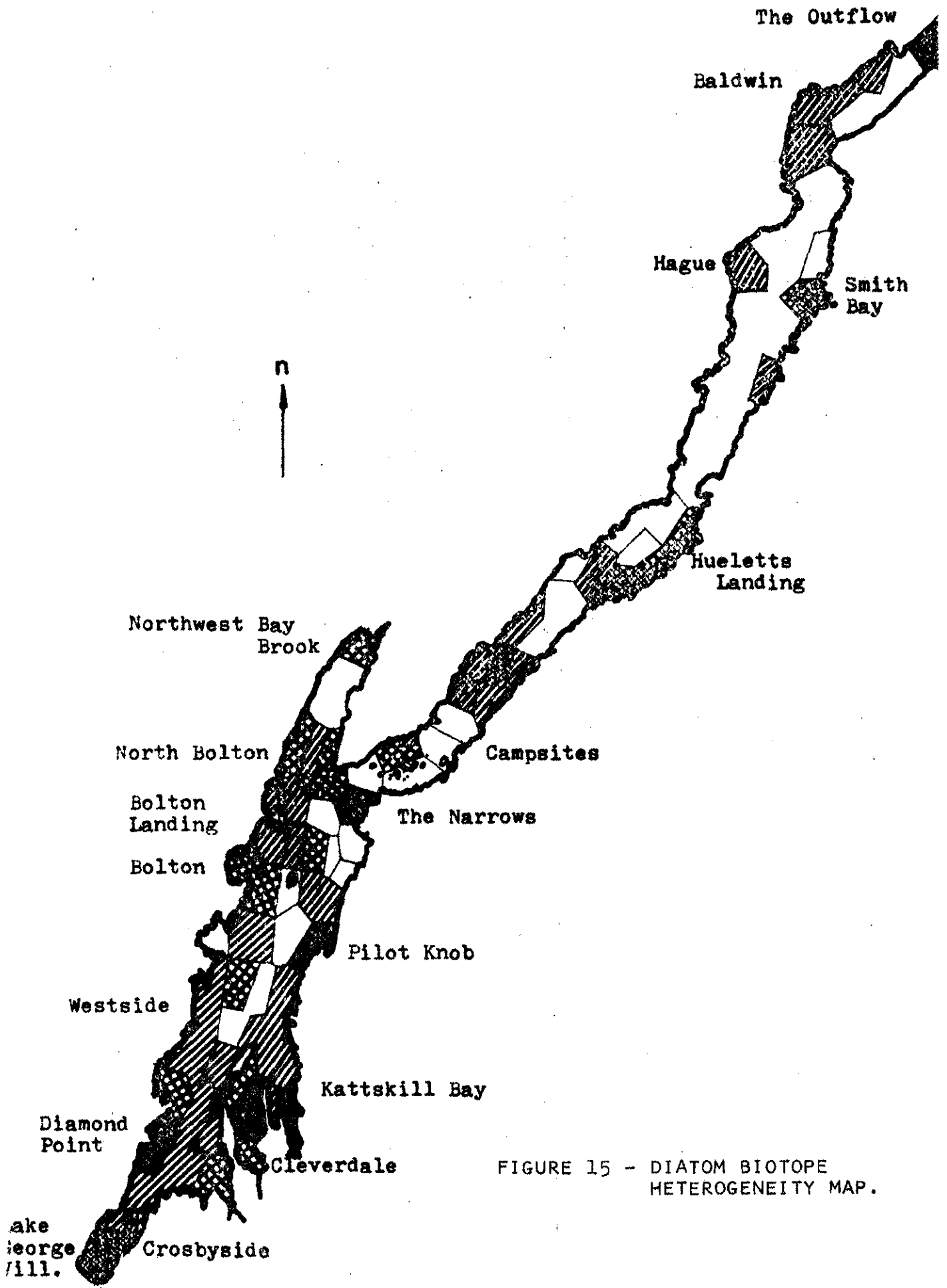


FIGURE 15 - DIATOM BIOTOPE HETEROGENEITY MAP.

Several large, relatively homogeneous lake segments, representative of differing natural and Man-induced environmental conditions, will be used as target areas in the simulation. Each area will be represented by a point model, with the model parameters being determined by the characteristics of the lake basin included in and impinging on that particular part of the lake. The target areas are being picked on the basis of the heterogeneity analysis and a consideration of the land-use, vegetational, hydrologic, topographic, and geologic patterns in the basin.

