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# A BIOLOGICAL PRODUCTION MODEL FOR GRAND TRAVERSE BAY

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THE UNIVERSITY OF MICHIGAN SEA GRANT PROGRAM

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## SUMMARY AND CONCLUSIONS

For the past three years researchers supported by The University of Michigan Sea Grant Program have conducted extensive field surveys in both arms of Grand Traverse Bay. These surveys have included observations of several physical, chemical, and biological characteristics of the Bay. A major goal of this field sampling program has been to provide data which can be used to construct mathematical models which specify interactions and mechanisms among the variables. Subsequent to verification, the models are intended to be used to predict certain measures of water quality which result from various pollution control schemes and alternate patterns of land use and zoning. This report describes the utilization of these data for the construction, verification, and application of a dynamic model for plankton and nutrients in the lower west arm of Grand Traverse Bay.

The model has been used to calculate the spatial and temporal distribution of dissolved and particulate phosphorus, particulate nitrogen, ammonia, nitrate, silicon, chlorophyll a, primary productivity, and total zooplankton. The seasonal dynamics of each of these variables has been determined at a number of locations within the bay by the integration of mass continuity equations which account for changes due to transport by water movements, growth, decomposition, and biological uptake.

The dynamics of the behavior of the chemical and biological variables of interest have been modeled in the lower part of the west arm of the bay using measured nutrient input fluxes and observed temperature and solar radiation patterns. The

mass continuity equations were integrated using a number of sophisticated numerical techniques. In general the model predictions compare favorably with data obtained during 50 separate Sea Grant surveys conducted during a period between 1970 and 1972. The model has been used to forecast the water quality in the bay which will result from alternate patterns of residential, commercial, and industrial growth, and varying degrees of phosphorus control in the Traverse City area. A nonlinear relation exists between the level of nutrients discharged to the Bay and the resulting plankton populations. This nonlinear relation was not anticipated and is a phenomenon which should be examined prior to recommendation of management alternatives in aquatic systems.

The model predictions indicate that, as water quality deteriorates in the bay, changes in algal species will occur due to silicon limitation. It is expected that the phytoplankton community will become dominated by green and blue-green forms. This contrasts to the present population which consists mainly of diatoms. The model suggests that the potential biomass of algal species, which do not have a major silicon requirement, is double that of a population consisting only of diatoms.

## INTRODUCTION

Researchers supported by The University of Michigan Sea Grant Program have conducted extensive limnological field surveys in both arms of Grand Traverse Bay since 1970. These surveys have included observations of several physical, chemical, and biological characteristics of the Bay. The major goal of this field sampling program has been to provide data which can be used to guide the construction of mathematical models which quantify the interactions among the variables. Subsequent to verification, the models are intended to be used to predict the water quality which results from different pollution control schemes and alternate patterns of land use in the Traverse City area. This predictive capability will facilitate the adaption of rational water-quality control programs designed to maintain the relatively high quality of the Bay waters. Other efforts in the program have resulted in hydrological models (Brater, 1972); models for water circulation (Smith, 1973; and models for coliform bacteria (Canale and Green, 1972; Canale, 1973). This report describes the utilization of Sea Grant field data for the construction, verification and application of a dynamic model for phytoplankton, nutrients, and zooplankton in the lower west arm of Grand Traverse Bay.

## SAMPLING PROGRAM

Data gathered through the field sampling program have been collected on more than 50 cruises since initiation of the program in July 1970. During the first stages of the program

13 open-water stations were sampled on a routine basis and 18 cruises were made to sample chemical characteristics of bay tributaries. A modified sampling scheme was instituted in January 1972 to provide greater focus on the west arm of the bay. Figure 1 displays the location of some of the sampling stations currently used, as well as some historical stations. The measured parameters which are directly compared with model results are listed in Table 1, along with methods of analysis and error estimates. Other parameters such as temperature, sunlight intensity, cloud cover, primary productivity, secchi disc and light extinction are also routinely observed. A report on additional details regarding the handling and storage of samples prior to analysis, and the analytic techniques is in preparation. Parameters, sampled at some point in the field program, but not used directly in the current model, include conservative ions, heavy metals, dissolved oxygen, hydrogen ion activity, alkalinity, conductivity, benthos organisms, and surficial sediment chemistry. The observations of all parameters are maintained in a computer file for convenient retrieval.

The data obtained during this program have supported the modeling activity in three different ways. The first use has been to aid in model construction through the quantification of coefficients in the model. An example is the use of light measurements at various depths to obtain regression estimates of the light intensity extinction coefficient. The second use of the data has been to provide inputs to the model; specifically,

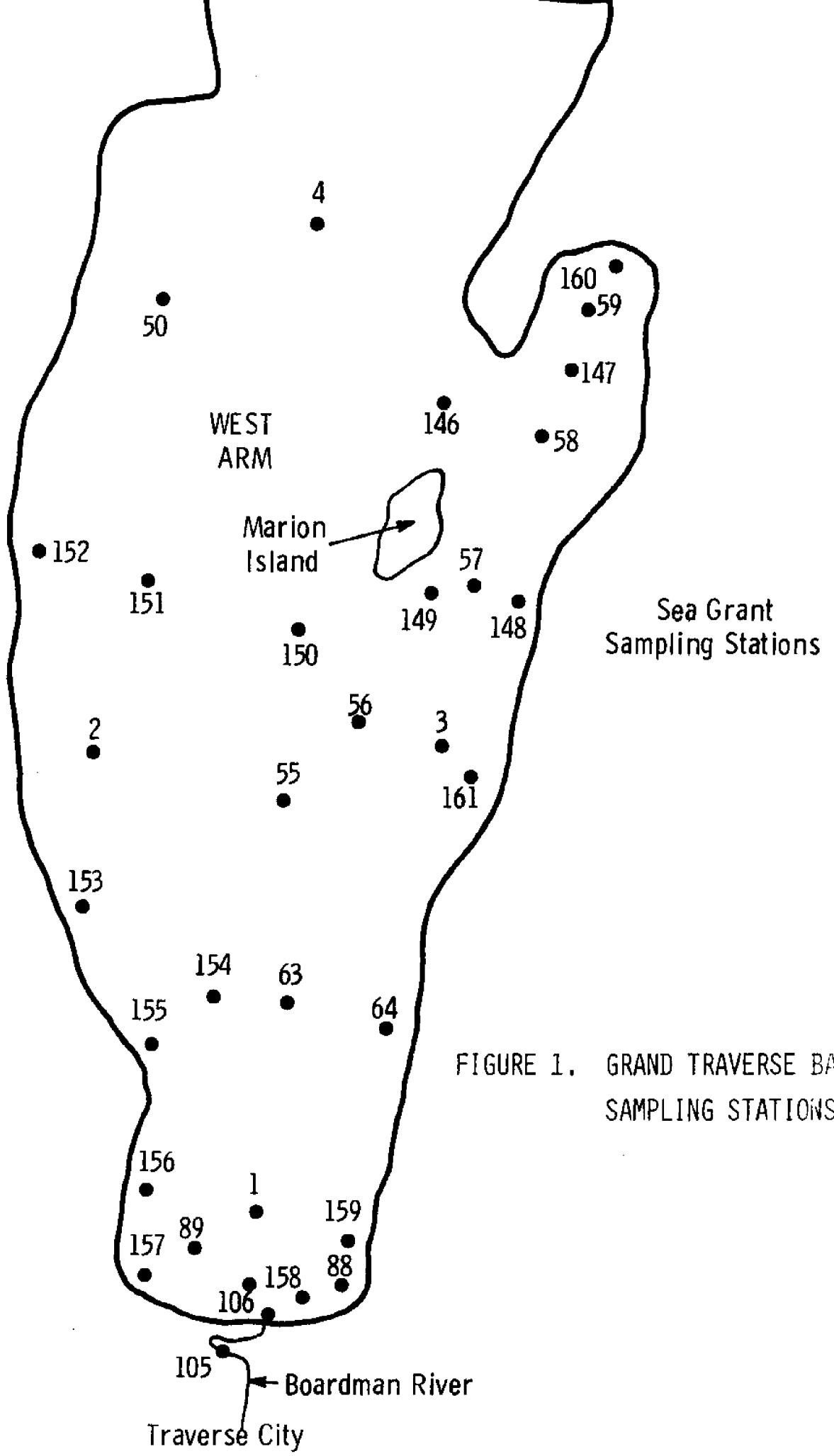


FIGURE 1. GRAND TRAVERSE BAY SAMPLING STATIONS



Parameter	Number of Stations	Number of Observations	Analytical Method	95% Confidence Limit on Analytical Error
Ammonia	18	142	Phenol-hypochlorite	$\pm 15\%$
NO <sub>2</sub> -NO <sub>3</sub>	18	146	Copperized Cadmium Reduction	$\pm 20\%$
Total Dissolved P	18	130	Ascorbic Acid (persulfate digestion)	$\pm 10\%$
Particulate P	18	130	Ascorbic Acid (persulfate digestion)	$\pm 20\%$
Silica - Si	18	146	Silicomolybdenum Blue	$\pm 10\%$
Chlorophyll <u>a</u>	18	117	Fluorometric	$\pm 10\%$
Zooplankton	9	36	Direct Count	$\pm 5\%$

TABLE 1. Measured parameters during field and modeling study of Traverse Bay, analytical methods, and estimated error by analysis.

system loadings, boundary conditions, and initial conditions. It has been determined from the data that the Boardman River and the upper bay are the major sources of nutrients for the lower west arm. Boardman loadings have been estimated using USGS discharge data and concentrations at the river mouth. Concentrations at the upper boundary of the model have been assumed to be representative of the upper bay. The field data have also been utilized in verification of the model. By comparing model-generated concentrations with concentrations at stations in the interior of the system, it is possible to assess the ability of the model to predict real-world conditions. Each of these uses of field data will be discussed in detail in later sections of this report.

In all cases the data presented here are composites of all applicable data collected during the 2-1/2 years of the sampling program. Furthermore, since it has been assumed in the present model that each segment is uniform, it is necessary to use depth-averaged data for input and verification purposes. This is not a serious limitation since a statistical analysis of the field data has failed to show significant variations over depth for the parameters of interest.

#### MODELING METHODOLOGY

In recent years the techniques of systems analysis, long the domain of defense and business practitioners, have begun to be applied to problems involving natural systems. These techniques, which involve the quantification of system components and interactions in an effort to understand or

manage the system, have been successfully employed in a number of studies related to environmental systems. Examples include models of a grassland ecosystem (Bledsoe et al., 1971), an insect population (Chapman, 1969), and a deer herd (Davis, 1967). Systems analysis is also being utilized in research on aquatic environments, examining such issues as the management of a harvestable resource (Beverton and Holt, 1957, and Paulik et al., 1967) and the control of the eutrophication process (Hydroscience, 1973). One of the many major goals of the University of Michigan Sea Grant program is to develop and apply systems analysis techniques to water quality problems of the Great Lakes.

Events of the recent past have made it evident that man, in the process of economic and political decision-making, has often neglected to fully anticipate or account for the effects his decisions have on the natural environment. As the environmental oversights of the past accumulate, it has become more of an economic and political necessity to gain a fuller understanding of the natural world. In so doing, it soon becomes apparent that any environmental system is an extremely complex entity, filled with numerous interrelationships and inclined toward nonintuitive behavior.

The complexity of such systems has two implications. First, the knowledge of a number of separate disciplines such as biology, chemistry, and physics must be brought together to gain an understanding of the system as a whole. And secondly, a procedure must be made available which can merge this diverse information into a clear picture of the system. This is the role played by systems analysis, or ecosystems analysis, as it

is called in such applications. Like systems analysis, the term ecosystems analysis is a general one and has been used to cover a number of analytical methods. The most common use of the term, however, is in situations where a mathematical simulation model of a natural system is constructed in conjunction with field data and experimental studies.

The steps commonly employed in ecosystems analysis include

1. identification of the problem to be addressed and definition of the system by enumeration of the variables or components of interest.
2. specification of the time and space scales which are compatible with the problem of interest and with practical considerations.
3. choice of the relationships between components which are to be modeled.
4. specification and quantification of the mechanisms by which these relationships operate.
5. construction of the mathematical equations which represent these reactions.
6. evaluation of constants contained in the equations.
7. validation of the resultant model.
8. application of the model to real-world situations.

It has been noted that each equation of such a model is, in effect, a hypothesis about the nature of its counterpart in the real world (Kowal, 1971). As such, it is important that the structure of these equations be constructed in compliance with the principles of natural and mathematical science and coupled with

an investigation of the scientific literature, field studies, and experimental research.

The mathematical model produced by an ecosystem analysis can be used to investigate properties of the system and, thus, can be a predictive device and an aid to the decision-making process. Equally important, however, is the activity of constructing the model. In following the steps outlined above, the analyst is forced to explicitly consider each interaction which is a part of his interpretation of the real-world system. This shifts his effort to measurement of important system variables, instead of relying on intuition, and diminishes the possibility of overlooking some important operator in the system. Construction of the model, coupled with its subsequent exercise, points out gaps in basic scientific knowledge and aids in the design of experimental studies to supply this information. In this way the abstract representation of the natural system can quicken the biological discovery process and thus constitutes a basic component of the scientific method (Milsum, 1966). Although model building cannot by itself add to scientific knowledge, it may convey insight to the investigator, who is now able to closely examine the process of interaction through which system components produce the eventual response of the system as a whole.

A model is desired which can be used to calculate the spatial and temporal distribution of dissolved and particulate phosphorus, particulate nitrogen, dissolved organic nitrogen, ammonia, nitrate, silicon, total algae, and total zooplankton. The assumed interactions among these variables, as incorporated

into the mathematical model, are illustrated in Figure 2. The seasonal dynamics of each of these variables will be determined at a number of locations within the bay by the integration of mass continuity equations which account for changes due to transport by water movements, growth, decomposition, biological uptake, exchange with Lake Michigan, direct input from the Boardman River, and exchange with the Bay sediments. The basic equations which comprise the model are developed by taking mass balances for the various model constituents about uniform cells. A system of cells coupled by advective and dispersive flows simulates the effects of water circulation, while sources and sinks within a cell represent the effects of chemical and biological reaction. A material balance equation for the  $i^{\text{th}}$  chemical or biological species about the  $j^{\text{th}}$  volume element can be written:

$$V_j \frac{dC_{ij}}{dt} = J_{ij}A_j + V_j S_{ij} + W_{ij} \quad (1)$$

where  $C_{ij}$  is the concentration of species  $i$  in segment  $j$ ,  $V_j$  is the volume of segment  $j$ ,  $J_{ij}$  is the net flux of species  $i$  into segment  $j$ ,  $A_j$  is the interfacial area of the  $j^{\text{th}}$  segment,  $S_{ij}$  is the summation of sources and sinks of species  $i$  in segment  $j$  which are associated with various biological, chemical, and physical reactions,  $W_{ij}$  represents the direct input of species  $i$  into segment  $j$ , and  $t$  is time.

### Fluid Transport

The physical transport of species due to fluid movements is represented by flux terms in Equation 1. Smith (1973) has developed a model for water circulation in Grand Traverse Bay by numerically integrating linearized equations of motion for

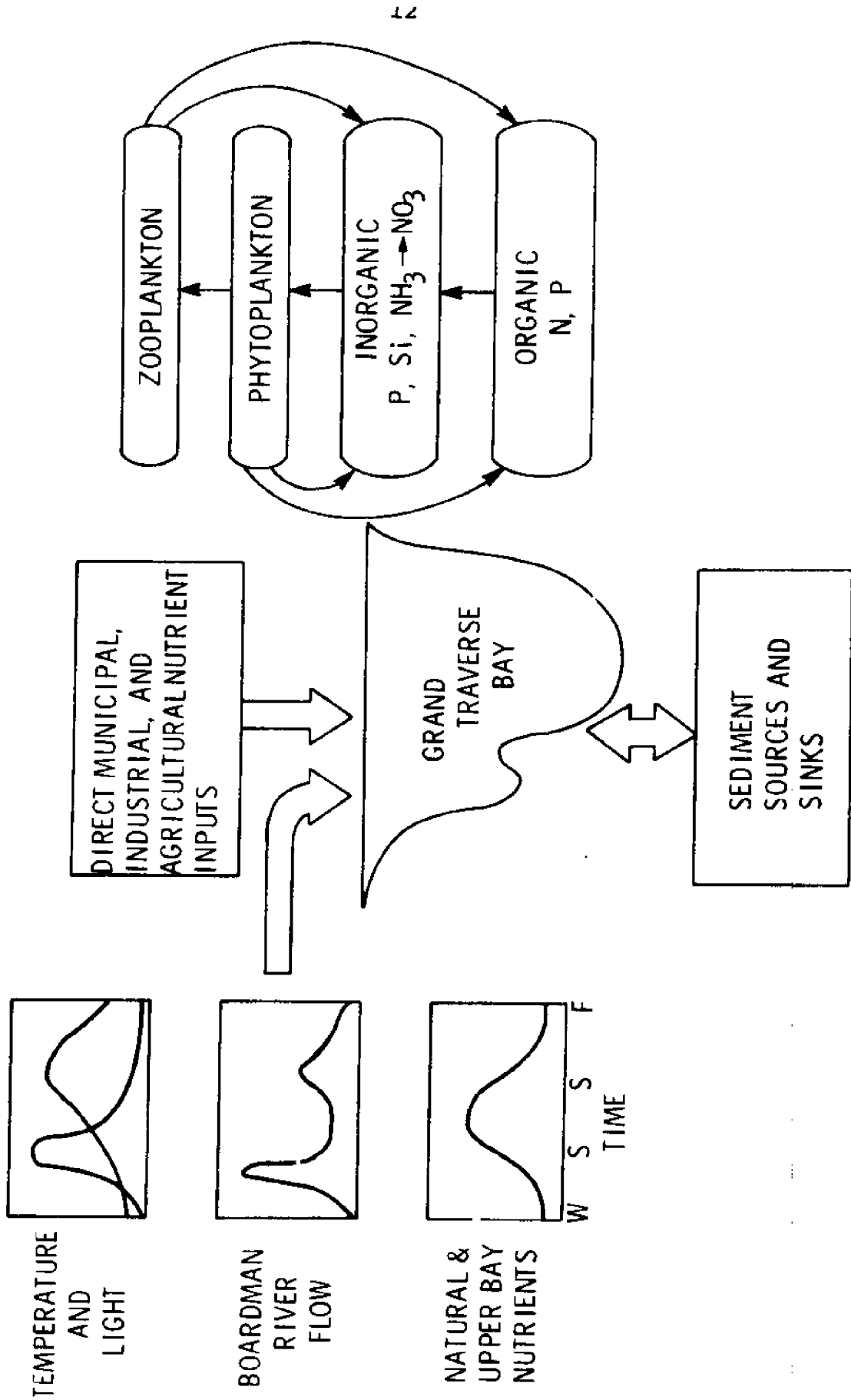


FIGURE 2. GRAND TRAVERSE BAY MODEL ECOSYSTEM INTERACTIONS

this system. This circulation model gives transient, depth averaged flows in response to forcing from winds. The general features of this model have been tested against field observations by Monahan et al. (1973).

The results of the numerical circulation model have been adapted to define typical advective and dispersive flux terms in Equation 1. The most typical magnitude and direction for these terms are shown in Figures 3 and 4 for circulation patterns which develop in the bay after 3 hours of forcing by 10 mph SW winds and after 3 hours of forcing by 10 mph NNW winds. It is observed that the circulation is strongly dependent on the wind direction. The model for biological production should accept time variable functions which represent the transfer terms. The transfer terms should be derived from a circulation model which is driven by actual wind forcing and oscillations from Lake Michigan. However, this approach is not practical in Grand Traverse Bay because of the extremely high cost of integrating the circulation model for a real time of one year. An alternate approach to this problem is necessary. The final form of the biological production model, as defined in detail in later sections, has been integrated for a one-year period using both flow patterns illustrated in Figures 3 and 4. In general the calculations indicate that SW winds result in relatively high phytoplankton in shoreline segments and relatively low phytoplankton in the deep-water segment. The model results for the NNW wind condition show smaller differences between offshore and near-shore stations with relatively high concentrations of phytoplankton in the deep-water segment. However the differences



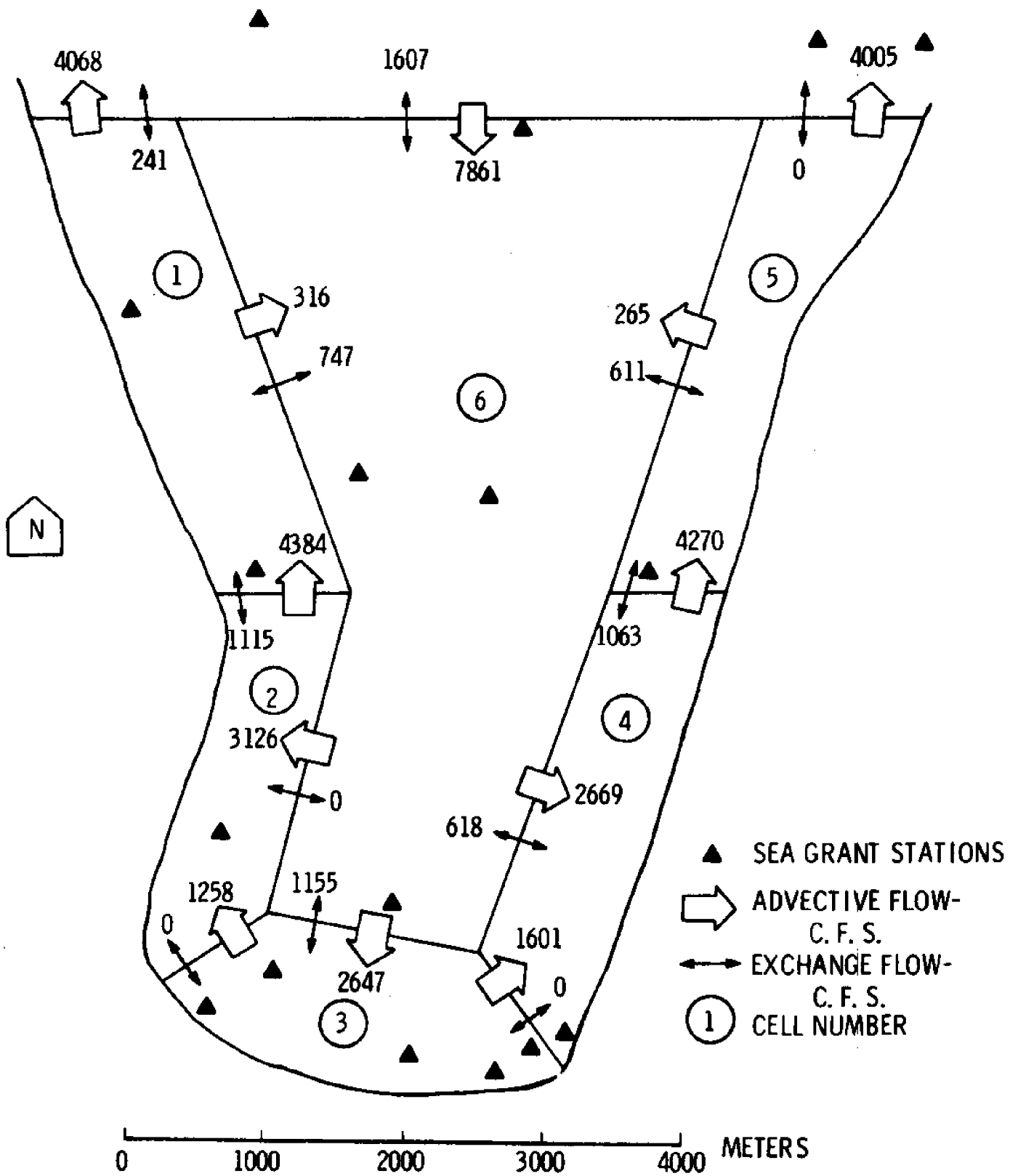


FIGURE 3. CIRCULATION IN GRAND TRAVERSE BAY WITH TYPICAL SW WINDS

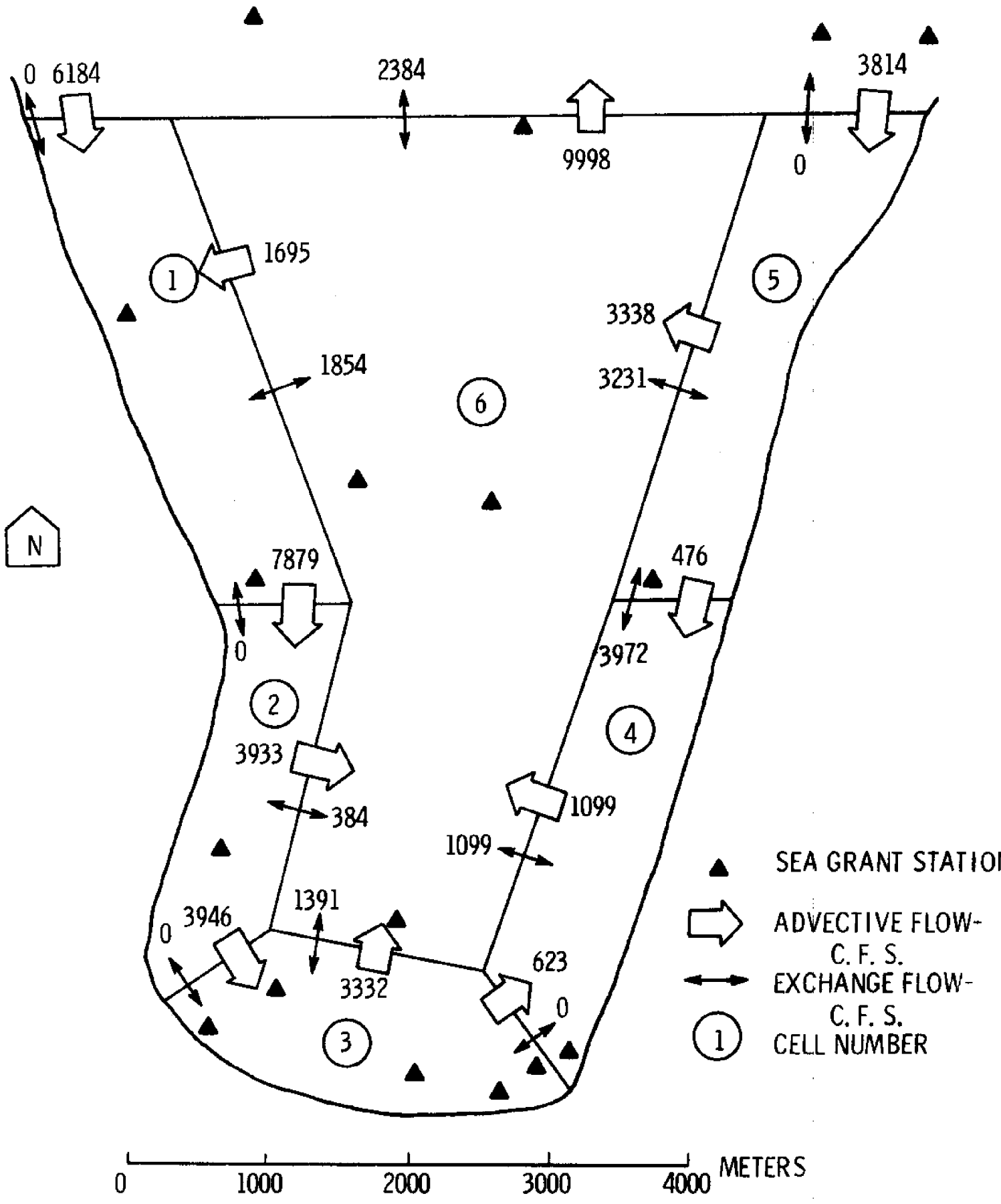


FIGURE 4. CIRCULATION IN GRAND TRAVERSE BAY WITH TYPICAL NNW WINDS

between the two flow conditions are relatively small. The maximum deviation between the two cases is approximately 20%, with most deviations being considerably less. All the calculations and predictions in this report are based on constant SW wind forcing since this gives insight into maximum potential phytoplankton concentrations in critical near-shore segments.

### Phytoplankton

Although it is known that the phytoplankton population of Grand Traverse Bay is composed of a number of ecologically important species (see Table 2), little information is available on the growth kinetics and specific nutrient requirements of each individual species. Therefore, it is convenient to characterize the phytoplankton as an entire population and to develop a growth rate expression which represents the performance of the population as a whole, realizing that this is a simplification of reality. Additional details regarding the dominant species which make up the phytoplankton assemblage in Grand Traverse Bay can be found in a report by Stoermer (1972). More advanced approaches to modeling the phytoplankton are being explored as part of an effort to model the Lake Michigan sport fishery ecosystem.

The accumulation or depletion of phytoplankton is governed by the mechanisms of fluid transport, growth, respiration, predation by zooplankton, sinking, and input from either the upper bay or the Boardman River. Although the actual phytoplankton population can be represented by numerous measures, it has been convenient to approximate the population present by

TABLE 2. Relative frequency of dominant taxa in samples from 5 m depth, Grand Traverse Bay, Lake Michigan on 18 May and 20 June 1970. A. = *Synedra filiformis* Grun.; B. = Unident. flagellates; C. = *Melosira islandica* O. Müll.; D. = *Fragilaria crotonensis* Kitton; E. = *Rhizosolenia gracilis* H.L. Smith; F. = *Stephanodiscus minutus* Grun.; G. = *Cyclotella stelligera* (Grun. & Cl.) V.H.; H. = *Tabellaria fenestrata* (Lyngb.) Kütz.; I. = *Rhizosolenia eriensis* H.L. Smith; J. = *Cyclotella michiganiana* Skv.; K. = *Melosira italica* subsp. *subarctica* O. Müll.; L. = *Asterionella formosa* Hass. species = Total number of species in sample; div. = Diversity; tot. = Percent of assemblage accounted for by dominants. (After Stoermer et al, 1972)

Sta- tion	18 May											20 June											species	div.	tot. %		
	A	B	C	D	E	F	G	H	I	J	K	L	A	B	C	D	E	F	G	H	I	J				K	L
1	21	26	8	12	5	5	7	3	1	0.8	1	0.6													57	2.3	90.4
2	23	20	10	5	4	7	9	6	2	0.6	1	1													58	2.4	88.6
3	23	20	7	11	6	8	7	3	1.	0.09	1	1													45	2.5	87.8
4	23	12	12	5	6	6	11	4	1	0.5	5	0.5													52	2.6	86.0
5	20	21	11	9	6	5	4	3	0.9	0.3	1	0.5													45	2.5	81.7
6	21	21	6	14	6	5	4	2	1	0.3	0.7	1													46	2.5	82.0
7	22	20	11	8	6	7	5	2	0.9	0.4	2	1													53	2.6	83.3
8	24	17	12	10	4	8	4	3	0.8	0.1	1	0.5													54	2.4	84.4
9	26	18	8	12	4	9	5	2	0.7	0.3	1	0.3													51	2.4	86.3
10	23	24	8	13	4	8	4	2	1	0.5	1	0.5													62	2.3	89.0
11	21	21	3	16	6	3	3	5	1	0.3	3	1													51	2.5	83.3
12	15	21	8	13	8	4	5	1	1	0.2	3	1													48	2.6	81.2
1	36	14	0.0	20	12	1	0.7	2	4	1	0.06	0.3													56	2.0	91.1
2	35	15	1	18	13	1	1	3	3	0.7	0.5	0.07													51	2.0	91.3
3	40	12	1	17	13	1	1	2	3	1	0.1	0.3													45	1.9	91.4
4	37	21	0.9	14	14	0.7	1	0.4	4	1	0.2	0.3													55	1.8	94.5
5	35	12	0.2	12	22	0.5	0.6	1	4	0.6	0.2	2													60	2.0	90.1
6	41	7	0	9	24	0.2	0.6	0.08	7	0.7	0	1													50	1.8	90.6
7	47	7	0.4	17	12	2	0.8	2	2	0.9	0.2	0.4													59	1.8	91.7
8	46	9	0.5	20	9	2	0.4	2	2	0.8	0.2	0.2													54	1.8	92.1
9	46	12	0.4	17	9	2	0.6	2	2	0.9	0.1	0.2													55	1.8	92.2
10	39	18	1	16	9	2	0.4	2	2	0.8	0.3	0.3													59	1.9	90.8
11	44	13	0	14	15	1	0.8	0.5	3	1	0	0.4													47	1.8	92.7
12	16	15	0.8	26	15	1	1	1	3	0.08	0.03	0.5													48	2.2	79.4

the concentration of chlorophyll a, which is denoted by  $P_j$ . The continuity of phytoplankton chlorophyll a in the  $j^{\text{th}}$  segment is defined by:

$$V_j \frac{dP_j}{dt} = J_{Pj} A_j + V_j [G_{Pj}(T, I, N_j) - D_{Pj}(T) - C_g(T, P_j) Z_j] P_j + W_{Pj} \quad (2)$$

In Equation 2, the growth of the phytoplankton is assumed proportional to the concentration of phytoplankton and an overall growth coefficient  $G_{Pj}$ . The growth coefficient is a function of temperature,  $T$ ; sunlight intensity,  $I$ ; photoperiod; and nutrient concentrations,  $N_j$ . The influence of light on the growth of the phytoplankton is further dependent on vertical light extinction and self-shading effects. The disappearance of phytoplankton due to excretion, respiration, and sinking is also considered proportional to the concentration of phytoplankton and is represented by a temperature dependent overall death coefficient  $D_{Pj}$ . The rate of phytoplankton depletion due to zooplankton predation is assumed to be proportional to the product of the phytoplankton concentration, the zooplankton concentration, and the grazing rate  $C_g$ . The grazing rate is a function of temperature and the phytoplankton concentration. The remaining terms in Equation 2,  $J_{Pj}$  and  $W_{Pj}$ , represent the phytoplankton flux and input contributions to the rate of change of the phytoplankton concentration.

The first growth-rate determining factor to be considered is temperature. Under optimum light and nutrient conditions phytoplankton growth is an increasing function of temperature, although the relationship may not be strictly linear. A quadratic function has been used in the model to quantify the relationship between temperature and growth rate:

$$G_{pj}(T) = a_1 + a_2 * T + a_3 * T^2 \quad (3)$$

where  $a_1$ ,  $a_2$  and  $a_3$  are constants and  $T$  is temperature in degrees C. Justification of this quadratic relationship is discussed in a later section.

Next it is necessary to consider the effect of light intensity on the phytoplankton growth rate. It is known that there exists for phytoplankton a light intensity at which photosynthesis can proceed at its maximum rate (Ryther, 1956). Intensity values above and below this light intensity, called  $I_S$ , will cause a reduction in the growth rate which could be realized at  $I_S$ . The effect of a saturating light intensity is that the growth rate of the phytoplankton is not uniform throughout the water column. Instead, growth rates at lower depths are depressed by lack of light, and growth rates near the surface may be inhibited by radiation levels above  $I_S$ . To describe this effect, Steele (1965) has developed the following equation:

$$r(I) = \frac{I}{I_S} e^{[-\frac{I}{I_S} + 1]} \quad (4)$$

where  $r(I)$  is the reduction factor of the growth rate,  $I$  is the light intensity incident on the phytoplankton population, and  $e$  is the base of the natural logarithm system. This equation only describes the effective growth rate at a given depth. However, a relationship representing the average growth rate over the depth of the experimental volume is required. To account for this, use is made of the fact that light attenuation with depth through a body of water occurs exponentially according to the equation:

$$I(X) = I_0 e^{-k_e X} \quad (5)$$

where  $X$  is the depth measured downward. At the water surface  $X = 0$ . As before,  $e$  is the base of the natural logarithm system;  $k_e$  is the extinction coefficient describing the rate at which light decays with depth. By combining equations 4 and 5 and averaging over depth, a reduction factor is obtained which represents the average reduction of the growth rate due to light intensity in the experimental volume. DiToro et al. (1971) have shown that the result of integrating this function over depth is

$$r(I) = \frac{e}{k_e H} \left( \frac{I_0}{I_S} (e^{-k_e H}) - \frac{I_0}{I_S} \right) \quad (6)$$

where  $r(I)$  is the growth rate reduction due to nonoptimum light and  $H$  is the depth of the water segment.

The final factor normally believed to affect the phytoplankton growth rate is that of nutrient limitation. A number of investigators have found it reasonable to assume that the uptake of important nutrients follows Monod growth kinetics; with growth rate being unaffected by nutrient concentration when nutrient supply exceeds some minimum level and being linearly proportional to nutrient concentrations below this level (Dugdale, 1967; Eppley et al., 1969; DiToro et al., 1971). Ongerth (1973) and Koonce and Hasler (1972) have reviewed the phenomenon of growth as controlled by internal nutrient concentrations. Although this effect appears significant in some cases, a traditional approach to algal uptake has been explored in this case. This approach is

characterized by assuming:

$$r(N) = \left[ \frac{N}{K + N} \right] \quad (7)$$

where  $r(N)$  is a reduction factor due to nutrient limitation at a given level of temperature and light intensity;  $N$  is a limiting nutrient concentration; and  $K$  is the half-saturation or Michaelis constant, which is that limiting nutrient concentration that supports half the maximum growth rate. In the model, it is assumed that nutrient limitation of the algal growth rate can occur due to critical concentrations of any of three major nutrients: phosphorus, nitrogen, and silicon. Accordingly, an expression representing nutrient limitation is included for each of these three nutrients.

By combining all of the growth-limiting effects outlined above, it is seen that the growth rate of phytoplankton becomes

$$G_{Pj}(T, I, N) = \left[ a_1 + a_2 T + a_3 * T^2 \right] \left[ \frac{2.718f}{k_e H} e^{-\frac{I_0}{I_S} (e^{-k_e H})} - e^{-\frac{I_0}{I_S}} \right] \cdot \left[ \frac{Nit}{K_N + Nit} \right] \left[ \frac{Ph}{K_{Ph} + Ph} \right] \left[ \frac{Si}{K_{Si} + Si} \right] \quad (8)$$

where Nit, Ph, Si and  $K_N$ ,  $K_{Ph}$ ,  $K_{Si}$  are the concentrations and Michaelis constants for inorganic nitrogen, total dissolved phosphorus, and silicon, respectively. Note that a term,  $f$ , has been included to represent the photoperiod, acknowledging the fact that phytoplankton growth is directly related to its photosynthesis during daylight hours. The carbon uptake rate is proportional to the growth rate of the phytoplankton and the chlorophyll a concentration in the water. In the model, it is assumed that the carbon uptake rate ( $\mu\text{gC}/\ell/\text{hr}$ ) is given by



$G_{pj} * P_j * Y_8 / 24$ , where  $Y_8$  is the carbon/Ch a ratio in the phytoplankton.

Phytoplankton respiration, like growth, is known to be an increasing function of temperature. Riley (1965) has suggested that respiration is an exponential function of temperature while DiToro et al. (1971) have proposed that linear formulas are adequate. The present form of the model assumes that

$$R = a_4 + a_5 * T \quad (9)$$

where  $a_4$  and  $a_5$  are constants and where  $R$  is the respiration rate coefficient ( $\text{day}^{-1}$ ).

The decrease of phytoplankton due to sinking is considered in the model. The amount of phytoplankton loss is considered to be directly proportional to the concentration of the phytoplankton and the sinking velocity ( $v_s$ ) and inversely proportional to the depth of the segment. Although the sinking velocity may be a complex function of temperature, light, and nutrients, as well as species and natural turbulence, the inclusion of such detail does not seem warranted at this point of development. Thus, the model formulation has been written assuming that  $v_s$  is constant. This assumption can be easily modified if justified in the future. Thus, the overall death coefficient of the phytoplankton in the model is given by

$$D_{pj}(T) = a_4 + a_5 * T + v_s / H \quad (10)$$

The losses due to zooplankton grazing are considered proportional to the product of the grazing rate of the zooplankton  $C_g$ , and the zooplankton concentration  $Z_j$  as described in Equation 2.

### Zooplankton

The Sea Grant sampling program has identified the spatial and temporal distribution of zooplankton species in Grand Traverse Bay. The major species and the 1971 average value for each species are listed in Table 3. It is observed that the zooplankton population is composed of a number of ecologically important species. The feeding mechanisms of these species are diversified with unselective and selective filter feeders and raptorial feeders being represented in the community. The present form of the model is limited to consideration of the total zooplankton effect, despite the existence of complex interactions within the zooplankton trophic level. More advanced modeling approaches to this community are currently being explored as part of an effort to describe the Lake Michigan sport fishery ecosystem.

Changes in the total zooplankton concentration can be described by a mass balance equation for the  $j^{\text{th}}$  segment:

$$V_j \frac{dz_j}{dt} = J_{Z_j} A_j + V_j [G_{Z_j}(T, P_j) - D_{Z_j}(T)] Z_j + W_{Z_j} \quad (11)$$

where the zooplankton population is expressed as mg of zooplankton dry weight per liter. The overall growth rate of the zooplankton is proportional to the concentration of zooplankton and an overall growth rate coefficient,  $G_{Z_j}$ . The growth rate coefficient is dependent on the zooplankton grazing rate and the phytoplankton absorption efficiency of the zooplankton, as well as on the temperature and the concentration of phytoplankton. The depletion of zooplankton is assumed proportional to the concentration of zooplankton and an overall temperature dependent death rate coefficient,  $D_{Z_j}$ , which

ZOOPLANKTER	% OF POPULATION BY NUMBER (Collected by a #10 Mesh Net)
Copepoda	
Diaptomids	23.1450
<u>Senecella calanoides</u>	0.0053
<u>Limnocalanus macrurus</u>	0.0711
<u>Epischura lacustris</u>	0.0324
<u>Eurytemora affinis</u>	0.0019
Cyclopoids	51.3059
Harpacticoids	0.0064
Cladocera	
Daphnids	5.0549
<u>Bosmina</u>	18.9881
<u>Leptodora kindtii</u>	0.0549
<u>Polyphemus pediculus</u>	0.1149
<u>Holopedium gibberum</u>	0.6985
<u>Chydorus</u>	0.0041
<u>Diaphanasoma</u>	0.0711
<u>Eurycercus lamellatus</u>	0.0012
<u>Alona</u>	0.0006
Rotifera	
<u>Asplanchna</u>	0.4445
Other Zooplankton	
<u>Mysis relicta</u>	0.0006
Conchostracans	0.0006
Ostracods	0.0012

TABLE 3. Average Composition of Grand Traverse Bay Zooplankton

accounts for respiration and predation by other elements in the food web. The zooplankton flux and input terms are given by  $J_{Zj}$  and  $W_{Zj}$  in Equation 11.