It was previously thought that the lake could be relatively well represented by a few point models and that interpolation procedures could be used to represent the intervening areas (Park and Wilkinson, 1970). However, the lake is more heterogeneous than originally assumed (Fig. 15) so that this approach is not readily applicable, although it might be quite useful in more homogeneous lakes.

In order to fully develop the simulation capability, data in computer accessible form were obtained on the land uses for the Lake George Basin. These data were drawn from the Land Use and Natural Resources Inventory (LUNR), an aerial photographic study recently completed by the New York State Office of Planning Services. In addition, tapes containing 1970 census data were obtained and are operational. A library of comprehensive sewage survey reports for the basin has also been established. These supplement the vegetational data collected by the site terrestrial research group so that the modeling parameters can be based on all the available data and information.

FORECASTING

One of the most difficult tasks is the development of models that are sufficiently robust to permit prediction of future ecosystem states based on a variety of possible natural and Man-induced perturbations. Because of the complexity of the ecosystem, it is doubtful that a high degree of precision and resolution could ever be achieved. However, by using a limited number of driving variables and by employing functional models that realistically represent most key processes, it should be possible to forecast the general consequences of such environmental changes as increased urbanization, improved sewage treatment, and higher water temperature.

Evaluation of predictive validity of an overall model with a time frame of one year will be a slow process, so it is anticipated that this task will begin as soon as the model is reasonably complete. Because modeling is an iterative, hypothesis-testing procedure, preliminary experimentation with forecasting should be considered a part of the general strategy of model refinement.

Of course, forecasting is not merely an academic exercise. When the model has been shown to have reasonable predictive validity it should be used to educate planners and politicians who have a decision-making role in the management of the ecosystem. One of the most promising techniques is the use of computer gaming, with the individuals assuming their real-life roles. Such gaming models have already proven useful in educating city planners (Feldt, 1966; Meier and Duke, 1966) and air pollution control officers (Anon. 1971).

APPLICATION TO WATER QUALITY MANAGEMENT

In order to assure the applicability of the ecosystem model, it is necessary to express the output in terms that directly pertain to environmental quality. Unfortunately, the definition of objective functions seems to have been overlooked in many ecosystem studies, perhaps because most studies stop short of development of management models.

The Lake George study is fortunate to have access to data that permit establishment of a variety of objective functions based on the reactions of differing groups of tourists and residents. A unique study conducted by Mr. Jack Kooyoomjian and funded by the New York State Science and Technology Foundation has resulted in the return of over 4500 questionnaires giving detailed information on recreationists, cottage owners, and others and how they perceived environmental quality at times when water quality measurements were taken. The Lake George modeling group has given programming support to this study in order to obtain the data in a form compatible with IBP objectives.

One of the ways in which these data will be used will be to differentiate between "good" and "bad" water quality for any particular user group, such as swimmers or fishermen. Discriminant function analysis is well suited for this, as shown in a hypothetical example (Fig. 16). Two populations of water quality samples, good represented by "+"s and bad represented by "-"s, are recognized on the basis of individual respondent's reactions. Each of these samples has associated with it a variety of chemical, physical, and biologic