The gross growth rate of the zooplankton is formulated mathematically by assuming that the whole population feeds as a selective filterer. In this case,

$$G_{Zj} = C_g * P_j * \epsilon * Y_1 \quad (12)$$

where  $C_g$  is the zooplankton grazing rate in  $\ell/\text{day}/\text{mg}$  of dry weight of zooplankton;  $\epsilon$  is the assimilation efficiency of the zooplankton; and  $Y_1$  is the ratio of the dry weight of zooplankton in  $\text{mg}$  to the chlorophyll a of the phytoplankton in  $\mu\text{g}$ . The grazing rate,  $C_g$ , is dependent on temperature and the phytoplankton availability. This dependency is expressed mathematically as

$$C_g = C_{g,\text{max}} \left[ a_6 + \frac{(1-a_6)K_{pe}}{K_{pe} + P_j} \right] \quad (13)$$

where  $C_{g,\text{max}}$  is the maximum grazing rate at a given temperature;  $a_6$  is the fraction of the maximum grazing rate at high phytoplankton levels; and  $K_{pe}$  is a saturation constant. The maximum grazing rate, following DiToro et al. (1970), is assumed to be a linear function of temperature:

$$C_{g,\text{max}} = a_7 + a_8 * T \quad (14)$$

where  $a_7$  and  $a_8$  are constants and  $T$  is the temperature in degrees C.

Zooplankton respiration, like grazing activity, is temperature dependent. In the present form of the model, it has been assumed that respiration is a linear function of

temperature. Zooplankton depletion also results from predation losses to upper trophic levels. These upper trophic levels are not explicitly included in the system state equations. However the influence of these organisms is included as a term ( $a_{11}$ ), which contributes to the value of  $D_{Zj}$ . The overall equation for  $D_{Zj}$  subject to the above assumption becomes:

$$D_{Zj} = a_9 + a_{10} * T + a_{11} \quad (15)$$

where  $a_9$ ,  $a_{10}$  and  $a_{11}$  are constants.

### Nutrients

The important algal nutrients in Traverse Bay are believed to be silicon, nitrogen, and phosphorus. These elements may occur in inorganic, organic, soluble, or particulate form. Furthermore, inorganic forms may appear with alternate states of oxidation: for example, inorganic nitrogen may occur as ammonia, nitrite, or nitrate. The mass balance equations for each of these nutrients involves the three mechanisms as discussed in Equation 1.

A mass balance for the soluble organic form of the nutrients in the  $j^{\text{th}}$  segment can be written in the form:

$$V_j \frac{dON_j}{dt} = J_{ONj} A_j - D_{ON}(T) ON_j V_j + E_j(T, P_j, Z_j) V_j + W_{ONj} \quad (16)$$

In Equation 16 the sources of soluble organic nutrients due to excretion and respiration, zooplankton grazing, and hydrolysis of particulate nutrient forms are explicitly included in the term,  $E_j$ , which is a function of temperature and the phytoplankton and zooplankton concentration. The conversion of organic forms to inorganic forms is accounted for by  $D_{ON}$  in Equations 16 and 17.

A mass balance equation for the inorganic form of each of the nutrients in segment  $j$  can be written as:

$$V_j \frac{dN_j}{dt} = J_{Nj} A_j - Y_{NP} G_{Pj} P_j V_j + D_{ON}(T) ON_j V_j + W_{Nj} \quad (17)$$

where  $N_j$  is the concentration of inorganic nutrient and  $ON_j$  is the concentration of the soluble organic form of the nutrient. In Equation 17 nutrient utilization by the phytoplankton is related to the phytoplankton growth by a stoichiometric conversion factor  $Y_{NP}$ , where  $Y_{NP}$  is the weight of nutrient required per weight of new phytoplankton produced. Nutrient regeneration is assumed to be proportional to the concentration of the soluble organic form and a temperature dependent regeneration rate coefficient,  $D_{ON}(T)$ . The flux and input of nutrients are included in the  $J_{Nj}$  and  $W_{Nj}$  terms. The exchange of nutrients with the sediments is included in the  $J_{Nj}$  or  $J_{ONj}$  terms. However, in Grand Traverse Bay, the release of nutrients such as phosphorus from the sediments is considered small.<sup>1</sup> Therefore, in subsequent calculations, the input of nutrients to the water from the sediments is assumed negligible.

Figure 2 indicates, that upon the death of phytoplankton or zooplankton by respiration, nutrients contained in the cells of these organisms become a part of the pool of non-living organic matter in the system. These nutrients may not be immediately utilizable by phytoplankton for further growth, but must be transformed by dissolution or bacterial action into a utilizable, often inorganic form. The component of the model labeled organic nitrogen represents an intermediate phase of nitrogen between that bound in particulate form and that in

<sup>1</sup>Personal Communication, Professor Edward Callender, Department of Atmospheric and Oceanic Science, University of Michigan

inorganic forms. It is assumed in the model that detritus nitrogen is negligible. There are, therefore, two positive terms in the rate expression for the change in the concentration of organic nitrogen. These represent the nitrogen released during phytoplankton and zooplankton respiration. Organic nitrogen is also introduced into the system as a result of zooplankton grazing since the assimilation efficiency of the zooplankton is always less than 1. In the current model the organic nitrogen released due to phytoplankton or zooplankton death is considered proportional to the biomass losses of these organisms. Thus for nitrogen:

$$E_j(T, P_j, Z_j) = D_{Zj} * Z_j * Y_2 + (a_4 + a_5 * T) * P_j * Y_3 + Y_3 * C_g * Z_j * P_j - G_{Zj} * Z_j * Y_2 \quad (18)$$

where  $Y_2$  is the nitrogen to dry weight ratio in the zooplankton and  $Y_3$  is the nitrogen to chlorophyll a ratio in the phytoplankton.

The major negative term in the organic nitrogen balance equation results from ammonification. An additional sink term for organic nitrogen could conceivably be included, since it has been found that some nitrogen-containing organic compounds can be used as a nutrient by some phytoplankton species (Brezonik, 1972; Hunter and Provasoli, 1964; and Guillard, 1963). However, this is not believed to be an important sink when compared to ammonification, and this term is not considered in the current model. The ammonification term is assumed to be dependent on the concentration of organic nitrogen and temperature, therefore,

$$D_{ON} = (a_{12} + a_{13} * T) * N_O \quad (19)$$

where  $a_{12}$  and  $a_{13}$  are constants and  $N_O$  is the concentration of organic nitrogen.

Following a sequential breakdown, the change in ammonia is due to gains from ammonification, losses through nitrification into nitrite and nitrate, and through uptake by the phytoplankton. The uptake of ammonia by the phytoplankton is considered proportional to the product of the phytoplankton concentration and the phytoplankton growth rate. The uptake is also dependent on the algal preference for ammonia and ammonia availability. Therefore, the algal uptake is equal to  $G_{Pj} * P_j * PNH_3 * Y_3$ , where  $PNH_3$  is the algal preference for ammonia which is a function of ammonia and nitrate availability and where  $Y_3$  is the nitrogen to chlorophyll a ratio in the phytoplankton. The nitrification losses are assumed to be proportional to the ammonia concentration and are temperature dependent. Therefore for ammonia, the sources and sinks are:

$$\begin{array}{l} \text{Ammonia Sources} \\ \text{and Sinks} \end{array} - G_{Pj} * P_j * PNH_3 * Y_3 + (a_{12} + a_{13} * T) * N_O - (a_{14} + a_{15} * T) * N_a \quad (20)$$

where  $a_{14}$  and  $a_{15}$  are constants and  $N_a$  is the concentration of ammonia.

The reactions determining the rate of change of nitrate consist of gains from nitrification and of losses by phytoplankton uptake. The nitrite concentration in Grand Traverse Bay is quite low and, therefore, not explicitly included in the model. Field data for nitrate and nitrite are added and compared to model predicted values. The oxygen content of Grand Traverse Bay waters is near saturation throughout the year, even at deep water stations. Therefore, denitrification mechanisms are not included in the model. The kinetic terms



in the nitrate equation therefore become:

$$\begin{array}{l} \text{Nitrate Sources} \\ \text{and Sinks} \end{array} - G_{Pj} * P_j * (1 - \text{PNH}_3) * Y_3 + (a_{14} + a_{15} * T) * N_a \quad (21)$$

The preference for the ammonia term included in the above equations (20 and 21) represents the preference by phytoplankton for ammonia as a nitrogen-source as opposed to nitrate. It is known that, although algae can utilize either form of inorganic nitrogen as a nutrient, there is often a preferential uptake of ammonia, often in the presence of substantially higher nitrate concentrations (Vaccaro, 1963; Strickland, 1965; Provasoli, 1958; and Brezonik, 1972). This preference, then, is expressed by a preference function which takes account of the concentrations of both ammonia ( $N_a$ ) and nitrate ( $N_i$ ):

$$\text{PNH}_3 = \frac{a_{16} N_a}{a_{16} N_a + (1 - a_{16}) N_i} \quad (22)$$

where  $a_{16}$  is a constant. A plot of this function for  $a_{16} = 0.95$  is shown in Figure 5.

The phosphorus cycle in this system operates in a manner similar to the nitrogen cycle, with the difference that there is only one inorganic form of the nutrient considered by the model. Also, it has been found that phosphorus is converted to an inorganic form faster than is nitrogen (Kramer et al. 1972; Kerr et al. 1970; and Redfield et al. 1963). It is assumed that this regeneration rate occurs rapidly, relative to the other rates in the model and can be considered instantaneous. Therefore, soluble organic P and inorganic P are lumped together into one component. The reactions concerning this phosphorus component, then, are gains from phytoplankton and zooplankton respiration, gains resulting from zooplankton

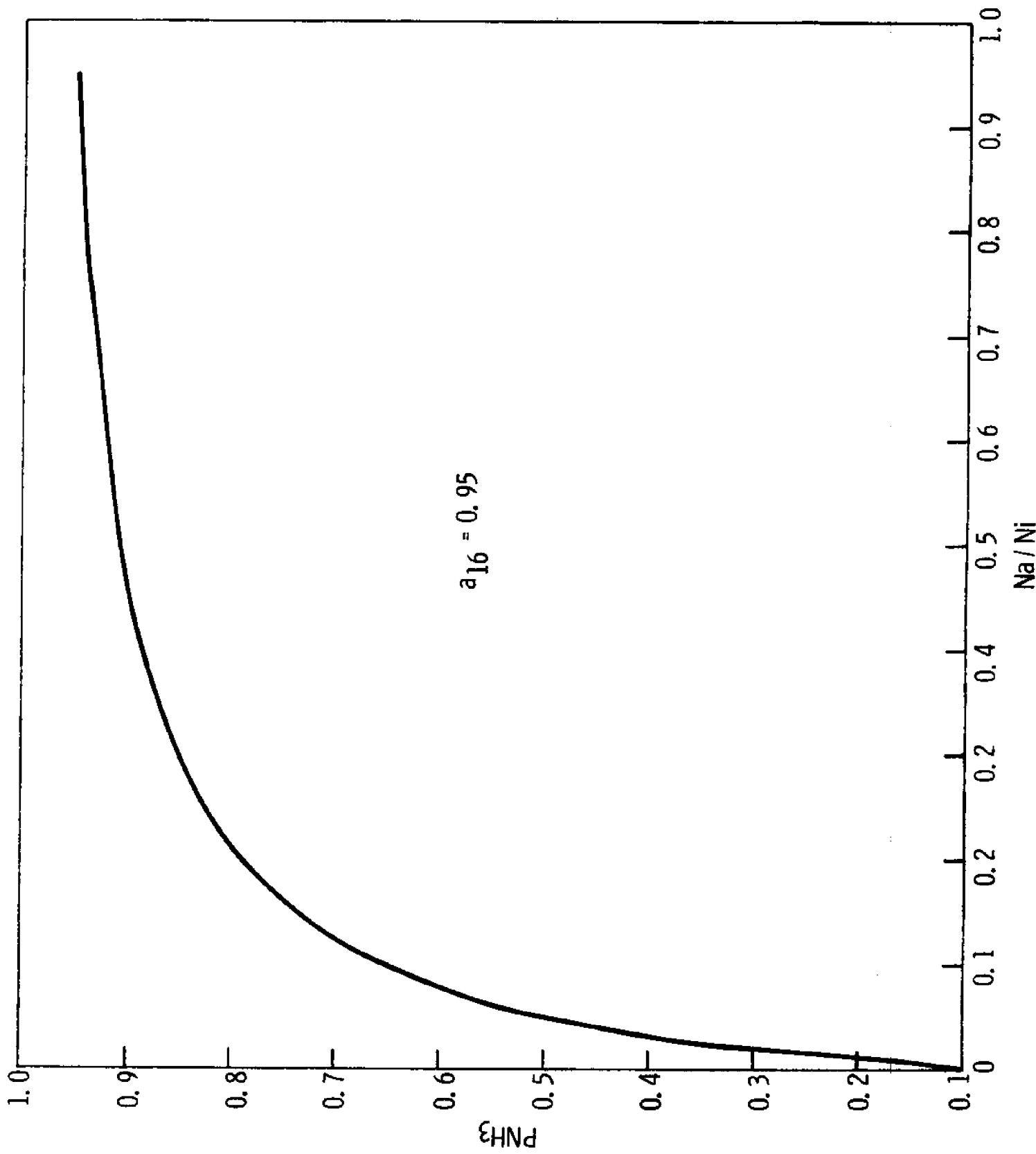


FIGURE 5. PREFERENCE FOR AMMONIA VS RATIO OF AMMONIA TO NITRATE CONCENTRATION

grazing, and losses due to phytoplankton uptake. The validity of this approach is supported by observations by Kuenzler (1965), which demonstrate the utilization of soluble organic phosphorus by certain algal species.

The total soluble phosphorus increase due to phytoplankton and zooplankton respiration is assumed to be proportional to the product of the populations and their specific death rates. The phosphorus released as a result of zooplankton grazing is a function of the grazing rate, assimilation efficiency, phytoplankton and zooplankton populations, and temperature. The uptake of soluble phosphorus is assumed to be directly proportional to the growth rate and level of phytoplankton.

The soluble phosphorus sources and sinks are expressed mathematically as follows:

$$\begin{aligned} \text{Soluble Phosphorus} &= D_{Zj} * Z_j * Y_2 * Y_4 + Y_5 * C_g * Z_j * P_j - G_{Zj} * Z_j * Y_2 * Y_4 \\ \text{Sources and Sinks} & \qquad \qquad \qquad + (a_4 + a_5 * T) * P_j * Y_5 - G_{Pj} * P_j * Y_5 \end{aligned} \quad (23)$$

where  $Y_4$  is the phosphorus to nitrogen ratio in the zooplankton;  $Y_5$  is the phosphorus to chlorophyll a ratio in the phytoplankton;  $Y_2$  is the nitrogen to dry weight ratio in the zooplankton; and  $Y_6$  is the phosphorus to nitrogen ratio in phytoplankton.

The silicon cycle is analogous to the phosphorus cycle. In this case, however, the silicon released by phytoplankton during respiration, primarily in the form of diatom frustules, is believed to be composed of a readily soluble component and another component which is relatively insoluble and released to the nutrient pool fairly slowly (Grill and Richards, 1964; Raymont, 1963; and Armstrong, 1965). Hence, it is necessary to introduce a variable,  $\theta$ , representing the percentage of silicon

which is regenerated upon release by phytoplankton and is made available again to the nutrient pool. The equation representing gains and losses of soluble silicon due to interactions with the phytoplankton is given by:

$$\text{Silicon Sources and Sinks} = ((a_4 + a_5 * T) + C_g * Z_j) * Y_7 * P_j * \theta - G_{Pj} * Y_7 * P_j \quad (24)$$

where  $Y_7$  is the silicon to chlorophyll a ratio in the phytoplankton.

#### PARAMETER ESTIMATION

The evaluation of the parameters in the biological production model is a critical step which must be considered very carefully to insure model credibility for predictive purposes. Two different techniques have been used to obtain initial estimates of model parameters in this study. The first technique consists of simply using laboratory and field empirical estimates as published in the scientific literature. The second technique involves the use of Sea Grant experimental results (Schelske et al., 1973) to estimate the kinetic and stoichiometric coefficients in the model. The experiments were conducted under controlled laboratory conditions with Grand Traverse Bay waters. Estimates of the coefficients, obtained by either of the above methods, can then be used to predict field conditions. If the model-predicted results compare favorably with the field data, with only minor modifications of parameter values, the model is considered verified or calibrated. If significant deviations exist between the model calculated values and the field data, the model structure or mechanisms must be assumed to be incorrect and fundamental modifications are probably in order.

The first parameters to be considered concern the variation of nutrient and light-saturated phytoplankton growth rates as a function of temperature. Table 4 contains growth rates obtained from the literature for phytoplankton growth under optimal light and nutrient conditions. This information has been combined with similar values previously tabulated by Canale and Vogel (1973) and by DiToro et al. (1971) and plotted against temperature in Figure 6. An examination of this graph leads to the conclusion that algal growth rate is an increasing function of temperature. It also appears that the function may not be strictly linear. A quadratic equation has been applied to the data in an attempt to quantify this relationship, considering only the diatom, green, and blue-green groups. There are two reasons for dropping flagellates from the analysis. First, flagellates are a minor component of the natural phytoplankton population in Grand Traverse Bay and, secondly, their growth rates are generally lower than for the other three groups. It should be noted that the data used in this analysis is in the form of specific growth rates. Assuming, then, that all of these values are indeed valid estimates of optimum growth rates, it is possible for the composite growth rate for a natural population to vary over the entire range of values shown in Figure 6. The actual growth rate attained by a natural population under optimum conditions would depend upon the species composition of the population and the optimum growth rates characterizing those species.

Equation 3 implies that the light-saturated growth rate is a monotonically increasing function of temperature, but the optimum temperature for algal growth is in the range of 20-35°C.

Organism	Temperature (°C)	Growth Rate (day <sup>-1</sup> )	Reference
<u>Diatoms</u>			
<u>Chaetoceros</u> sp.	18	2.10	Parsons et al., 1961
<u>Cyclotella</u> nana	22	1.60	Fuhs et al, 1970
<u>Nitzschia closterium</u>	9	1.07	Spencer, 1954
	14	1.55	Spencer, 1954
	18	2.18	Spencer, 1954
	25	2.29	Spencer, 1954
	20	2.73	Paasche, 1973
	20	2.77	Paasche, 1973
	20	2.52	Paasche, 1973
<u>Phaeodactylum</u> <u>tricornutum</u>	18	1.10	Parsons et al., 1961
	25	4.25	Spencer, 1954
<u>Skeletonema</u> <u>costatum</u>	18	3.40	Parsons et al., 1960
<u>Thalassiosira</u> <u>fluviatilis</u>	22	1.60	Fuhs et al, 1970
	21	3.11	Thomas & Dodson, 1968
	4	0.50	Lewin & Guillard, 1963
	8	0.55	Lewin & Guillard, 1963
	25	2.75	Lewin & Guillard, 1963
<u>Green Algae</u>			
<u>Chlorella</u> <u>pyrenoidosa</u>	25	2.80	Myers, 1964
<u>Chlorella</u> <u>pyrenoidosa</u>	10	0.40	Sorokin & Kraus, 1962
(synchronized and high temper- ature strain)	15	1.50	Sorokin & Kraus, 1962
	20	3.30	Sorokin & Kraus, 1962
	25	5.70	Sorokin & Kraus, 1962
<u>Chlorella</u> <u>ellipsoidea</u>	15	1.71	Tamiya et al, 1964
	25	4.49	Tamiya et al, 1964
<u>Scenedesmus</u> <u>quadricauda</u>	25	2.89	Myers, 1964
<u>Blue-Green Algae</u>			
<u>Agmenellum</u> <u>quadruplicatum</u>	18	2.55	Parsons et al., 1961

Table 4. Phytoplankton Saturated Growth Rates

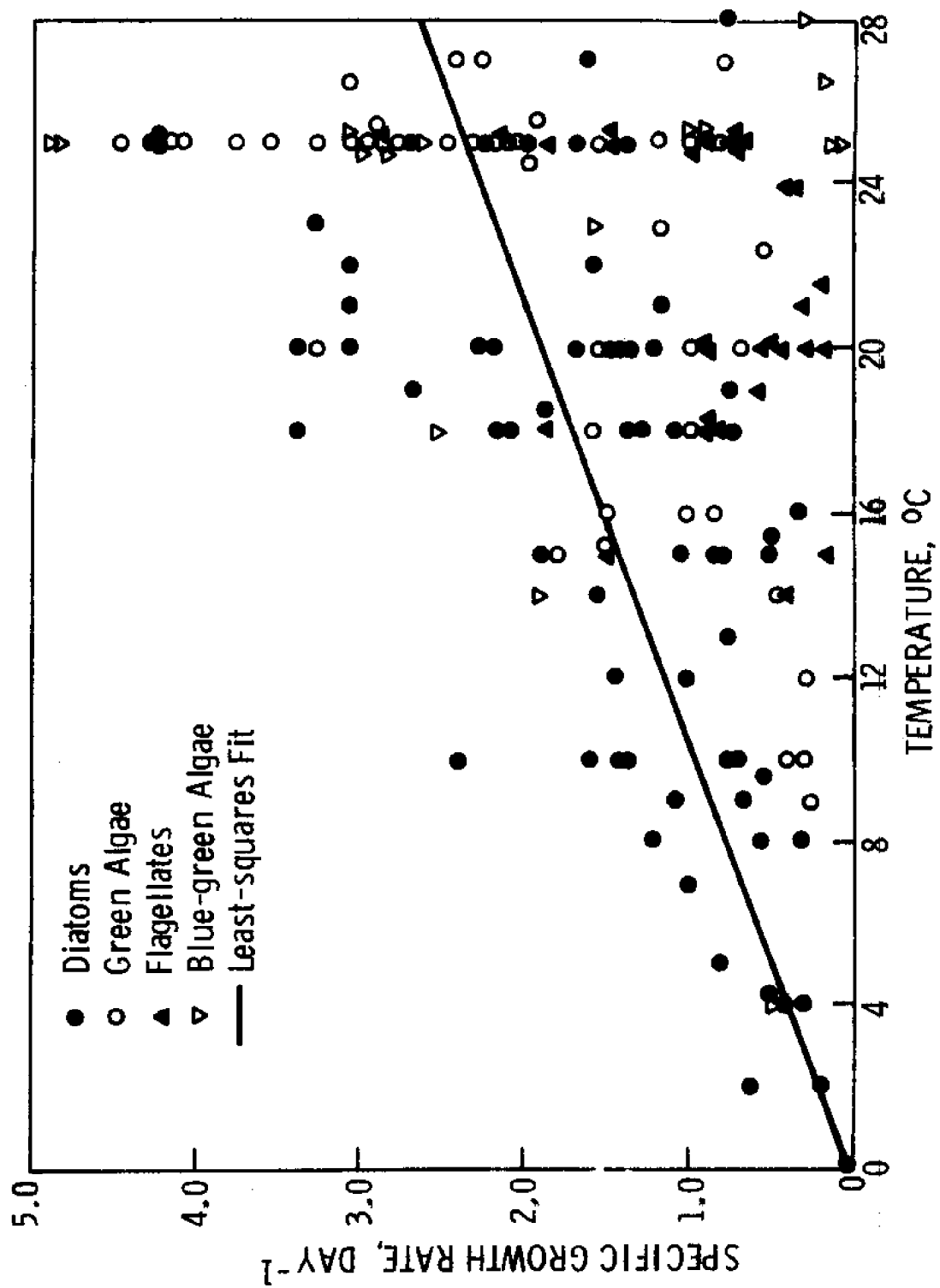


FIGURE 6. ALGAL GROWTH RATE AS A FUNCTION OF TEMPERATURE

Above these values the growth rate is usually depressed. Fortunately, in the natural waters where the model will be applied, the maximum water temperature will not exceed these values. Hence the discrepancy between Equation 3 and the true relationship of growth rate and temperature will not hinder the use of this relationship in the model.