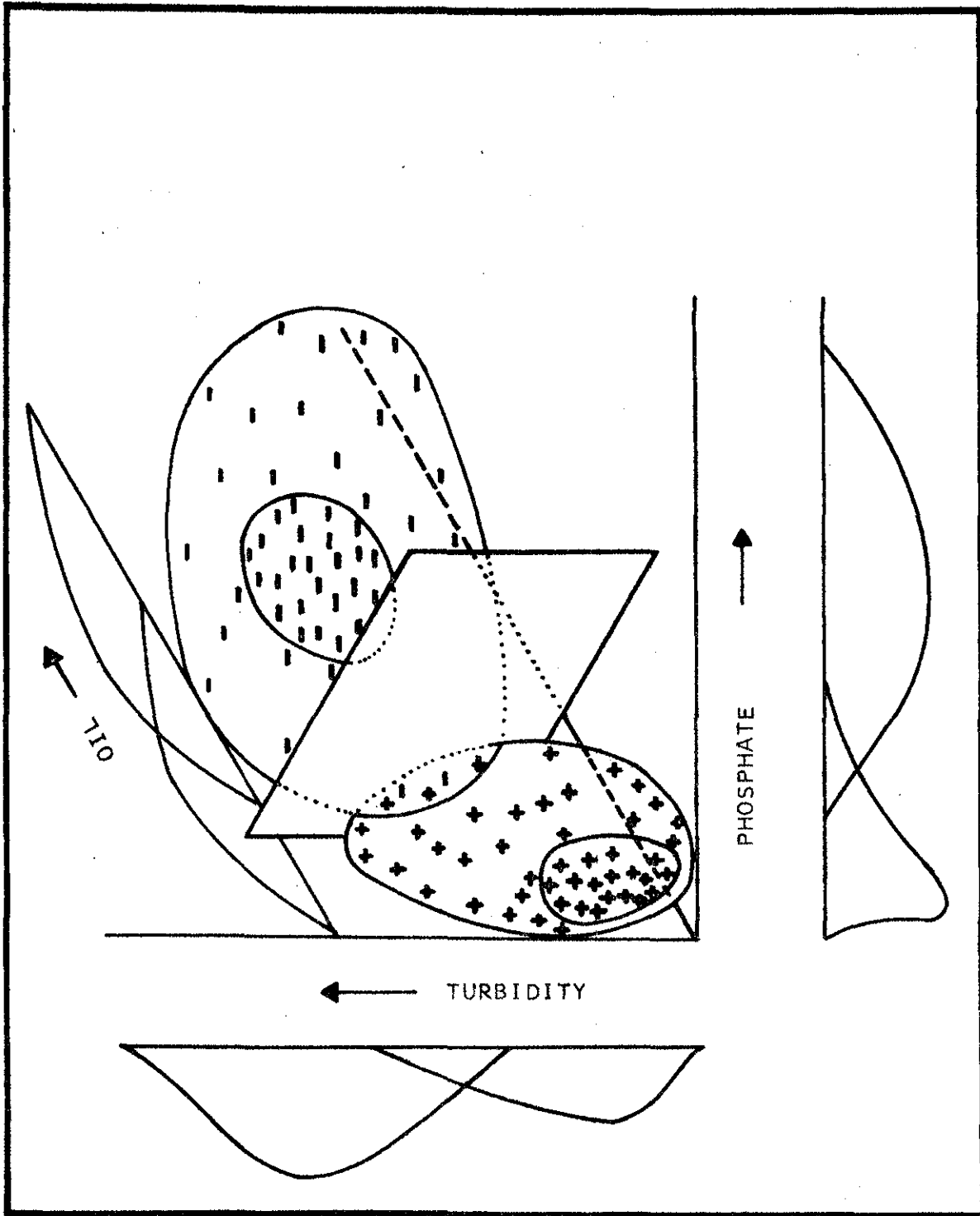


FIGURE 16 - HYPOTHETICAL DISCRIMINANT FUNCTION ANALYSIS OF WATER QUALITY DATA.

characteristics measured at the time the questionnaire was distributed. The analysis provides an objective means of discriminating between combinations of environmental characteristics that usually result in good water quality and those that usually result in bad water quality. The discriminant function equation can then be used to transform model output into a direct expression of predicted water quality. Thus, environmental effects can be balanced against the operating and economic-development costs of various management practices.

MACROMODELS

In order to achieve efficient computing, aggregate or macromodels which will be used for specific purposes should contain only those submodels that contribute to the computation of the target variables. The development of macromodels therefore entails carefully considered simplification. This is consistent with the concept of content validity in that content is determined by the objectives and desired resolution.

Because not all functional models are needed for any particular macromodel, it is possible to begin developing certain macromodels while development of the various functional models is proceeding. In keeping with the philosophy of parallel, iterative development of different levels of models (Fig. 1), the Lake George group is now engaged in refinement of a population-pollution macromodel developed as a class exercise in cooperation with the IBP study (Stern, 1971). The model is self-contained and includes a simple population forecasting submodel (Fig. 17), thus permitting experimentation