Some reported values for the parameters which characterize phytoplankton response to temperature are listed in Table 5. Included in the table are parameter values used by DiToro et al. (1971) for the Mossdale phytoplankton model and values incorporated by Hydrosience, Inc. (1973) in the model for phytoplankton in the western basin of Lake Erie. Hineman (1973) has estimated similar model parameter values using parameter optimization techniques and laboratory data generated by an experimental study by Schelske et al. (1973) with Grand Traverse Bay waters. The Traverse Bay model values are final estimates of the parameters obtained following a comparison of the model results with field data.

Equation 4 describes the assumed effect of light on phytoplankton growth in the model. It is known that the parameter  $I_S$  varies among species. However all models to date consider  $I_S$  constant. Table 5 lists values for  $I_S$  as used in five models, including a model for Lake George described by Park and Wilkinson (1971).

In Equation 8 nutrient limitation of the phytoplankton growth is expressed mathematically as the product of three Michaelis terms. Some reported Michaelis half-saturation constants for nitrogen, phosphorus, and silicon are listed in



Table 5. Model Parameter Values

Parameter	Units	Mosssdale Model	Lake George Model	Lake Erie	Laboratory Study	Traverse Bay Model
a <sub>1</sub>	day <sup>-1</sup>	0	--	.1	0	0
a <sub>2</sub>	day <sup>-1</sup> °C <sup>-1</sup>	.1	--	.06	.0405	.047
a <sub>3</sub>	day <sup>-1</sup> °C <sup>-2</sup>	0	--	0	.0033	.0066
I <sub>S</sub>	langleys day <sup>-1</sup>	300	300	350	350	350
a <sub>4</sub>	day <sup>-1</sup>	0	--	0	0	0
a <sub>5</sub>	day <sup>-1</sup> °C <sup>-1</sup>	.005	--	.004	.0054	.003
V <sub>S</sub>	m day <sup>-1</sup>	0	--	0	0	0
Y <sub>1</sub>	mg d.w. Ch a <sub>1</sub> <sup>-1</sup>	0	--	0	0	.15
a <sub>6</sub>	dimensionless	0	--	0	0	.1
K <sub>pe</sub>	µg Ch a <sub>1</sub> <sup>-1</sup>	60	13	60	--	5.0
a <sub>7</sub>	ℓ mg d.w. <sup>-1</sup> day <sup>-1</sup>	.13	2.0	.012	--	0
a <sub>8</sub>	ℓ mg d.w. <sup>-1</sup> day <sup>-1</sup> °C <sup>-1</sup>	0	0	.021	--	.08
ε	dimensionless	.6	.75	.65	--	.65
a <sub>9</sub>	day <sup>-1</sup>	--	--	--	--	0
a <sub>10</sub>	day <sup>-1</sup> °C <sup>-1</sup>	--	--	--	--	.005
a <sub>11</sub>	day <sup>-1</sup>	.075*	--	.015	--	.04
Y <sub>2</sub>	mg N mg d.w. <sup>-1</sup>	--	--	.14	--	.096
Y <sub>3</sub>	mg N mg Ch a <sub>1</sub> <sup>-1</sup>	.0085	--	.007	.012	.012
a <sub>12</sub>	day <sup>-1</sup>	--	--	--	.0125	0
a <sub>13</sub>	day <sup>-1</sup> °C <sup>-1</sup>	--	--	.002	--	.002
a <sub>14</sub>	day <sup>-1</sup>	--	--	.002	.0213	0
a <sub>15</sub>	day <sup>-1</sup> °C <sup>-1</sup>	--	--	.0025	--	.003
a <sub>16</sub>	dimensionless	--	--	--	.97	.95

Table 5. (continued)

Parameter	Units	Mossdale Model	Lake George Model	Lake Erie	Laboratory Study	Traverse Bay Model
Y <sub>4</sub>	mg P mg N <sup>-1</sup>	--	--	.143	--	.135
Y <sub>5</sub>	mg P mg Ch a <sup>-1</sup>	--	--	1.	1.5	1.5
Y <sub>6</sub>	mg P mg N <sup>-1</sup>	--	--	.143	.122	.125
Y <sub>7</sub>	mg Si mg Ch a <sup>-1</sup>	--	--	--	32	44
θ	dimensionless	--	--	--	.95	.80
K <sub>n</sub>	mg N ℓ <sup>-1</sup>	.025	.005	.025	.020	.015
K <sub>p</sub>	mg P ℓ <sup>-1</sup>	--	.001	.010	.0018	.003
K <sub>Si</sub>	mg Si ℓ <sup>-1</sup>	--	--	--	.029	.028
Y <sub>8</sub>	mg C mg Ch a <sup>-1</sup>	--	--	--	88	50

\*Includes both respiration and predation losses

-- Indicates that parameter was not included or different formulation was adopted

Table 6. Table 5 shows the values of the Michaelis constant obtained from the laboratory data of Schelske and Rothman (1973) and the analysis by Hineman (1973). The Traverse Bay model Michaelis constants are also listed in Table 5.

The algal respiration and sinking loss coefficients used in the model and obtained by Hineman (1973) are listed in Table 5. DiToro et al. (1971) have tabulated extensive data which supports the values used in the model.

The nutrient-phytoplankton stoichiometry is defined by the carbon, nitrogen, phosphorus, and silicon to chlorophyll a ratios, that is, by the parameters  $Y_8$ ,  $Y_3$ ,  $Y_5$ , and  $Y_7$ . It is known that phytoplankton stoichiometry is not constant and varies among species. The stoichiometry is also dependent on the availability of nutrients and the life history of the cells. In spite of these complications, restrictive ranges for the parameter values exist. Table 7 lists some typical stoichiometric coefficients for plankton communities. These values are in general agreement with the findings of Hineman (1973). The values of the coefficients used in the model for Grand Traverse Bay are listed in Table 5.

Scientific data defining the kinetic and stoichiometric metabolism coefficients for Grand Traverse Bay zooplankton are less abundant than similar data for phytoplankton. However, data do exist for similar zooplankters and for marine species. In most cases it has not been possible to match existing estimates of the coefficients with Grand Traverse Bay species, thus there is a need for further research on zooplankton growth and respiration dynamics.

The nitrogen and phosphorus content of the total zoo-

Table 6. Half-saturation constants for algal growth

Organism	K <sub>N</sub> ( $\mu\text{gN/L}$ )	K <sub>ph</sub> ( $\mu\text{gP/L}$ )	K <sub>Si</sub> ( $\mu\text{gSi/L}$ )	Reference
<u>Selenastrum capricornutum</u>	---	3.5-5.7	----	Toerien et al., 1964
<u>Nitzschia palea and Tabellaria flocculosa</u>	---	1.7	----	Chu, 1942
<u>Nitzschia closterium</u>	---	5.56*	----	Ketchum, 1939
<u>Cyclotella nana and Thalassiosira fluviatilis</u>	---	1.0	----	Fuhs et al., 1970
<u>Chaetoceros gracilis</u>	---	25.0	----	Thomas & Dodson, 1968
<u>Scenedesmus gracile</u>	150.0	10.0	----	
<u>Microcystis aeruginosa</u>	---	10.0*	----	
<u>Phaeodactylum tricornutum</u>	---	10.0	----	Ditoro et al., 1971
-----	25.0	10.0	----	Hydroscience, 1973
-----	---	10.5	----	Dugdale, 1967
Diatoms	---	2.48*	----	Goldberg et al., 1951
Tropical Oceanic Diatom	---	3.72	----	Thomas & Dodson, 1968
Oceanic Species	1.4-9.8 (NO <sub>3</sub> )	-----	----	Eppley et al., 1969
	1.4-7.0 (NH <sub>3</sub> )	-----	----	Eppley et al., 1969
Neritic Diatoms	6.3-39.2 (NO <sub>3</sub> )	-----	----	Eppley et al., 1969
	7.0-120.0 (NH <sub>3</sub> )	-----	----	Eppley et al., 1969
Neritic or Littoral Flagellates	1.4-140. (NO <sub>3</sub> )	-----	----	Eppley et al., 1969
	1.4-77. (NH <sub>3</sub> )	-----	----	Eppley et al., 1969
Natural Association	---	6.0*	----	Riley, 1963

Table 6. (Continued)

Organism	K <sub>N</sub> (μgN/ℓ)	K <sub>ph</sub> (μgP/ℓ)	K <sub>Si</sub> (μgSi/ℓ)	Reference
Natural Association Oligotrophic	2.8 (NO <sub>3</sub> ) 1.4-8.4 (NH <sub>3</sub> )	----- -----	----- -----	MacIsaac & Dugdale, 1969 MacIsaac & Dugdale, 1969
Natural Association Eutrophic	14. (NO <sub>3</sub> ) 18. (NH <sub>3</sub> )	----- -----	----- -----	MacIsaac & Dugdale, 1969 MacIsaac & Dugdale, 1969
Natural Association	-----	-----	16.-33.*	Strickland, 1965
<u>Cyclotella nana</u>	-----	-----	23.3-38.2	Paasche, 1973

\*Estimated by multiplying saturating concentration by 0.33.

Table 7. Stoichiometric ratios in various algal groups

Organism	$Y_8$ $(\frac{\mu\text{g C}}{\mu\text{g Chl a}})$	$Y_3$ $(\frac{\mu\text{g N}}{\mu\text{g Chl a}})$	$Y_5$ $(\frac{\mu\text{g P}}{\mu\text{g Chl a}})$	$Y_7$ $(\frac{\mu\text{g Si}}{\mu\text{g Chl a}})$	Reference
<u>Diatoms</u>					
<u>Chaetoceros sp.</u>	44	8	2.1	--	Parsons et al., 1961
<u>Cyclotella nana</u>	25-175	4.1	---	--	Fuhs et al., 1970
<u>Coscinodiscus sp.</u>	69	12	1.7	93.9	Parsons et al., 1961
<u>Phaeodactylum tricornutum</u>	26	4	1.4	0.21	Parsons et al., 1961
<u>Skeletonema costatum</u>	26	6	1.7	14.3	Parsons et al., 1961
-----	25-90	5-9	2-4	--	Strickland, 1965
<u>Green Algae</u>					
<u>Dunaliella salina</u>	19	4	1.5	0.09	Parsons et al., 1961
<u>Tetraselmis maculata</u>	32	7	2.9	1.04	Parsons et al., 1961
-----	25-40	5-9	2-4	--	Strickland, 1965
<u>Flagellates</u>					
<u>Amphidinium carteri</u>	48	5	1.4	0.06	Parsons et al., 1961
<u>Exuviella sp.</u>	62	7	1.8	0.27	Parsons et al., 1961
<u>Monochrysis lutheri</u>	97	14	5.5	2.92	Parsons et al., 1961
<u>Syracosphera carterae</u>	61	14	1.8	0.31	Parsons et al., 1961
-----	75-110	15	2.5-6.5	--	Strickland, 1965
-----	65-80	9	2	--	Strickland, 1965
<u>Blue-Green Algae</u>					
<u>Agmenellum quadruplicatum</u>	45	6	1.5	1.38	Parsons et al., 1961
<u>Marine Algae</u>					
-----	--	0.3-5.5	---	--	MacIsaac & Dugdale, 1969
<u>Open Ocean Crop</u>					
-----	65	15	2	--	Strickland, 1965
<u>Coastal Crop (mostly diatoms)</u>					
-----	25	10	1.5	--	Strickland, 1965
<u>Coastal Crop (mostly diatoms)</u>					
-----	60	16	2	--	Strickland, 1965

Table 7. (Continued)

Organism	$Y_8$ $(\frac{\mu\text{g C}}{\mu\text{g Chl a}})$	$Y_3$ $(\frac{\mu\text{g N}}{\mu\text{g Chl a}})$	$Y_5$ $(\frac{\mu\text{g P}}{\mu\text{g Chl a}})$	$Y_7$ $(\frac{\mu\text{g Si}}{\mu\text{g Chl a}})$	Reference
Natural Association	50	7	1.0	---	Hydroscience, 1973
Spring Community	76	---	---	---	Steele & Baird, 1961
Summer Community	47-260	---	---	---	Steele & Baird, 1961
Autumn Community	47-165	---	---	---	Steele & Baird, 1961
Winter Community	213	---	---	---	Steele & Baird, 1961
Estuarine Community	45	10	1.0	---	Jaworski et al., 1972

plankton is described by the parameters  $Y_2$  and  $Y_4$ . The values of the parameters as used in the model are listed in Table 5. These values are also compared with values adapted by other models in Table 5. Data published by Baudouin and Ravera (1972) for Daphnia hyalina supports the assumptions made in the model.

The grazing of the zooplankton is assumed to be dependent on temperature and the phytoplankton concentration in the water. The maximum grazing rate at any phytoplankton concentration is assumed to be linearly dependent on temperature. The coefficients defining the slope and intercept of this linear relation are listed in Table 5 along with the value of similar coefficients used in other models. These coefficients are based primarily on data summarized by DiToro et al. (1971). At a given temperature the filtering rate is assumed to be dependent on the phytoplankton concentration. The model assumes a formulation which results in high grazing rates at low phytoplankton concentrations and low grazing rates at high concentrations. Equation 13 is a mathematical representation of these ideas. The adopted model coefficients are based on data published for Daphnia pulex by Crowley (1973) and for Calanus helgoandicus by Mullin (1963).

The assimilation efficiency of zooplankton has been studied by several researchers. Conover (1966) has reported that the assimilation efficiency of Calanus hyperboreus is independent of temperature, the age of the food source, and the length of exposure to the food supply. Assimilation efficiencies have been reported between 63% and 90% by Mullin and Brooks (1970) and Waterman (1960). The assimilation



efficiency used in the Grand Traverse Bay model is listed in Table 5 and compared to similar parameter values used in other models.

The respiration mechanisms of zooplankton are difficult to quantify. It has been reported by Burns and Rigler (1967) that containment increases cladoceran respiration by a factor of 4.5. It is known that past history, temperature transients, and seasonal acclimation factors also affect respiration rates. These detailed phenomena are considered too complex to be included in the present form of the model. The respiration is considered to be a linear function of temperature which is similar to the assumption used by DiToro et al. (1971). DiToro et al. (1971) contains an extensive list of data supporting the model formulation. The parameters describing the respiration of the zooplankton, as used in the Grand Traverse Bay model, are listed in Table 5.

The rates of decomposition and oxidation of organic nitrogen and ammonia as used in the model are listed in Table 5. Table 5 also gives values of similar parameters used in other models. Brezonik (1972) has given rates of ammonification between .01 and .6 day<sup>-1</sup>. Jaworski et al. (1972) have found nitrification rates ranging from 0.005 to 0.4 day<sup>-1</sup>, depending upon temperature. At 9°C the nitrification rate was approximately 0.01 day<sup>-1</sup>. These data support the parameter values used in the Grand Traverse Bay model.

## LIGHT EXTINCTION

Knowledge of the pattern of light extinction in Grand Traverse Bay waters is required for the construction of the mathematical model for biological production. The penetration of light is limited by suspended materials such as clay and silt particles and by the plankton organisms. Sea Grant field data are available which describe light extinction in Grand Traverse Bay. This information can be summarized in terms of light extinction coefficients defined by the equation,

$$I/I_0 = e^{-k_e X} \quad (25)$$

where  $X$  is the depth,  $I$  is the light intensity at depth  $X$ ,  $I_0$  is the surface light intensity, and  $k_e$  is the extinction coefficient.

Estimates of  $k_e$  were obtained separately for stations 1, 2, 3, 4, and 5 on each of 17 different dates during 1971, 1972, and 1973. These estimates were obtained by fitting the above equation to data using a least-squares criterion. The number of depth-light intensity data pairs for a given least-squares regression (at a given station on a given date) was usually five. The resulting correlation coefficients ranged from 0.974 to 0.999. Typical results are shown in Figure 7.

Other attempts were also made to quantify the extinction coefficient. Riley (1956) proposed an approximating equation for  $k_e$  which takes the form

$$k_e = k'_e + 0.0088P + 0.054P^{2/3} \quad (26)$$

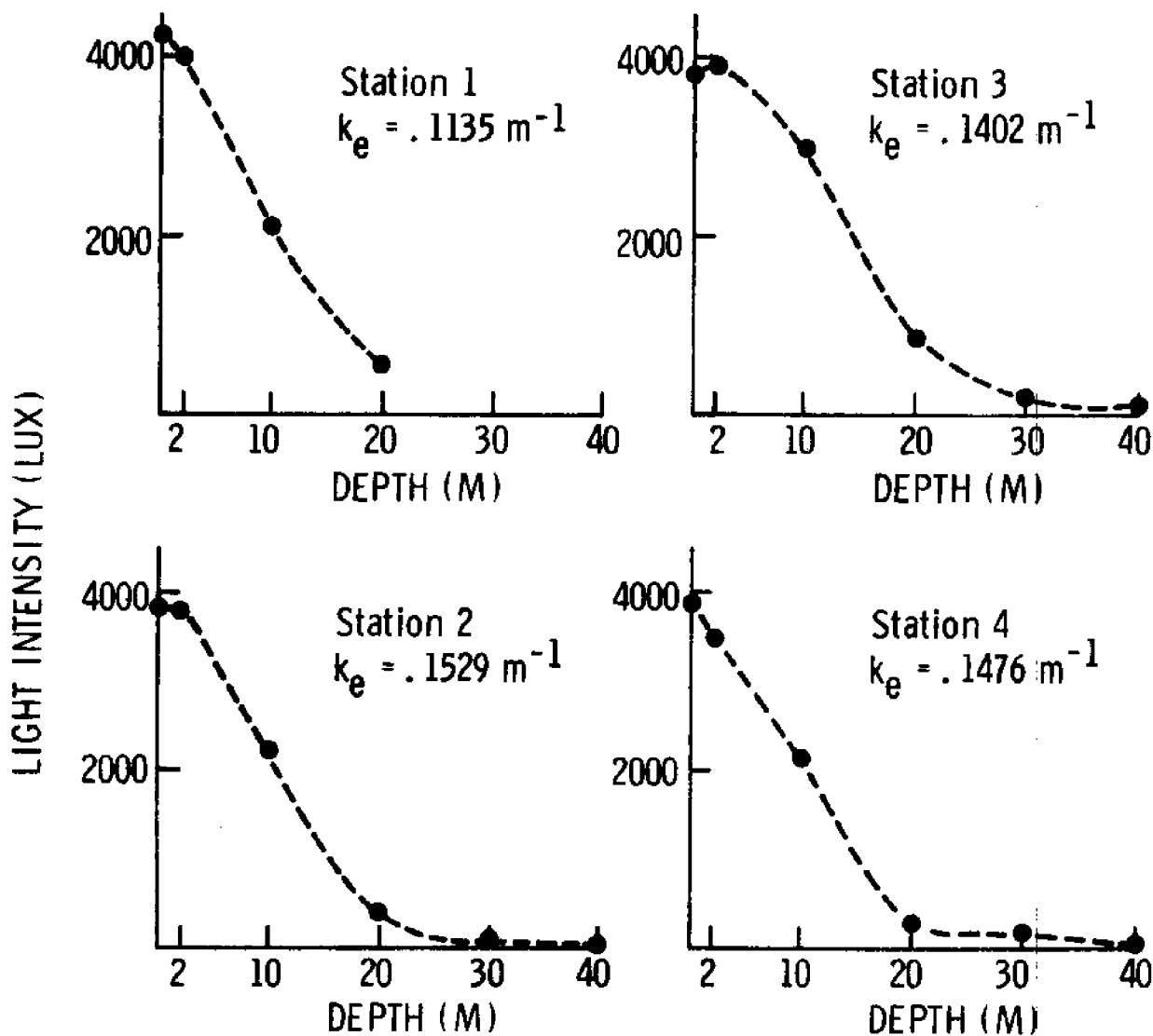


FIGURE 7. LIGHT INTENSITY AS A FUNCTION OF DEPTH AT STATIONS 1-4

where:  $k'_e$  = is the extinction coefficient due to other causes and

$P$  = is Chlorophyll a in  $\mu\text{g}/\ell$ .

Regression analysis on Grand Traverse Bay  $k_e$  and chlorophyll a data was performed in an attempt to derive a similar equation, with the following result:

$$k_e = 0.0752 - 0.0611P + 0.128P^{2/3} \quad (27)$$

The fit obtained by this equation was poor, yielding a correlation coefficient of only 0.16. Several other polynomial functions of chlorophyll a and particulate phosphorus, as well as combinations of the two, were tried as well. None were able to provide a good fit to the data. As Figures 8 and 9 indicate, the data do not show a strong relationship between  $k_e$  and either chlorophyll a or particulate phosphorus; and the self-shading effect of phytoplankton evidently cannot be accounted for in this way in Grand Traverse Bay.

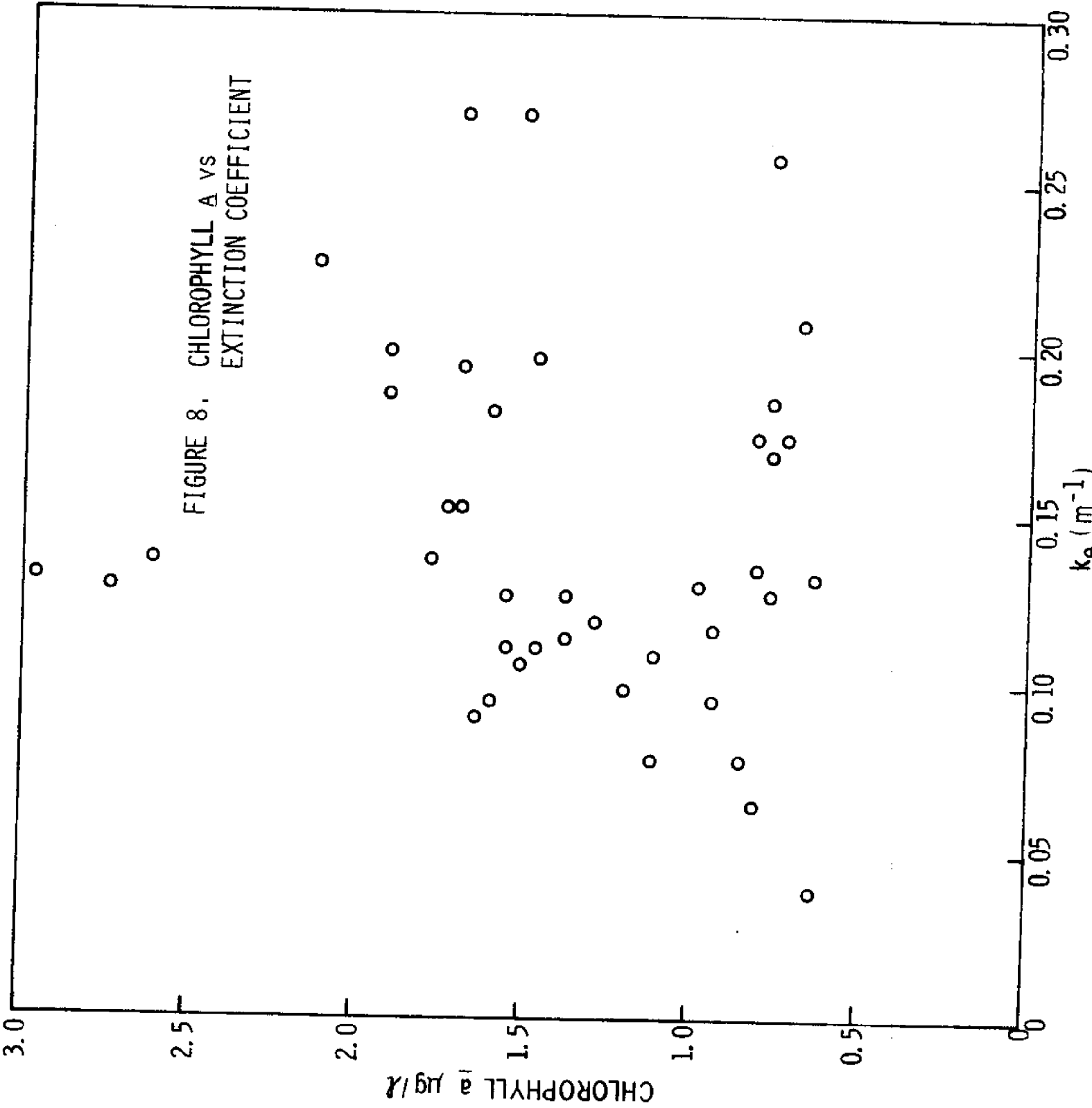
Another attempt involved the use of secchi disc measurements to estimate the extinction coefficient. A formula derived by Poole and Atkins (1929) and used by Saunders et al. (1962) expresses  $k_e$  as the following function of the secchi disc reading:

$$k_e = \frac{1.7}{\text{secchi reading}} \quad (28)$$

A least-squares regression analysis of values for these variables in Grand Traverse Bay yielded a coefficient of 0.836 and a correlation coefficient of 0.94. As Figure 10 indicates, there is a fairly strong relationship between secchi disc readings and the extinction coefficient.

The growth of phytoplankton is dependent on the extinction coefficient as shown by Equation 8. Values of the extinction

FIGURE 8. CHLOROPHYLL  $\Delta$  VS  
EXTINCTION COEFFICIENT



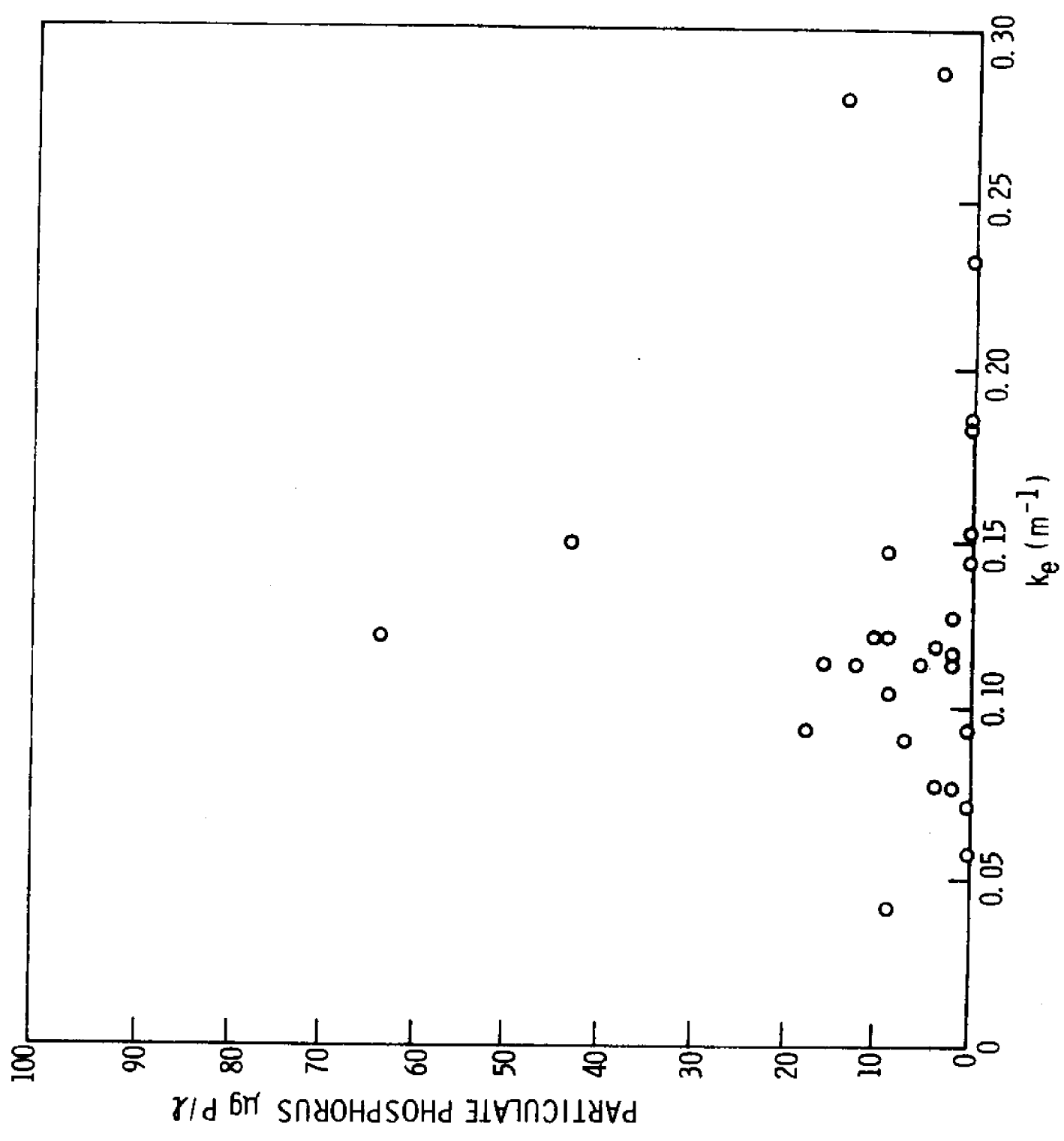


FIGURE 9. PARTICULATE PHOSPHORUS VS EXTINCTION COEFFICIENT

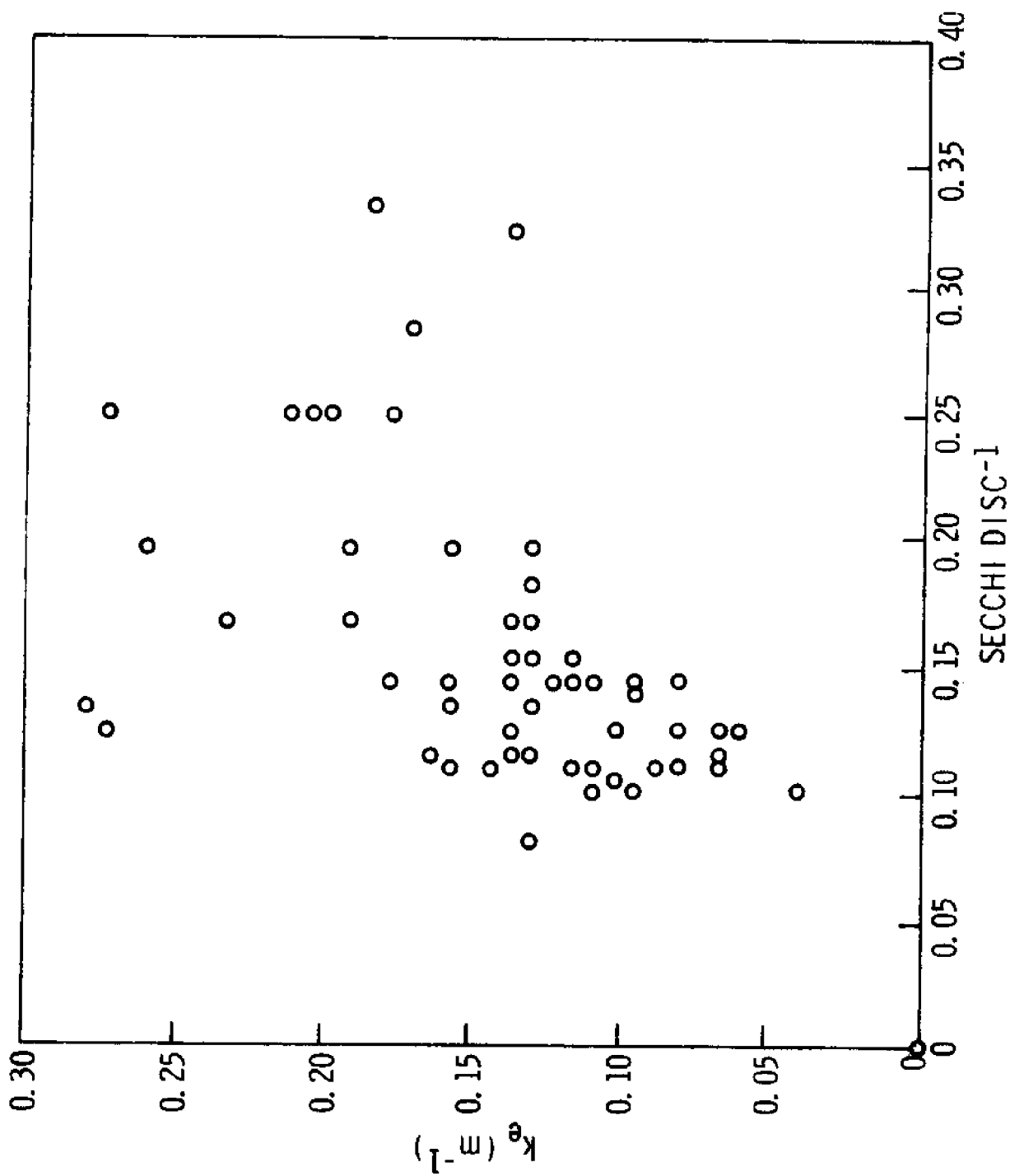


FIGURE 10. EXTINCTION COEFFICIENT vs SECCHI DISC READING<sup>-1</sup>

coefficient are input to the model as a time variable function. This function approximates measured extinction coefficients at stations 1, 2, and 3. The observations and the approximating function are illustrated in Figure 11.

#### FORCING FUNCTIONS

Forcing functions are defined as those variables which influence the system but are not themselves affected by conditions within the system. In the model for biological production there are three of these: temperature, solar radiation, and photoperiod. An initial attempt was made to obtain this information from Sea Grant data collected at Grand Traverse Bay. This was not possible in all cases, however, and data for photoperiod and solar radiation were acquired from other sources.

Fairly complete records for water temperature in the lower west arm are available from Sea Grant sampling stations 1, 2, and 3 starting in July 1970 (Figures 12 to 14). Measurements were usually taken at four different depths at each station on each cruise. This made it possible to obtain weighted averages over depth for each station. This information was then averaged again to yield a single time-series of depth-averaged temperature (Table 8). These points and linear interpolation schemes were used in the model.

Figures 12 through 14 also give insight into the timing of stratification of the bay waters. Since each point in the plots represents a measurement at a particular depth, several points are plotted for a given date. The relatively wide variation of summer temperatures with depth compared to