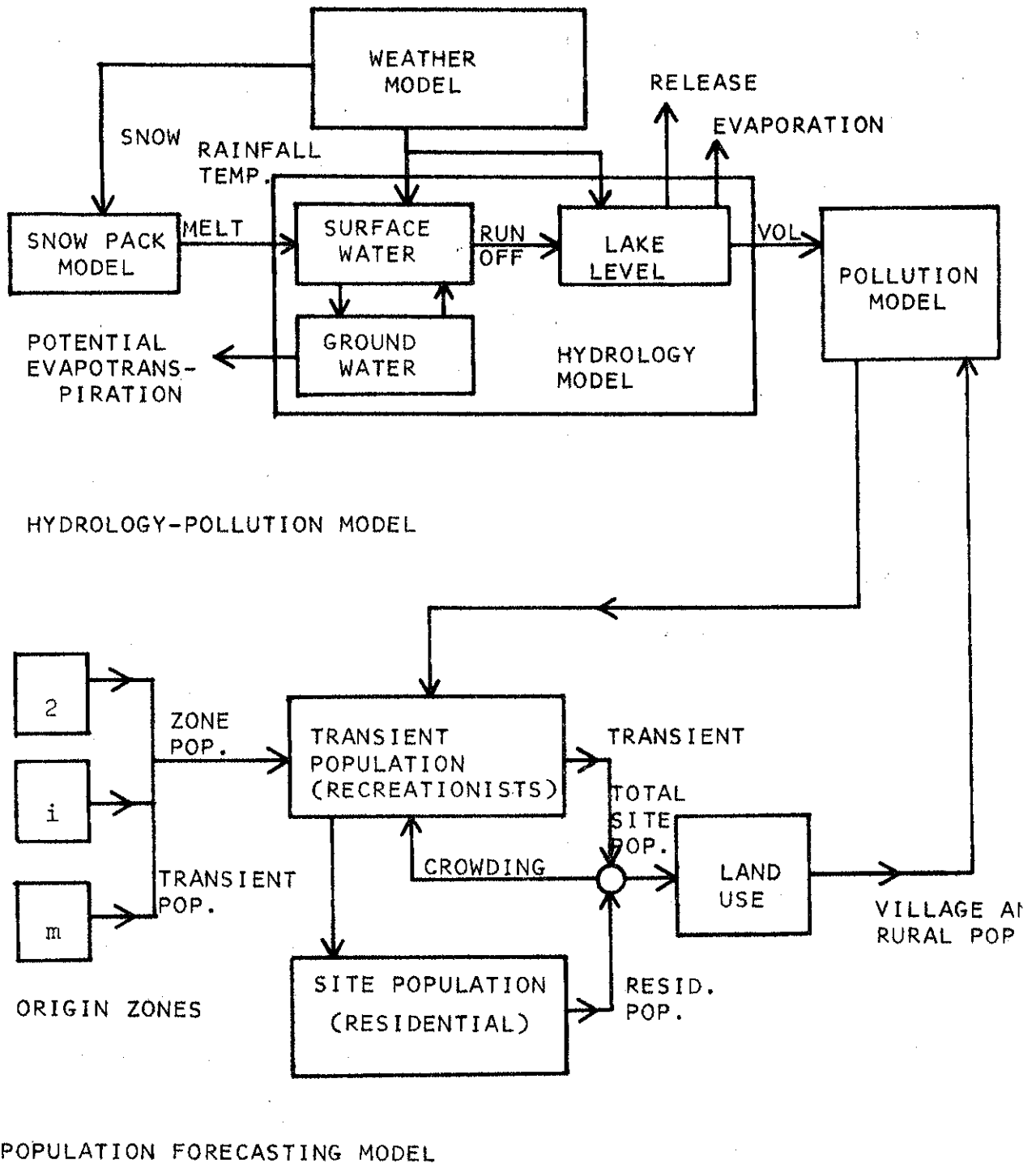


FIGURE 17 - A MODEL FOR POPULATION-RECREATIONAL QUALITY INTERACTIONS OF A FRESH WATER SITE

with system feedback. The present refinement involves disaggregation of recreationist response to various types of pollution, utilizing the environmental perception data. Similar macromodels are envisioned for other specific, well defined ecosystem feedback loops.

OPTIMIZATION

Following one objective of the IBP Analysis of Ecosystems, i.e. to be able to predict Man's impact on the ecosystems, research has begun on formulation of optimization models that represent ways in which Man could (or should) seek to manage his environment. Initial efforts were concerned with the development of a mathematical programming model for cultural eutrophication control within a lake basin. This approach seeks to find the "optimal" plan for sewage collection and treatment, which admittedly is an idealistic undertaking. However, sensitivity analyses can then be performed to see how deviations from this optimal management system would affect the ecosystem.

Any environmental management model constructed for a lake basin is closely tied to the corresponding ecosystem model. The interaction of these two models could be expressed as a feedback loop as shown in Figure 18. The results of experimentation with the feedback should lead to refinements of the environmental management model. Perturbation analyses performed on the ecosystem model might well serve as a basis for establishing appropriate water quality standards which, of course, would be time varying.