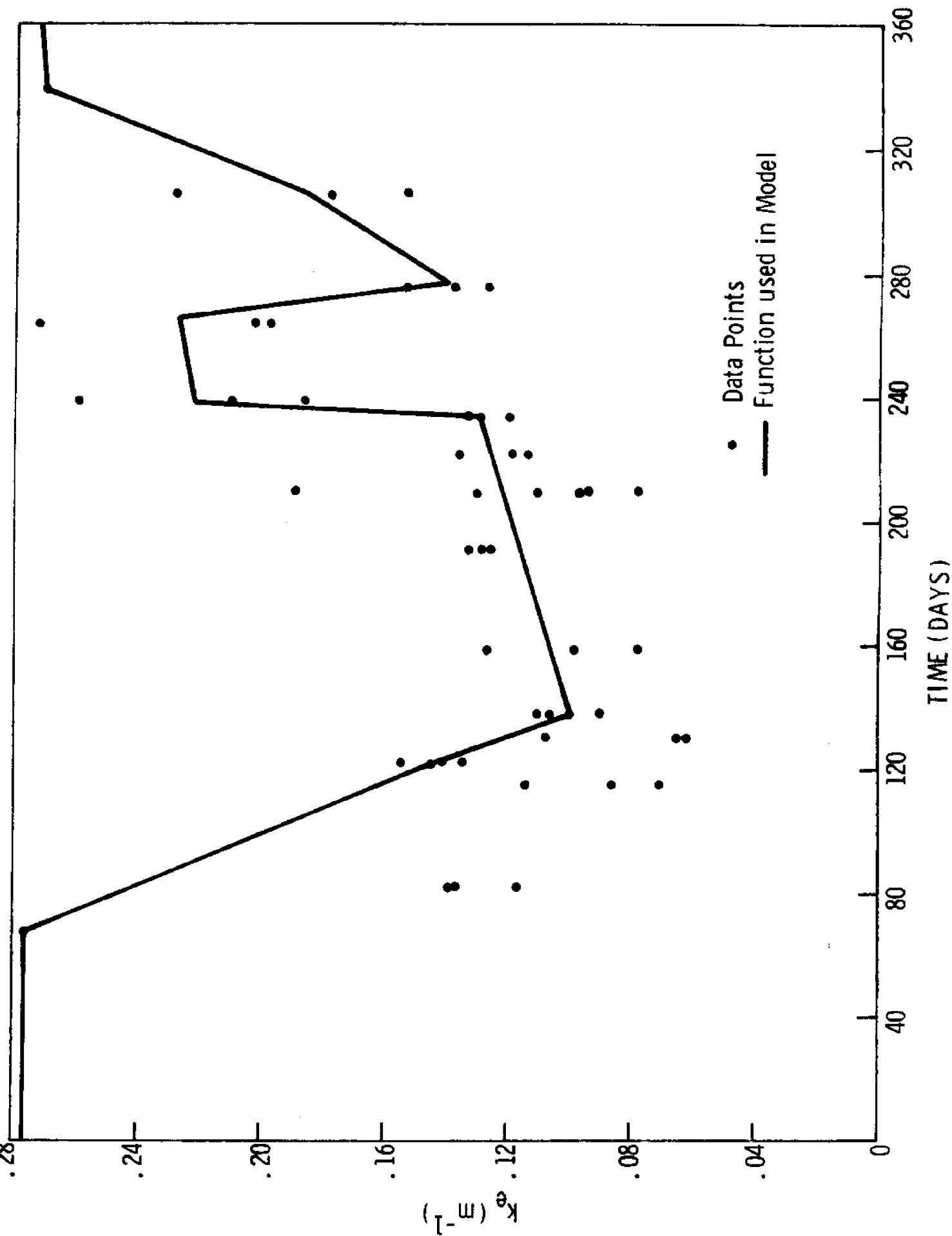


FIGURE 11. LIGHT INTENSITY EXTINCTION COEFFICIENT AT STATIONS 1-3

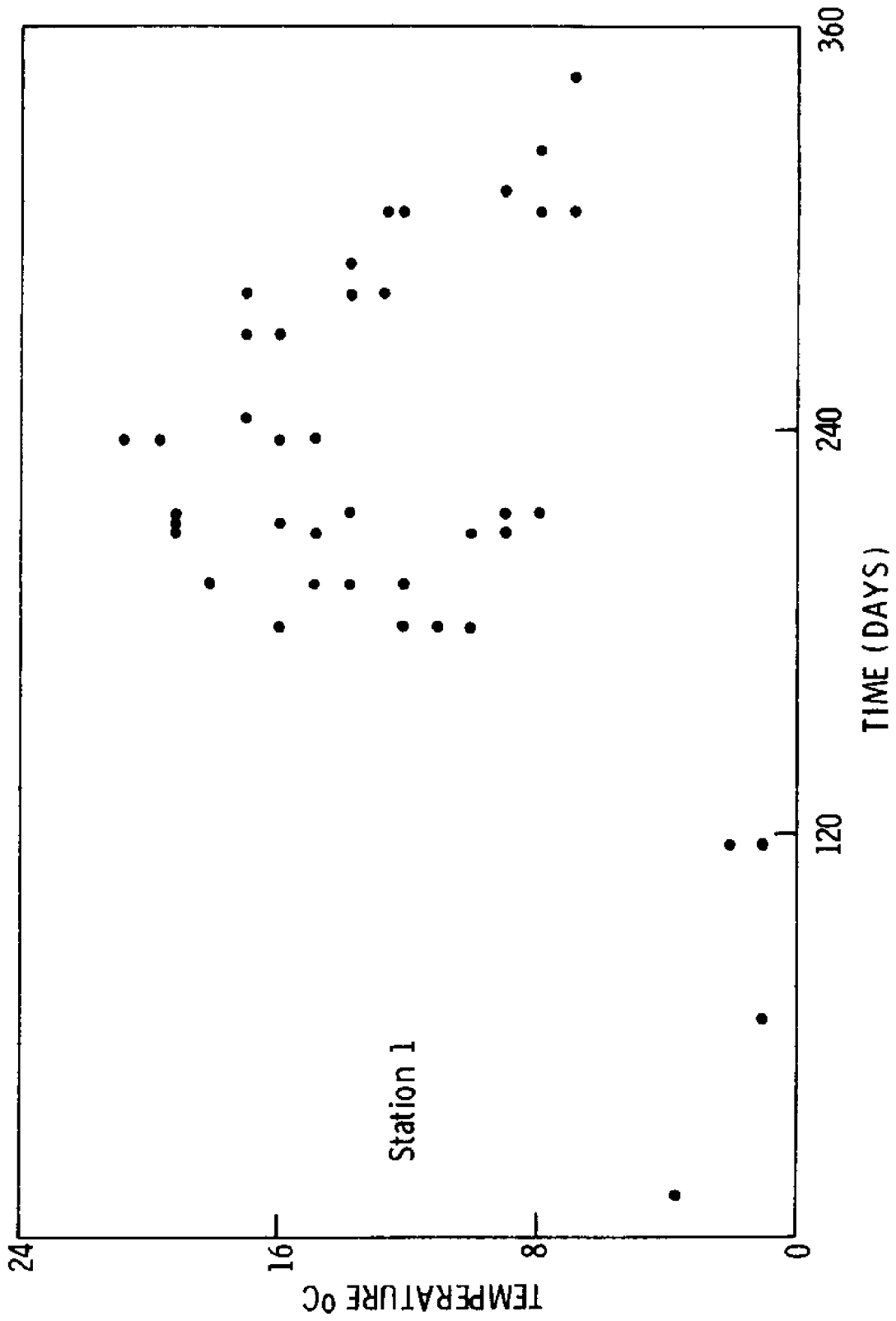


FIGURE 12. PLOT OF WATER TEMPERATURE AT VARIOUS DEPTHS AT STATION 1

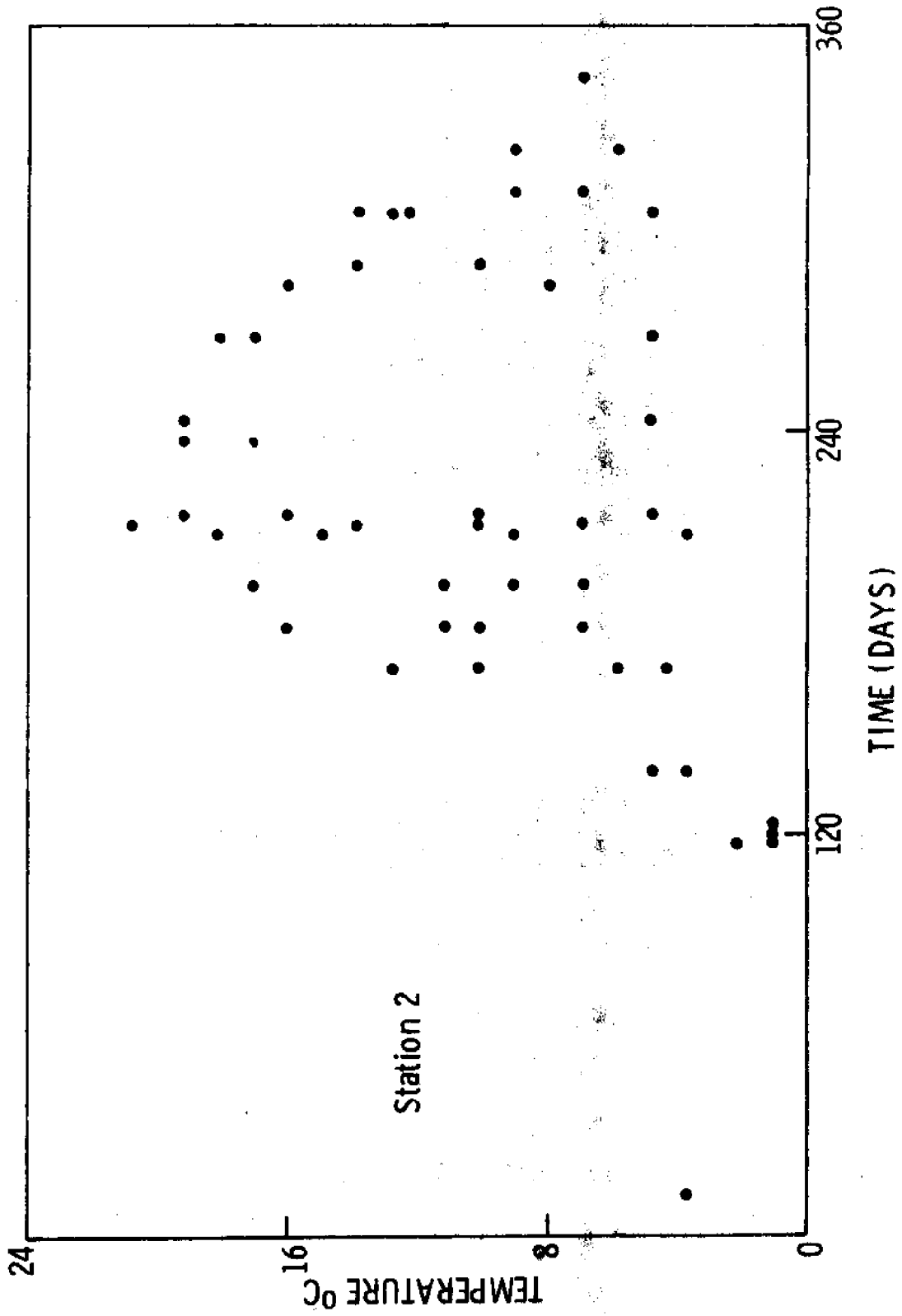


FIGURE 13. PLOT OF WATER TEMPERATURE AT VARIOUS DEPTHS AT STATION 2

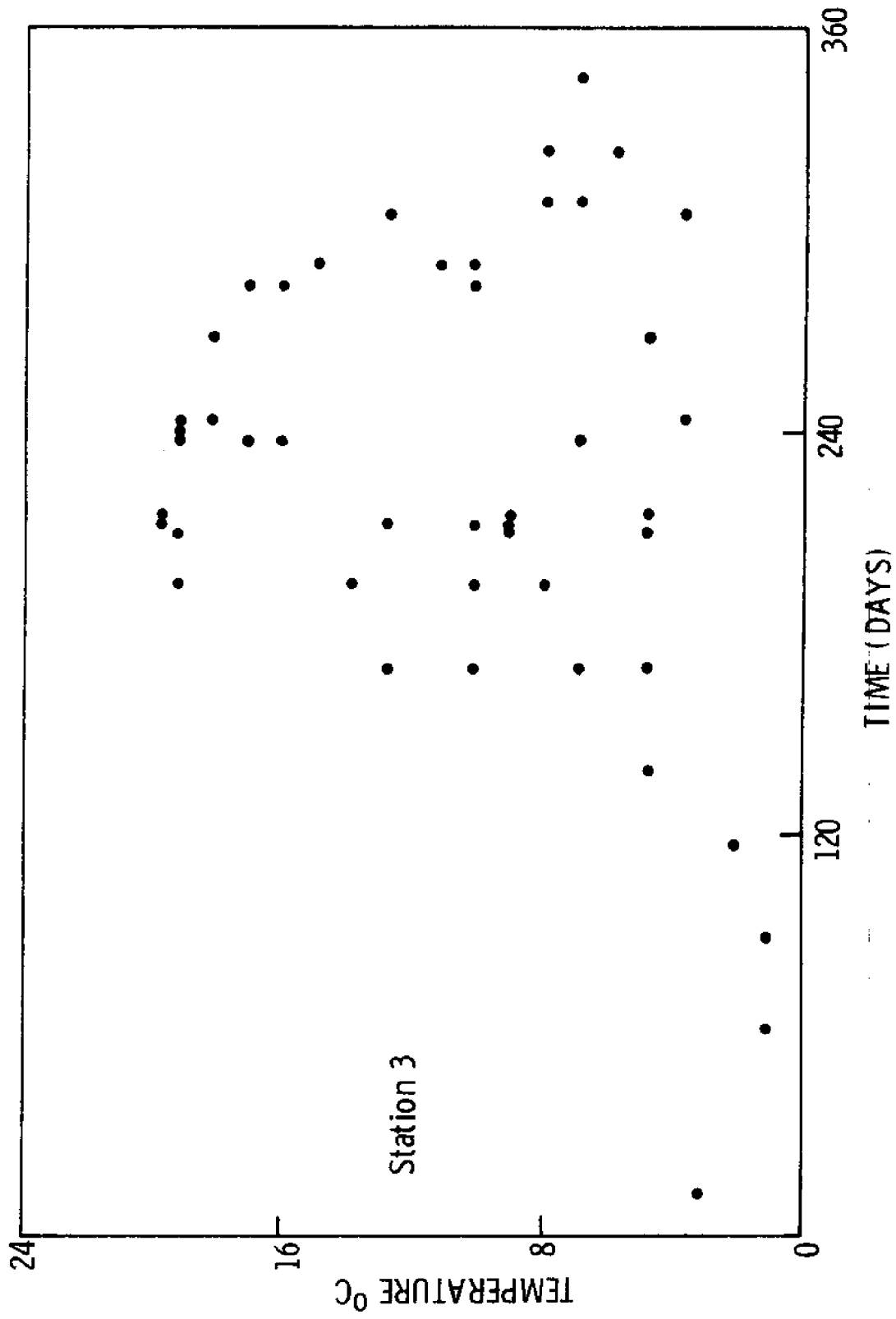


FIGURE 14. PLOT OF WATER TEMPERATURE AT VARIOUS DEPTHS AT STATION 3

Date	Light Intensity (Langleys/day)	Photoperiod (fraction)	Temperature (°C)
5	111	.43	4.0
35	175	.44	2.4
65	295	.52	1.5
100	430	.59	2.7
130	555	.60	5.2
160	623	.62	8.7
190	620	.60	13.0
220	540	.57	16.1
250	420	.52	16.5
280	280	.43	13.1
310	163	.40	9.4
340	100	.38	6.4

TABLE 8. Forcing Functions

winter temperatures with depth can be clearly seen. From this information it appears that the thermocline becomes established sometime between May 15 and June 15 and breaks up in late October or early November.

No Sea Grant data exists for photoperiod in the Grand Traverse Bay area. However a simulation model developed for Lake Erie by Hydroscience (1973) utilized photoperiod data for that region. Since Lake Erie and Grand Traverse Bay are in fairly close geographical proximity, it was felt that these data would be adequate for the bay.

Records of sunlight intensity in the West Arm have been collected by Sea Grant. However these records are instantaneous measures of illumination, recorded in units of lux, and applicable only to the visible spectrum. Since the model requires light intensity in langleys/day, a measure of irradiance energy, the Sea Grant data could not be utilized. A set of solar radiation measurements in the correct units and collected on the Great Lakes was located in the literature and used in the model (Great Lakes Institute 1962 and 1963). These data (Figures 15 and 16) agree well with values reported for the northeast and midwest regions of the United States (Odum, 1971).

#### BOUNDARY CONDITIONS

The behavior of biological and chemical variables in the lower west arm of the bay is affected by the inflow of upper bay water. These effects are quantified by calculating an indirect loading equal to the concentration of various components times the inflow current. The current direction and magnitude

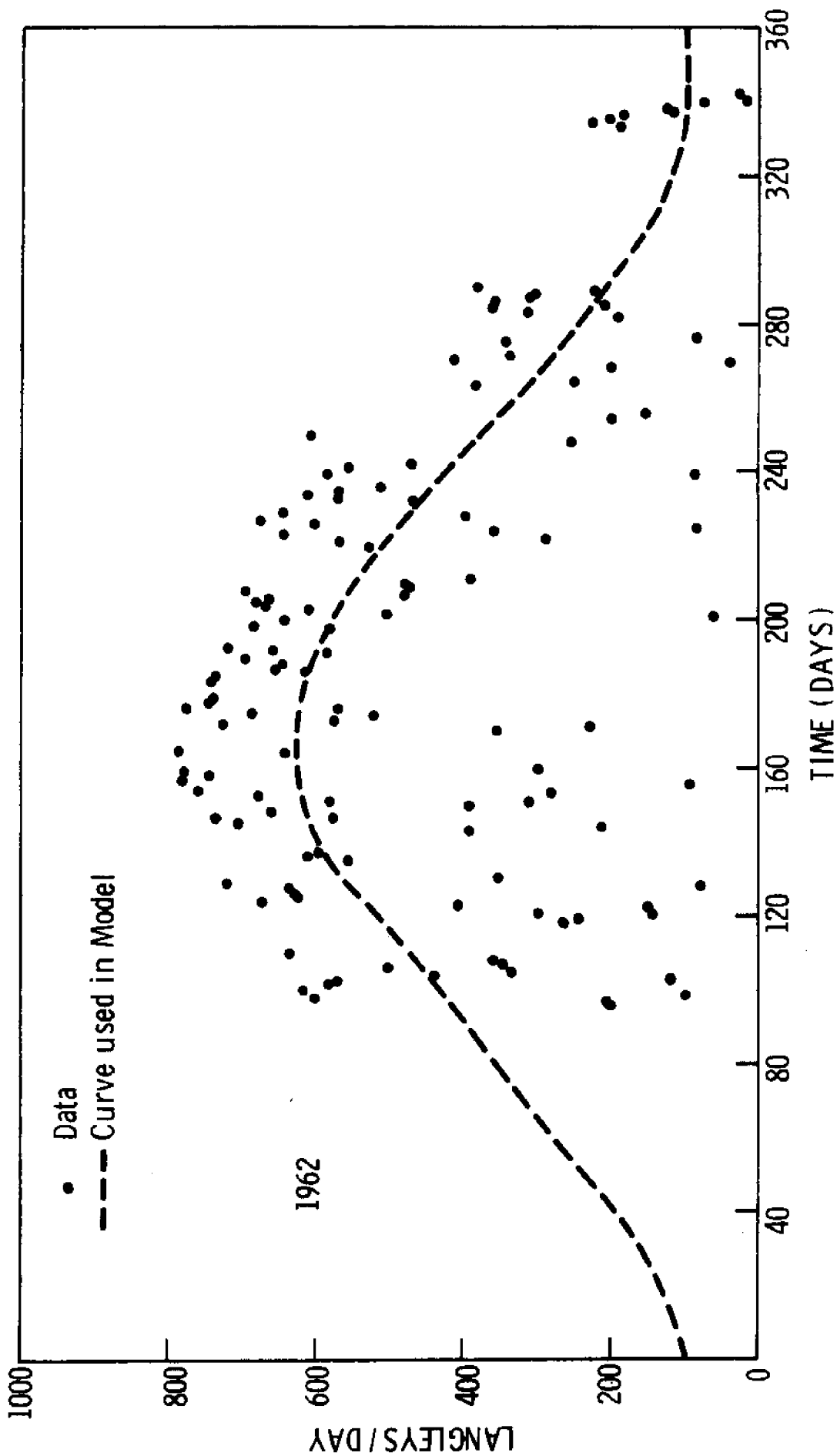


FIGURE 15. SOLAR RADIATION ON THE GREAT LAKES, 1962

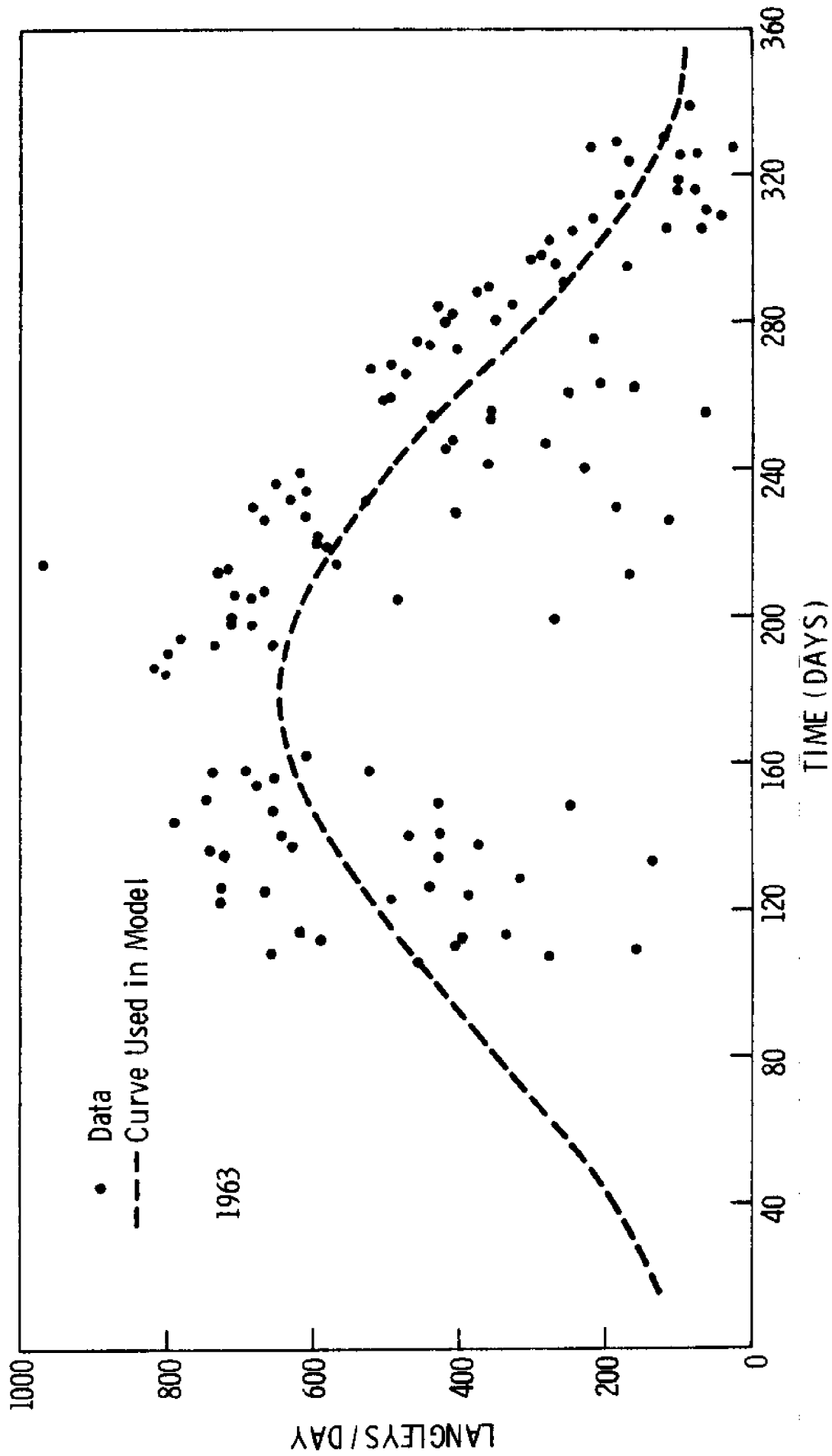


FIGURE 16. SOLAR RADIATION ON THE GREAT LAKES, 1963



were obtained from the numerical circulation model developed by Smith (1973). The boundary concentrations are time variable functions which must be estimated directly from available field data. These values were obtained by calculating depth-averaged concentrations for both stations 2 and 3 at each available time point. The available data and the functions used in the model are illustrated in Figures 17 through 22.

No direct measurements on non-living organic nitrogen are available for Grand Traverse Bay. Hence an indirect technique had to be employed in order to obtain an estimate of the boundary concentration of this parameter. In this system the non-living organic nitrogen can be defined as the difference between the total N and the sum of the inorganic N plus the N contained in the phytoplankton and zooplankton. A survey of the Sea Grant data base revealed that measurements of all of these variables (total N, inorganic N, phytoplankton and zooplankton) were made on four dates between 28 August 1970 and 30 March 1971. The phytoplankton and zooplankton counts were converted to their equivalent nitrogen content, and non-living organic nitrogen was computed. Due to the scarcity of information on this variable, its boundary concentration was taken as constant, equal to the average of the values obtained with the formula above, 0.153 mg N/l.