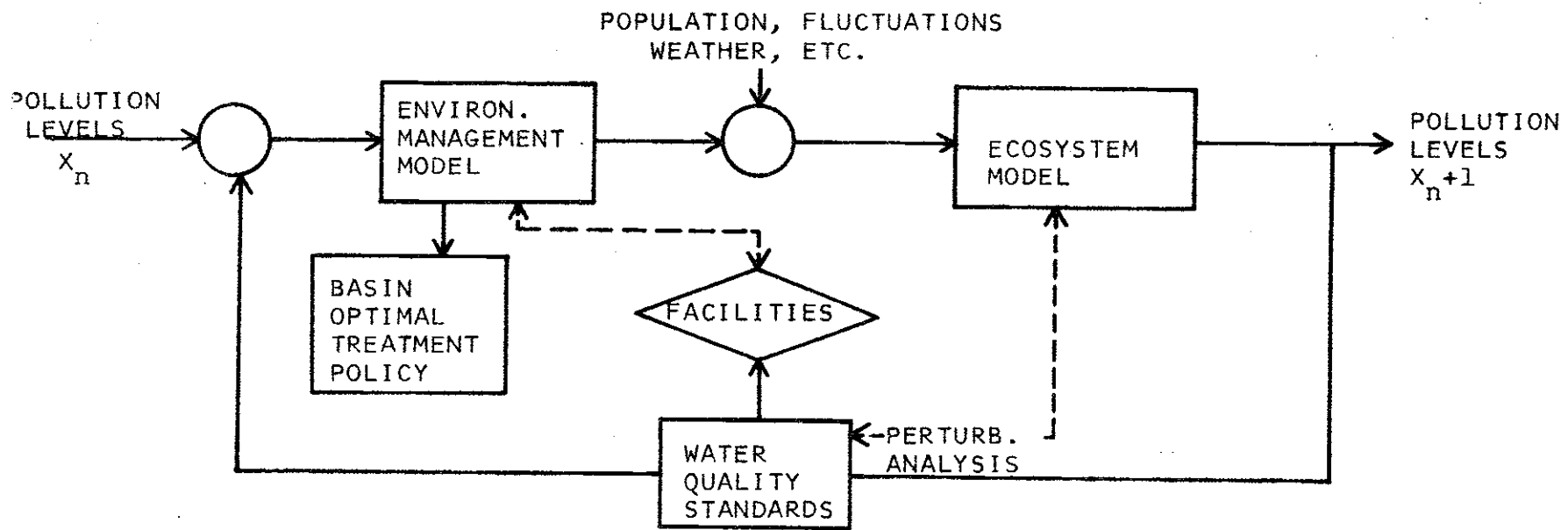


FIGURE 18 - ENVIRONMENTAL CONTROL: A CONCEPTUAL MODEL

Findings to date indicate that at least six mathematical programming formulations of the environmental management model of a lake basin are possible. They depend upon the characteristics and attributes of the particular lake basin under consideration.

These six possible formulations fall into three separate categories. Only one of these categories, however, applies specifically to the Lake George Basin; and the choice between the two possible formulations within this category was dependent upon the availability of computer programs.

The type of formulation recommended for the Lake George Basin is the network flow model as follows:

$$\text{Min. } \sum_i \sum_j F_{ij} (X_{ij})$$

$$\text{Subject to: } \sum_j X_{ij} - \sum_j X_{ji} = \sum_j (X_{ij} - X_{ji}) = a_i;$$

$$X_{ij} \geq 0; \sum_i a_i = 0;$$

where $x_{ij} \equiv$ the amount of waste transported from node i to node j ;

$F_{ij} (X_{ij}) \equiv$ cost of transporting X_{ij} units of waste from node i to node j ;

$a_i \geq 0$ implies an input node;

$a_i = 0$ implies a transshipment node; and

$a_i \leq 0$ implies an output node.

The form of the objective function to be used, where the function is the sum of the collection and treatment costs, specifies the type of computer program to be used. If a non-linear programming algorithm is available to solve the problem, the objective function can be put in its most

realistic form. If not, a linear approximation of the function is necessary.

SUMMARY

The philosophy of modeling at Lake George embodies a multi-pronged approach with models of differing complexity being developed simultaneously. In order to take full advantage of prior knowledge, preliminary models are developed from the literature at the same time that statistical models and process models are developed using data from ongoing studies. The resulting functional models are then subjected to content, construct, and concurrent validation as soon as they are operational. Because model refinement is a continuing process, even very simplistic models are considered to be useful. As soon as the functional models are reasonably valid they are aggregated into macromodels with varying objectives. These can then be used in determining predictive validity in succeeding years; they also serve as the basis for preliminary optimization leading eventually to management models.

ACKNOWLEDGEMENTS

Numerous individuals have aided in the Lake George modeling effort, including N. L. Clesceri, site director, L. S. Clesceri, R. G. Stross, D. C. McNaught, E. J. LaRow, R. Stewart, J. T. Scott, E. M. Colon, S. Kobayashi, S. L. Williams, and K. J. Kooyoomjian; their help is gratefully acknowledged, for without the scientific insights they have provided the modeling would be meaningless. In addition to the members of the modeling group who contributed directly to this paper, H. I. Stern, R. B. Simpson, J. G. Ecker, F. DiCesare, J. M. Hill, R. J. Ashdown, and E. P. Rodriguez also influenced the model development, as did R. V. O'Neill Biome modeling coordinator. However, the authors take full responsibility for the views expressed. The research was supported by the Deciduous Forest Biome Project, International Biological Program, funded by the National Science Foundation under Interagency Agreement Ag-199, 40-193-69 with the Atomic Energy Commission - Oak Ridge National Laboratory, with additional support from the Office of Water Resources Research (OWRR Contract No. 14-31-001-3387) and New York State Science and Technology Foundation.

REFERENCES

- Anonymous. 1971. Computer game trains pollution officials. Environ. Sci. Tech. 5(3):202-203.
- Baisuck, A. and W. A. Wallace. 1970. A computer simulation approach to enrollment projection in higher education. Socio-Econ. Plan. Sci. 4:365-381.
- Bella, D. A. 1970. Simulating the effect of sinking and vertical mixing on algal population dynamics. J. of Wat. Poll. Contr. Fed. 42(5):R140-R152.
- Burns, C. W. 1969. Relation between filtering rate, temperature, and body size in four species of Daphnia. Limnol. & Oceanogr. 15(5):693-700.
- Conover, R. J. 1966. Assimilation of organic matter by zooplankton. Limnol. & Oceanogr. 11:338-345.
- Dale, M. B. 1970. System analysis and ecology. Ecology. 51(1):2-16.
- Di Toro, D. M., O'Connor, D. J., and R. V. Thomann. 1970. A dynamic model of phytoplankton populations in natural waters. In press.
- Dugdale, R. C. 1967. Nutrient limitation in the sea: dynamics, identification, and significance. Limnol. & Oceanogr. 12(4):685-695.
- Epply, R. W., Rogers, J. N., and J. J. Mc Carthy. 1959. Half saturation constants for uptake of nitrate and ammonia by marine phytoplankton. Limnol. & Oceanogr. 14(6):912-920.
- Feldt, A. G. 1966. Operational gaming in planning education. J. of Am. Inst. Planners. 32:17-23.
- Fishman, G. S. and P. J. Kiviat. 1967. The analysis of simulation generated time series. Mgt. Sci. 13(7): 525-557.
- Mac Isaac, J. J. and R. C. Dugdale. 1969. The kinetics of nitrate and ammonia uptake by natural populations of marine phytoplankton. Deep-Sea Res. 16:45-57.
- Meier, R. L. and R. D. Duke. 1966. Gaming simulation for urban planning. J. of Am. Inst. Planners. 32:3-17.
- Naylor, T. H. and J. M. Finger. 1967. Verification of computer simulation models. Mgt. Sci. 14(2):B92-B101.
- Park, R. A. and J. W. Wilkinson. 1970. Lead-time study report, Lake George modelling project. IBP Prelim. Progr. Rept. 98pp.

Riley, G. A. 1963. Theory of food-chain relations in the ocean. The Sea, Intersci. Publications, N.Y. 438-463.

_____, Stommel, H. and E. F. Bumpus. 1949. Quantitative ecology of the plankton of the Western North Atlantic. Bull. of the Bingham Oceanogr. Coll. 12(3):1-169.

Stern, H. I. 1971. A model for population-recreational quality interactions of a fresh water site. RPI, Operations Res. and Stat. Res. Paper 37-71-P4, 24 pp.

Van Horn, R. L. 1971. Validation of simulation results. Mgt. Sci. 17(5):257-259.