#### LOADINGS

The present model covers the lower west arm of the bay. The only substantial loadings in this region of the bay enter through the Boardman River. Loadings from the Boardman River were calculated by first computing instantaneous loading rates

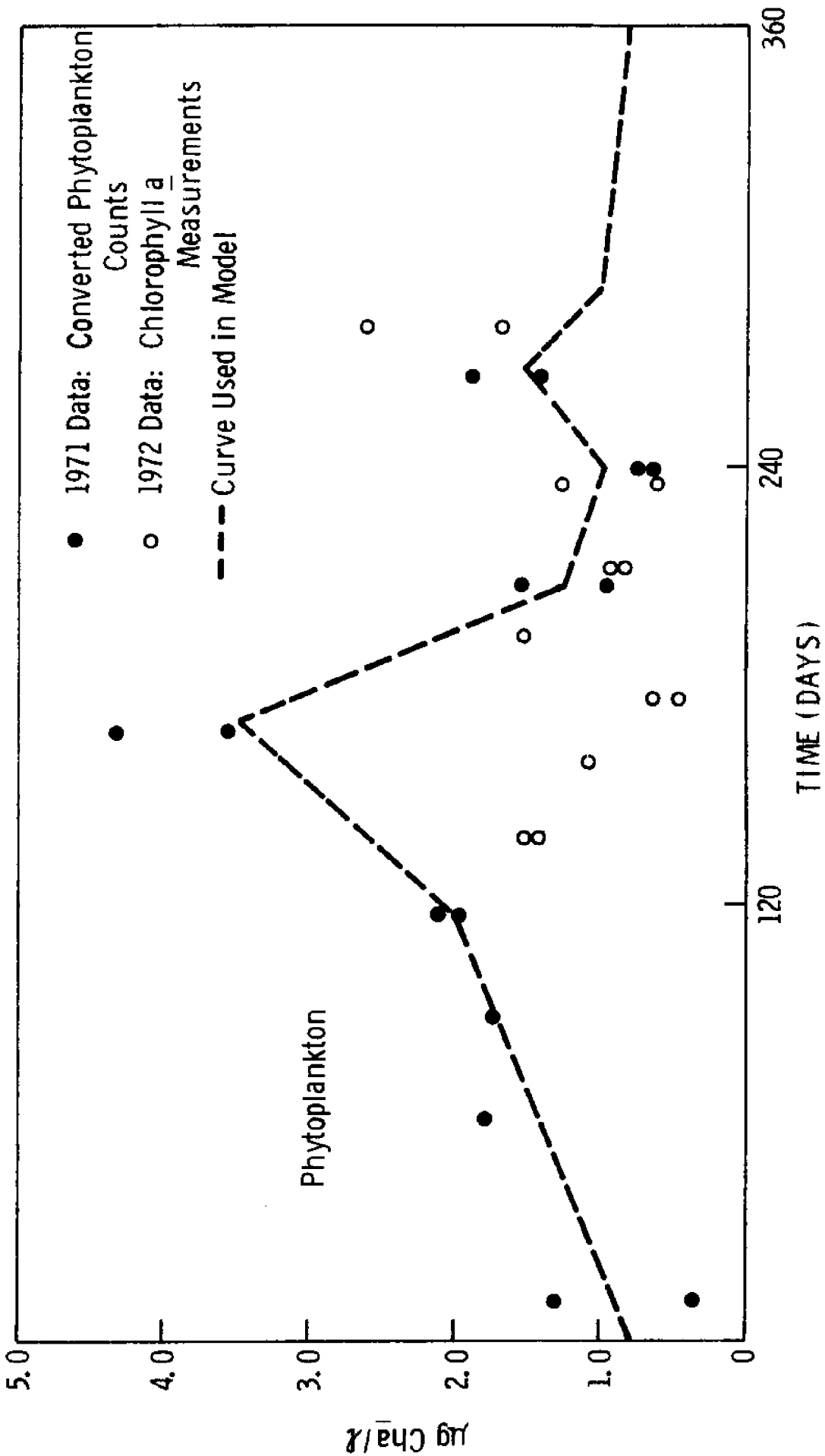


FIGURE 17. PHYTOPLANKTON AT BOUNDARY

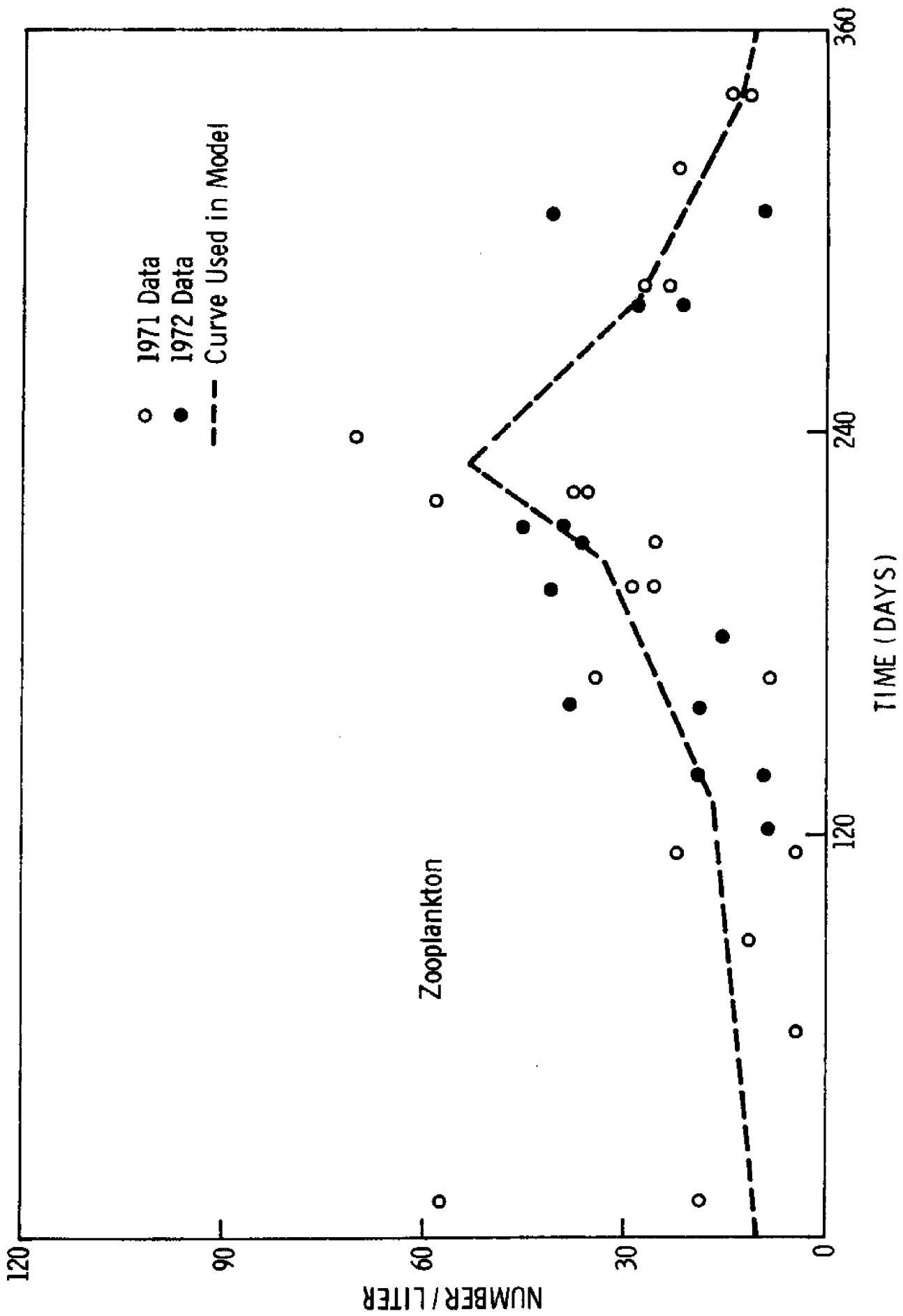


FIGURE 18. ZOOPLANKTON AT BOUNDARY

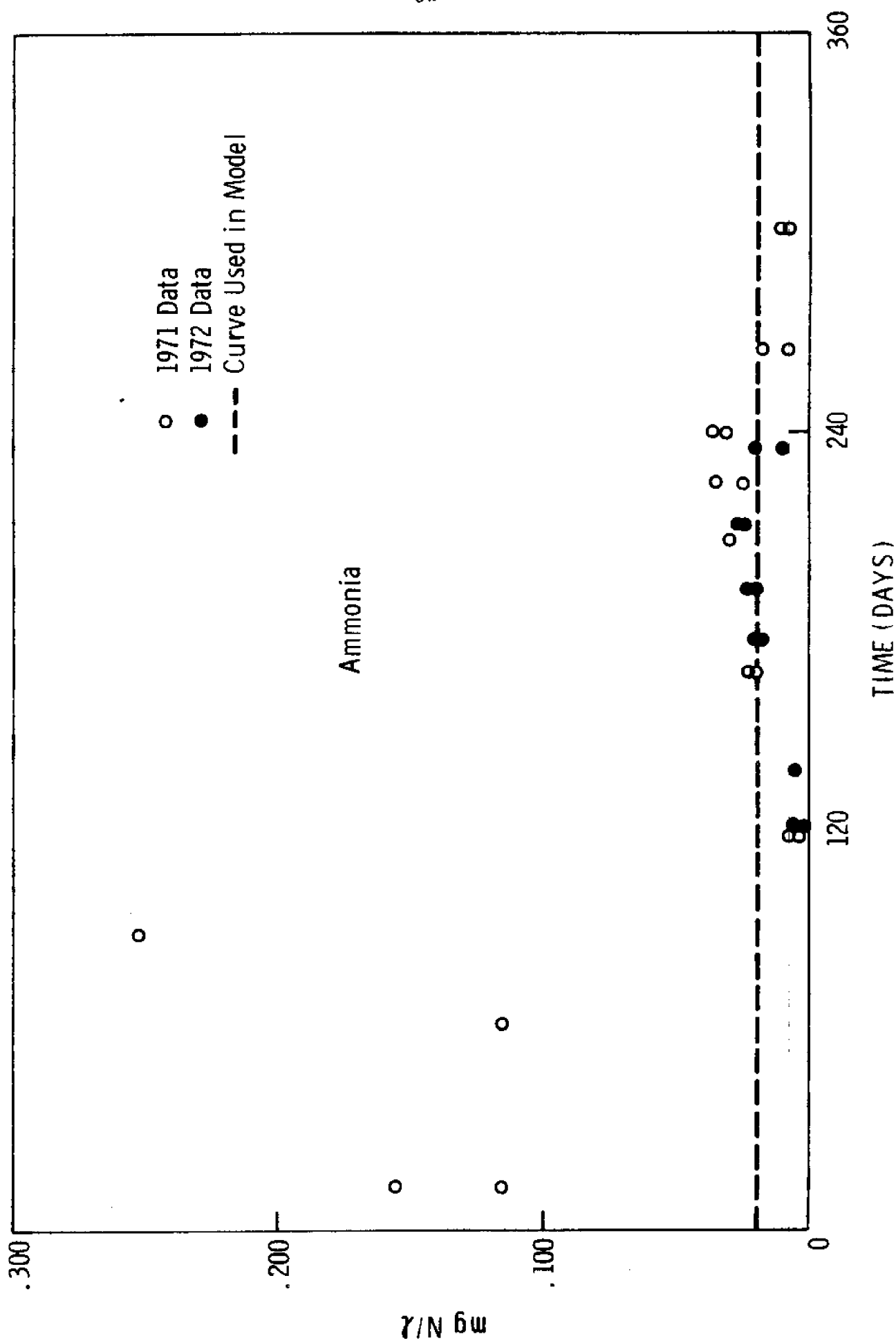


FIGURE 19. AMMONIA AT BOUNDARY

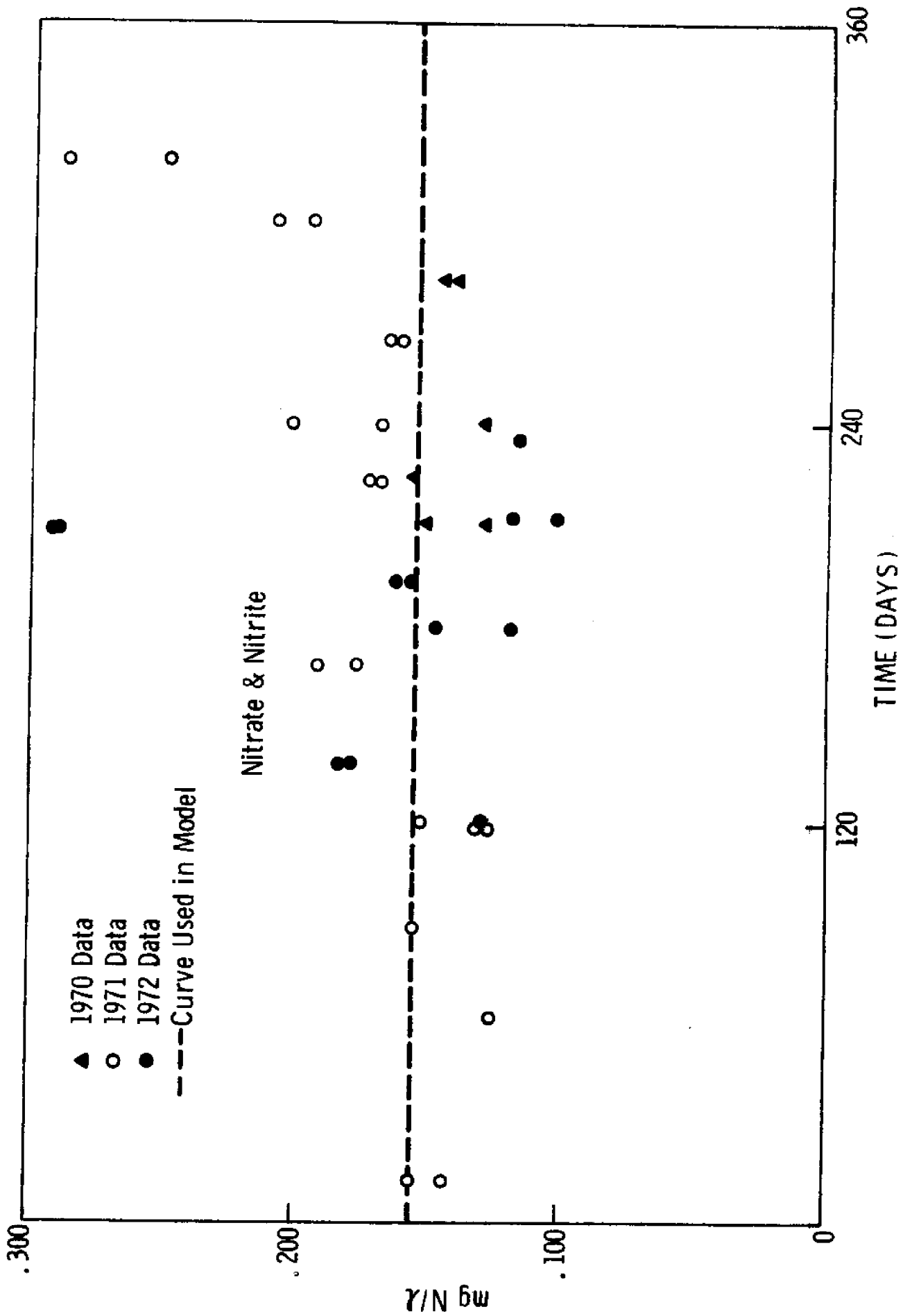


FIGURE 20. NITRATE-NITRITE AT BOUNDARY

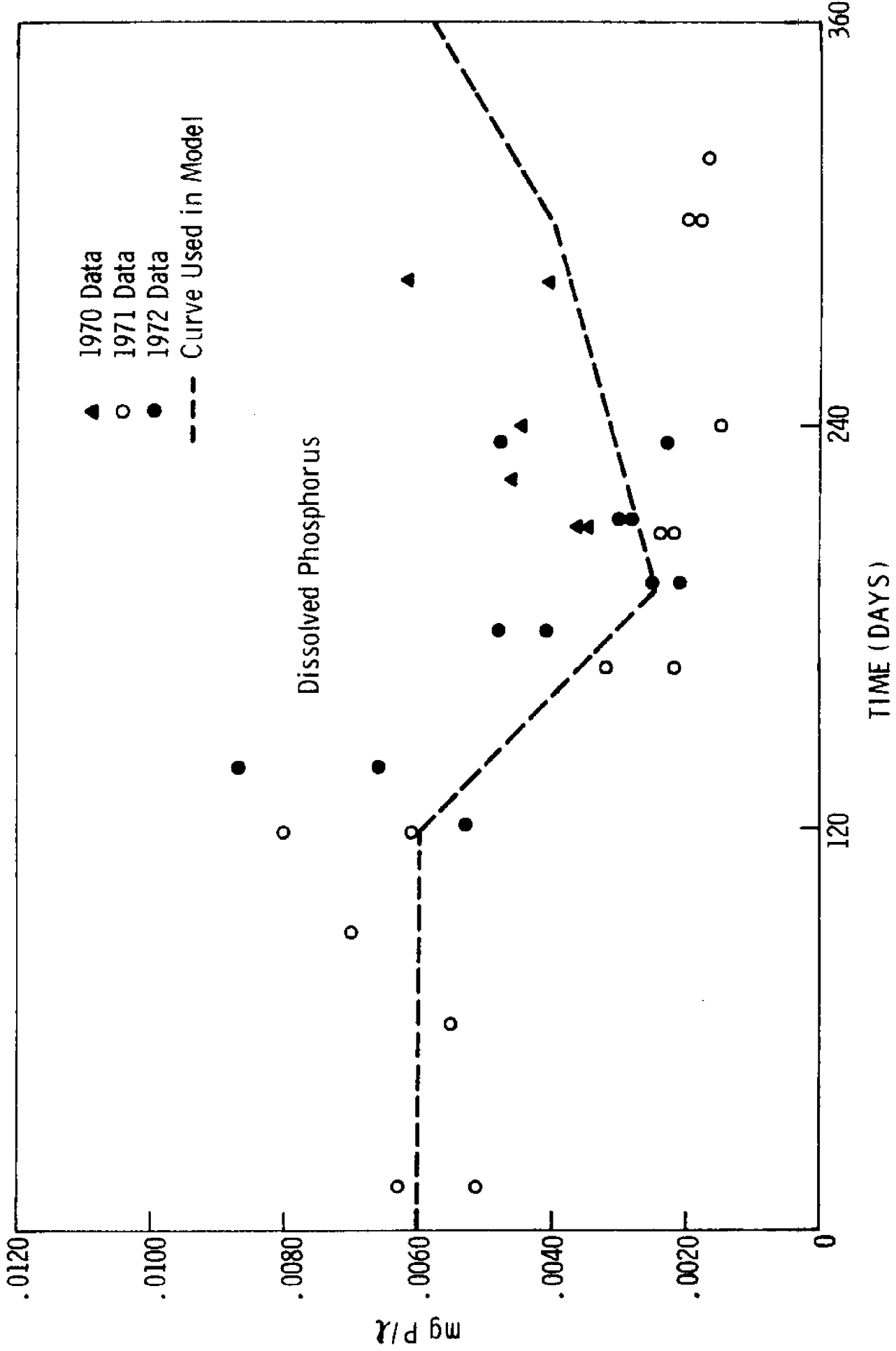


FIGURE 21. DISSOLVED PHOSPHORUS AT BOUNDARY

mg P/l

120

240

360

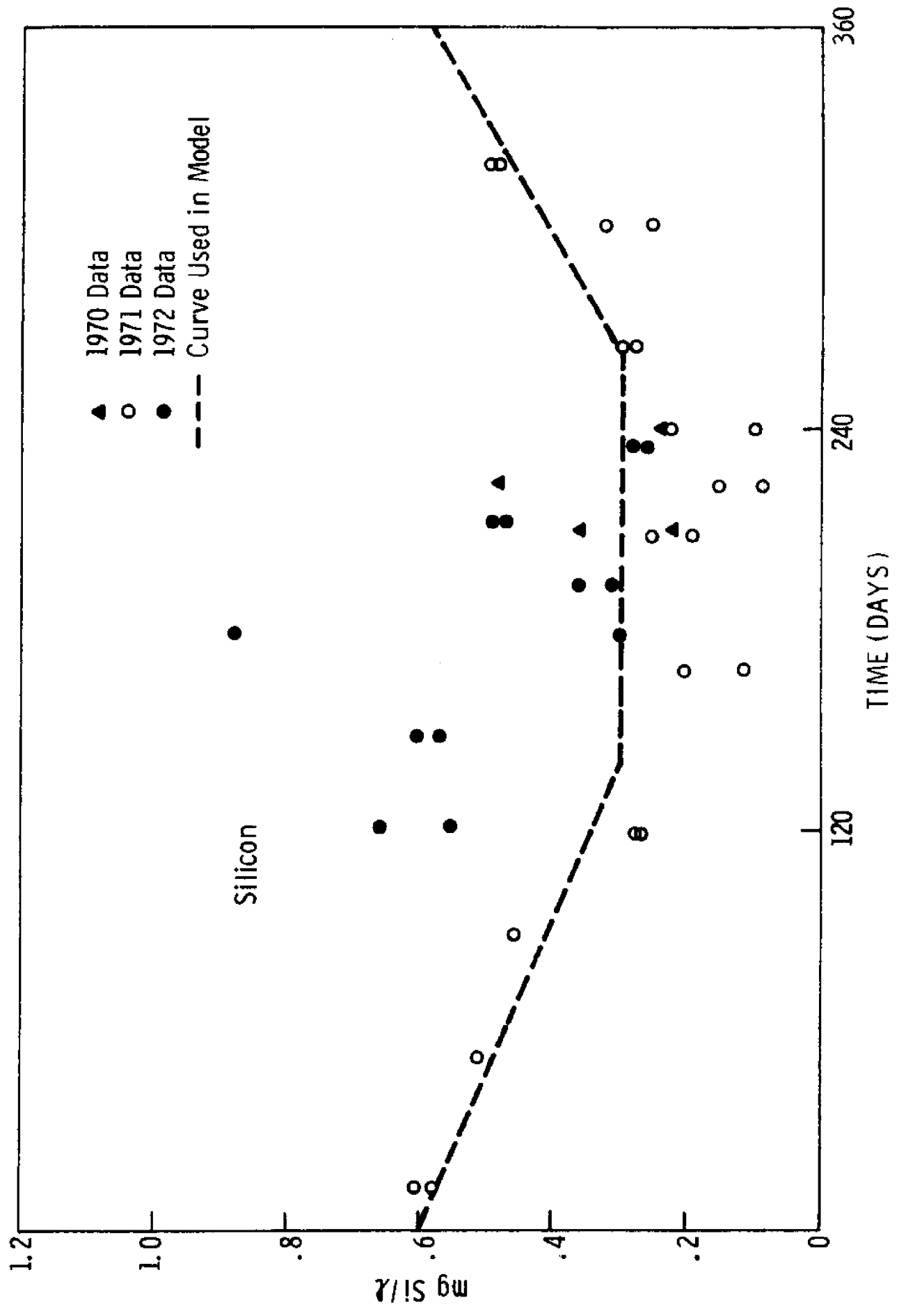


FIGURE 22. SILICON AT BOUNDARY

for a series of time points for which both river concentrations and flow rates were available. The discharge information was obtained from USGS records of discharge rates at the Mayfield gaging station (USGS, 1970, 1971 and 1972), and corrected to represent discharge at the mouth of the river by using a factor determined by Brater (1972). This procedure provided the loading time series shown in Figures 20 through 27.