Appendix A

Phytoplankton Model

1. Model Equation

$$dP/dt = (G_p - R_p - L_{hgz} - S_p) * P \quad (1)$$

where

$$G_p = K_{sg} * T_m * (2.718 * F_p / (K_e * D) * (\exp(-(I_o/I_s)) - \exp(-(I_o/I_s) * \exp(-K_e * D)))) * (N_p / (K_{mnp} + N_p)) * (N_a / (K_{mna} + N_a)) \quad (1.1)$$

$$R_p = K_{pr} * T_m \quad (1.2)$$

$$L_{hgz} = g_{hg} * Z_h \quad (1.3)$$

$$S_p = K_{sp} * T_m \quad (1.4)$$

$$F_p = .04167 * (12.10 + 3.150 * \sin(.017262 * (t - 81))) \quad (1.5)$$

$$T_m = 10.24 - 5.96 * \cos(2\pi t / 365) - 7.57 * \sin(2\pi t / 365) \quad (1.6)$$

2. Notation

- P = phytoplankton concentration (mg-C/l)
- G_p = phytoplankton growth rate (day^{-1})
- R_p = phytoplankton endogenous respiration rate (day^{-1})
- L_{hgz} = phytoplankton loss rate due to grazing by herbivorous zooplankton (day^{-1})
- S_p = phytoplankton sinking rate (day^{-1})
- t = Time of year (day)
- K_{sg} = phytoplankton saturated growth rate ($\text{day}^{-1}\text{-}^\circ\text{C}^{-1}$)
- T_m = water temperature ($^\circ\text{C}$)
- F_p = photoperiod (day)
- K_e = extinction coefficient (m^{-1})
- D = chosen depth in euphotic zone (m)
- I_o = Incident solar radiation intensity at water surface (ly/day)
- N_p = concentration of limiting nutrient (phosphate) (mg-P/l)
- K_{mnp} = Michaelis-Menten constant for phosphate (mg-P/l)
- N_a = concentration of limiting nutrient (ammonia) (mg-N/l)
- K_{mna} = Michaelis-Menten constant for ammonia (mg-P/l)
- K_{pr} = phytoplankton endogenous respiration coefficient ($\text{day}^{-1}\text{-}^\circ\text{C}^{-1}$)
- g_{hg} = Herbivorous zooplankton grazing rate (1/mg-C-day)
- Z_h = Herbivorous zooplankton concentration (mg-C/l)
- K_{sp} = phytoplankton sinking coefficient ($\text{day}^{-1}\text{-}^\circ\text{C}^{-1}$)

Appendix B

Herbivorous Zooplankton Model

1. Model Equation

$$dZ_h/dt = (G_{hz} - R_{hz} - L_{pzg} - S_{hz}) * Z_h \quad (2)$$

where

$$G_{hz} = a_{hzp} * f_{hg} * K_{mp} * (P / (K_{mp} + P)) \quad (2.1)$$

$$R_{hz} = K_{h zr} * T_m \quad (2.2)$$

$$L_{pzg} = g_{zp} * Z_p \quad (2.3)$$

2. Notation

Z_h = Herbivorous zooplankton concentration (mg-C/l)

G_{hz} = Herbivorous zooplankton growth rate (day^{-1})

R_{hz} = Herbivorous zooplankton respiration rate (day^{-1})

L_{pzg} = Herbivorous zooplankton loss rate due to the grazing by predatory zooplankton (day^{-1})

S_{hz} = Herbivorous zooplankton rate of loss due to normal mortality (day^{-1})

t = Time of year (day)

a_{hzp} = Herbivorous zooplankton conversion factor (mg-C/mg-C)

f_{hg} = Herbivorous zooplankton filtering rate (l/mg-C-day)

K_{mp} = Michaelis-Menten constant for phytoplankton (mg-C/l)

P = Phytoplankton concentration (mg-C/l)

$K_{h zr}$ = Herbivorous zooplankton respiration rate ($\text{day}^{-1} \cdot ^\circ\text{C}^{-1}$)

T_m = Water temperature ($^\circ\text{C}$)

g_{zp} = Predatory zooplankton grazing rate (l/mg-C-day)

Z_p = Predatory zooplankton concentration (mg-C/l)

Appendix C

Predatory Zooplankton Model

1. The Model Equation

$$dZ_p/dt = (G_{pz} R_{pz} - L_{pz}) * Z_p \quad (3)$$

where

$$G_p = a_{pzh} * f_{pg} * K_{mh} * (Z_h / (K_{mh} + Z_h)) \quad (3.1)$$

$$R_{pz} = K_{pzt} * T_m \quad (3.2)$$

2. Notation

Z_p = predatory zooplankton concentration (mg-C/l)

G_{pz} = predatory zooplankton growth rate (day⁻¹)

R_{pz} = predatory zooplankton respiration rate (day⁻¹)

L_{pz} = predatory zooplankton loss rate due to predation and natural mortality (day⁻¹)

t = time of year (day)

a_{pzh} = predatory zooplankton conversion factor (mg-C/mg-C)

f_{zg} = predatory zooplankton filtering rate (l/mg-C-day)

K_{mh} = Michaelis-Menten constant for herbivorous zooplankton (mg-C/l)

Z_h = herbivorous zooplankton concentration (mg-C/l)

K_{pzt} = predatory zooplankton respiration rate (day⁻¹-°C⁻¹)

T_m = water temperature (°C)

Appendix D

Nutrient Submodel

1. Model Equation

$$dN/dt = (A_m + A_n + P_d + Z_e + Z_d + F_{ed}) - L_{pa} - L_s \quad (4)$$

where

$$A_m = k_m * N \quad (4.1)$$

$$A_n = k_n * N \quad (4.2)$$

$$P_d = a_{np} * K_{pr} * T_m * P \quad (4.3)$$

$$Z_e = a_{np} * f_{hg} * Z_h * P * (1 - (a_{hzp} * K_{mp}) / (K_{mp} + P)) + a_{nzh} * f_{pg} * Z_p * Z_h * (1 - (a_{pzh} * K_{mh}) / (K_{mh} + Z_h)) \quad (4.4)$$

$$Z_d = a_{nzh} * K_{h zr} * T_m * Z_h + a_{nzp} * K_{p zr} * T_m * Z_p \quad (4.5)$$

$$L_{pa} = a_{np} * G_p * P \quad (4.6)$$

$$L_s = K_s * N \quad (4.7)$$

2. Notation

N = Nutrient concentration (mg-N or P/l)

A_m = Nutrient addition rate due to various man-made inputs (mg-N or P/l-day)

A_n = Nutrient addition rate due to various natural inputs

P_d = Nutrient release rate by the death of phytoplankton (mg-N or P/l-day)

Z_e = Nutrient release rate by the excretion of zooplankton (mg-N or P/l-day)

Z_d = Nutrient release rate by the death of zooplankton

- F_{ed} = Nutrient release rate by the death and excretion of higher food-chain elements (mg-N or P/l-day)
- L_{pa} = Nutrient loss rate due to assimilation by phytoplankton (mg-N or P/l-day)
- L_s = Nutrient loss rate due to sediments (mg-N or P/l-day)
- k_m = Nutrient addition rate constant due to man-made inputs (day⁻¹)
- k_n = Nutrient addition rate constant due to natural inputs (day⁻¹)
- a_{np} = Ratio of nutrient to phytoplankton biomass (mg-N or P/mg-C)
- K_{pr} = Phytoplankton respiration coefficient (day⁻¹-°C⁻¹)
- T_m = Water temperature (°C)
- t = Time of year (day)
- p = Phytoplankton concentration (mg-C/l)
- f_{hg} = Herbivorous zooplankton filtering rate (l/mg-C-day)
- Z_h = Herbivorous zooplankton concentration (mg-C/l)
- a_{hzp} = Herbivorous zooplankton conversion factor (mg-C/mg-C)
- K_{mp} = Michaelis-Menten constant for phytoplankton (mg-C/l)
- a_{nzh} = Ratio of nutrient to herbivorous zooplankton biomass (mg-N or P/mg-C)
- f_{pg} = Predatory zooplankton filtering rate (l/mg-C-day)
- Z_p = Predatory zooplankton concentration (mg-C/l)
- a_{pzh} = predatory zooplankton conversion factor (mg-C/mg-C)
- K_{mh} = Michaelis-Menten constant for herbivorous zooplankton (mg-C/l)
- $K_{h zr}$ = Herbivorous zooplankton respiration coefficient (day⁻¹-°C⁻¹)
- a_{nzp} = Ratio of nutrient to predatory zooplankton biomass (mg-N or P/mg-C)
- $K_{p zr}$ = Predatory zooplankton respiration coefficient (day⁻¹-°C⁻¹)
- G_p = Phytoplankton growth rate (day⁻¹)
- K_s = Nutrient loss rate due to sediments (day⁻¹)