No measurements of zooplankton concentrations in the Boardman River are available. However, it is believed that the zooplankton contribution from the river is negligible; hence, it is assumed that the zooplankton loading to the system is zero. Similarly, no data were available for non-living organic nitrogen concentrations in the river. However, the Michigan Water Resources Commission has taken some direct measurements of organic N and inorganic N on the river (Water Resources Commission, 1969, 1970, and 1971). These data were used to compute the ratio of organic N to inorganic N. The resulting ratio was then applied to the sum of ammonia and nitrate-nitrite loading. It was thus estimated that the average loading of this component was  $2.607 \times 10^8$  mg N/day.

#### NUMERICAL METHODS

The dynamics of the behavior of the chemical and biological species in the model are obtained by using measured patterns of nutrient inputs from the Boardman River and the upper bay and observed cycles of temperature, solar radiation, photoperiod, and vertical light extinction in the model. Forty eight nonlinear differential equations with time variable coefficients representing the continuity of eight species in



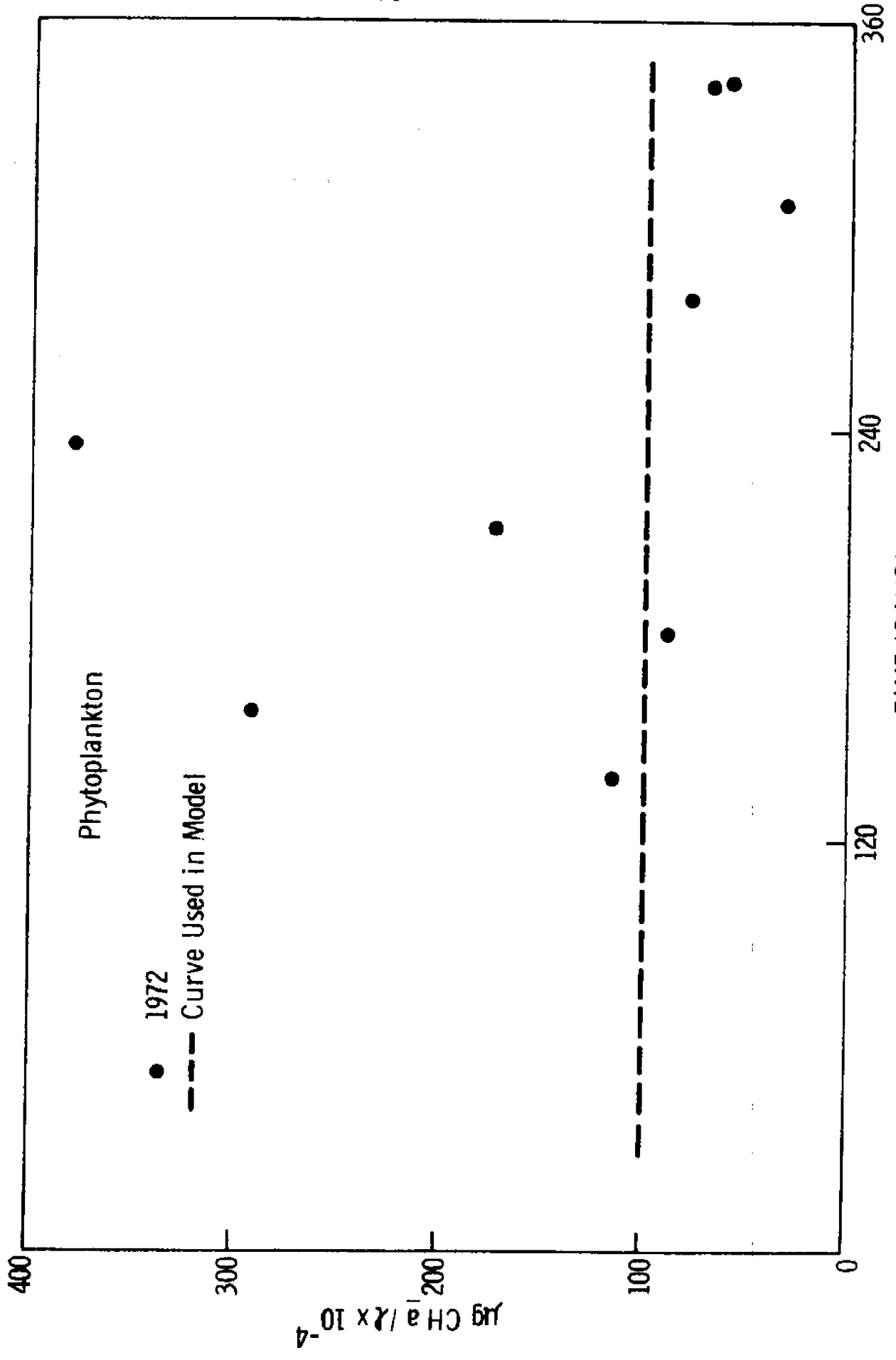


FIGURE 23. PHYTOPLANKTON LOADING

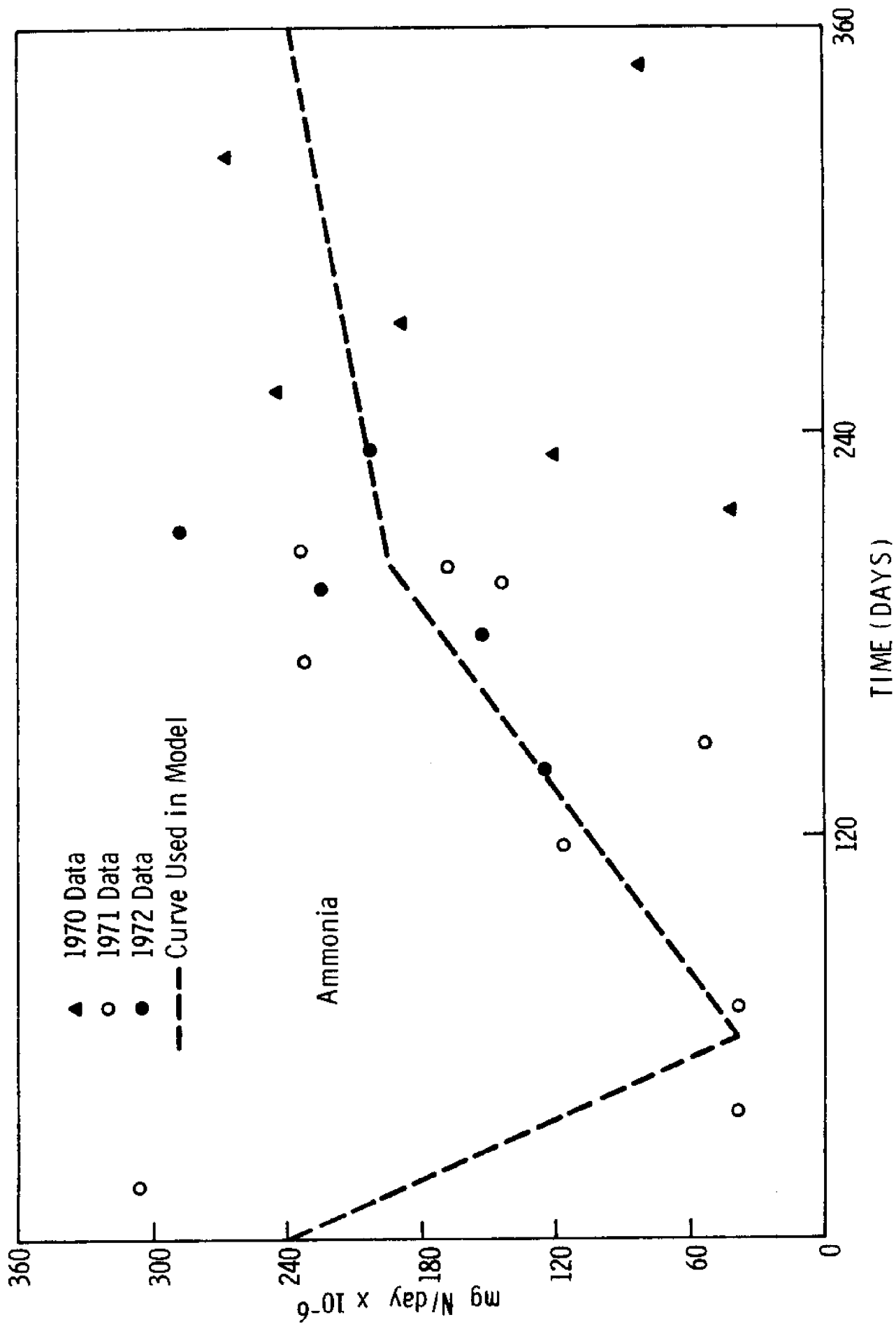


FIGURE 24. AMMONIA LOADING

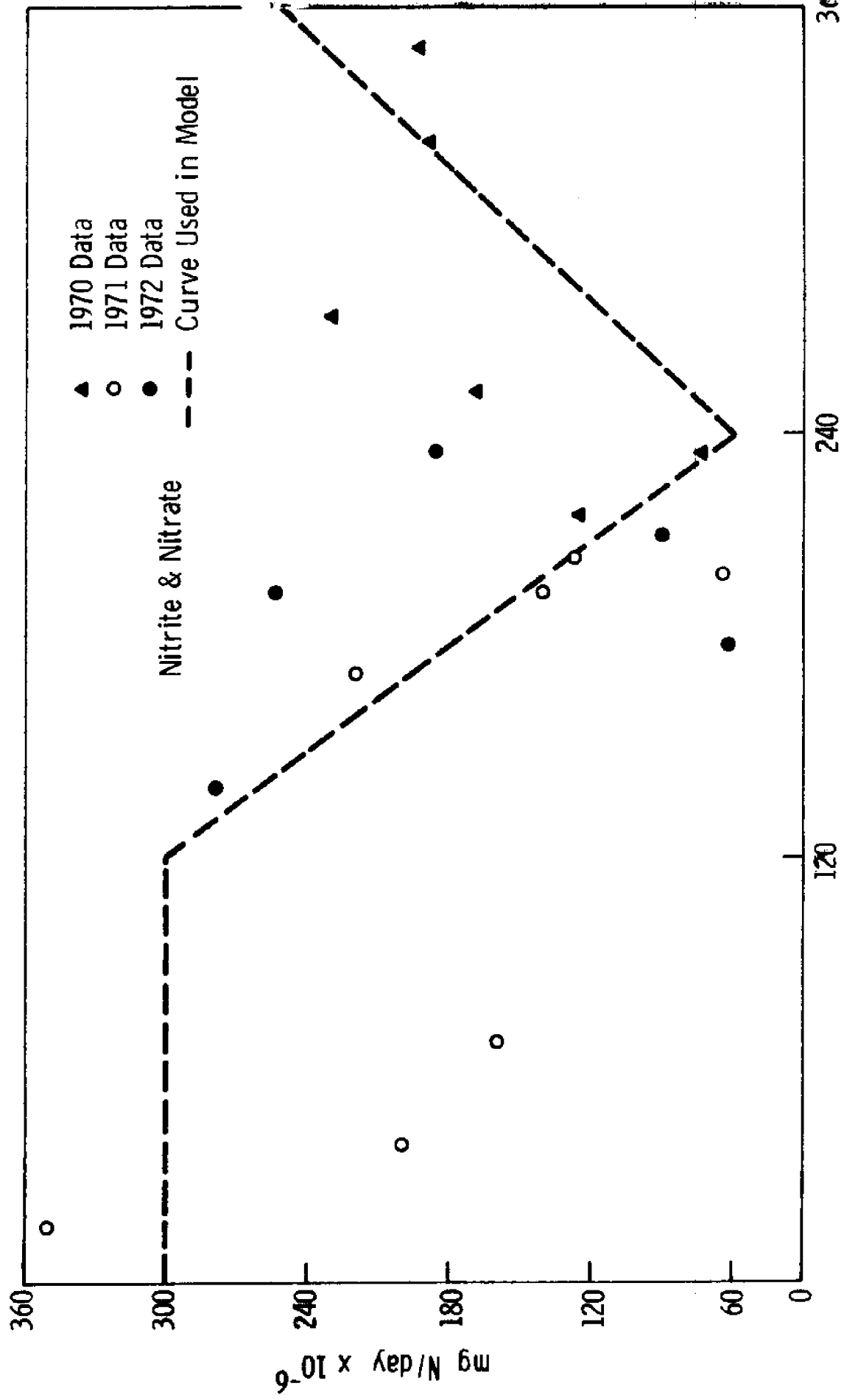


FIGURE 25 NITRITE-NITRATE LOADING

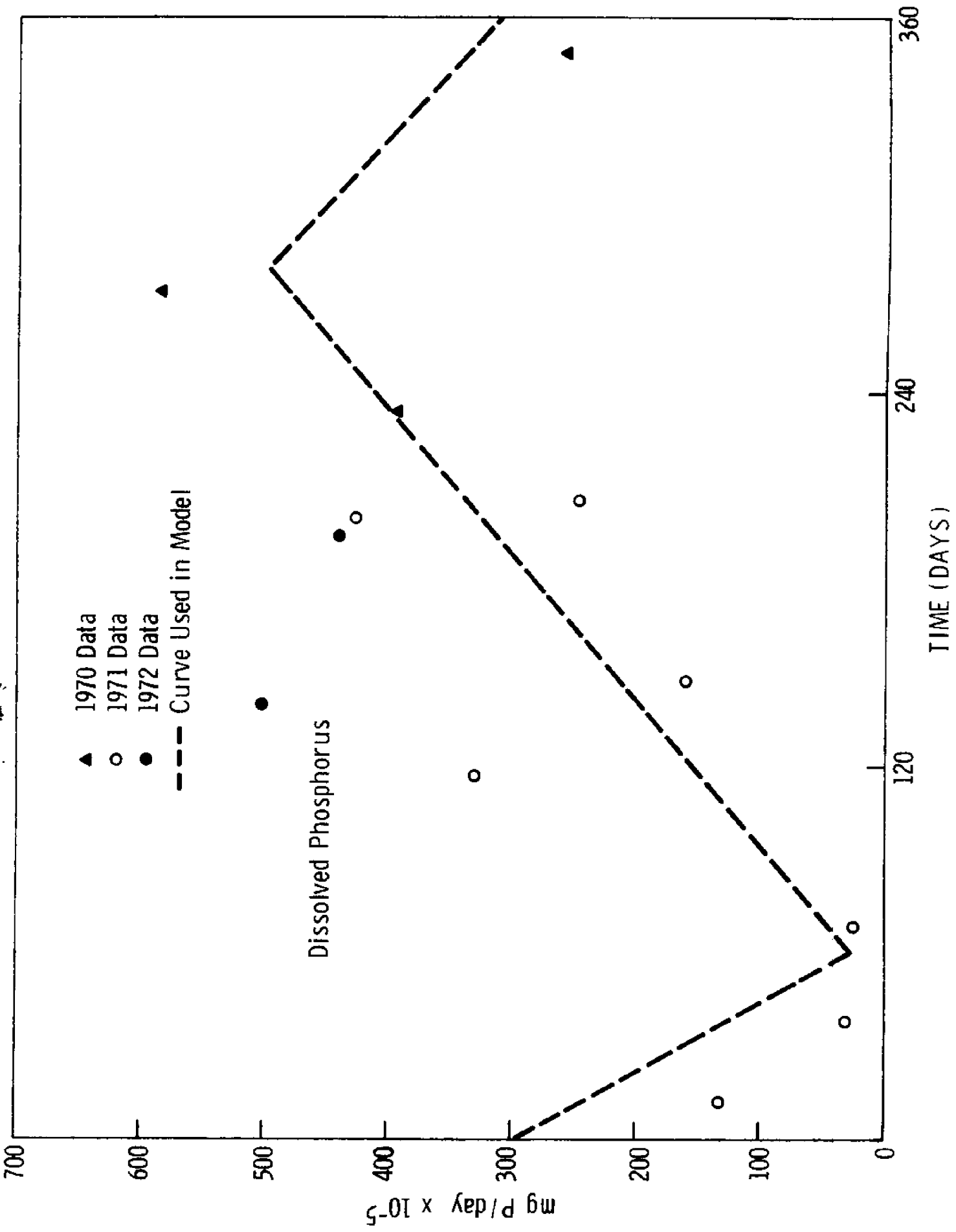


FIGURE 26. DISSOLVED PHOSPHORUS LOADING

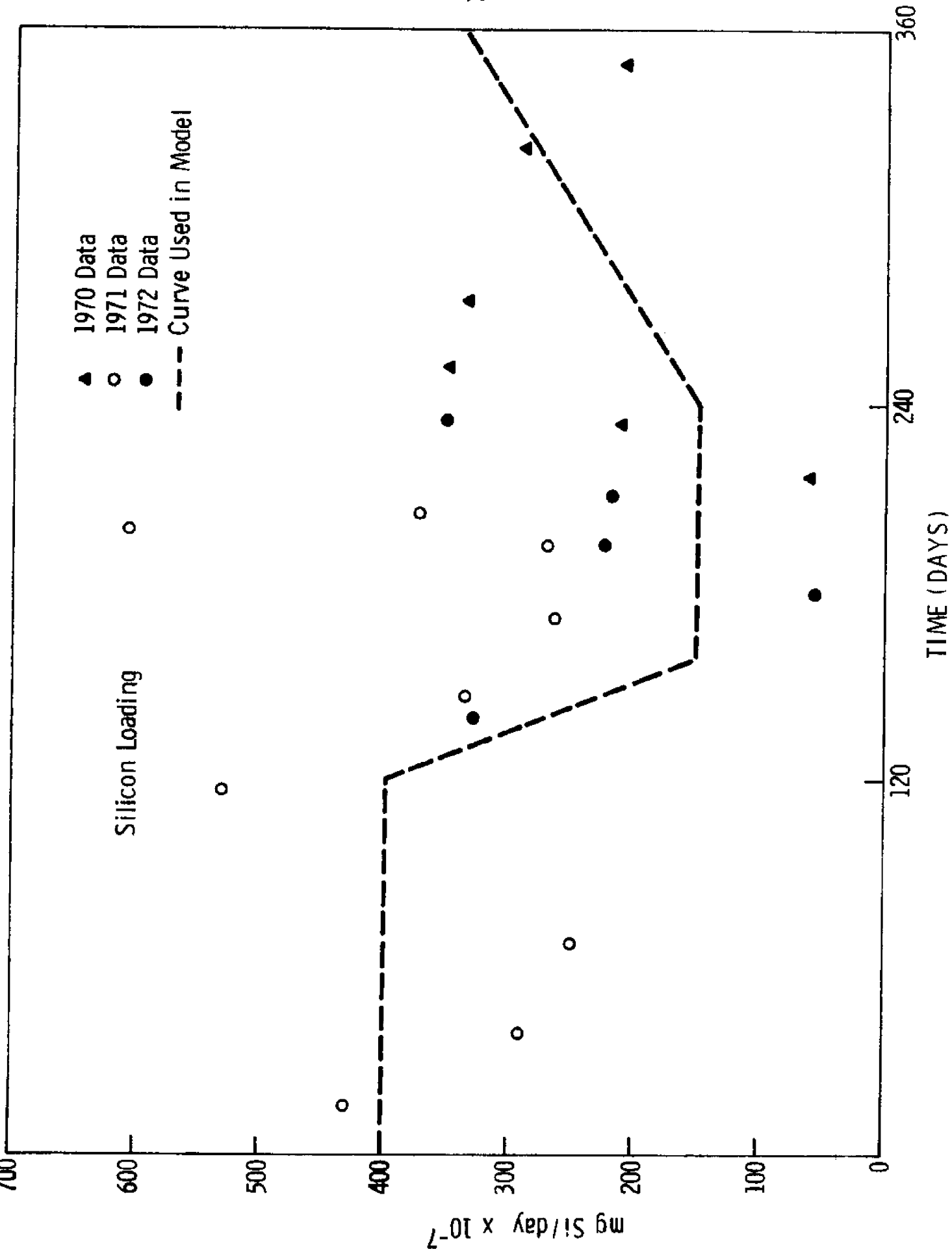


FIGURE 27. SILICON LOADING

six segments have been constructed. These mass continuity equations can be integrated numerically using a number of different numerical integration algorithms. These methods include fourth-order variable step-size Runge-Kutta schemes and variable step-size, variable order predictor-corrector schemes of the Adams type.

Early calculations using the model were performed using a simulation language called CSMP (Continuous Systems Modeling Program). However, this procedure proved to be inefficient and limited because of the large number of differential equations which must be integrated in this case. Subsequent to these efforts, a new software package was developed. This program uses an integrator subroutine available at The University of Michigan called DVDQ. DVDQ uses a variable order variable step-size predictor-corrector algorithm for numerical integration. This method has proven to be very efficient and reliable and has been used to obtain the results presented in the following sections. A more detailed discussion of DVDQ which includes comparisons with other types of integration schemes is presented by Frazho et al. (1973).

A typical run of the model consists of integrating the system of forty-eight equations over a period of one year. This requires the simultaneous use of a linear interpolation subroutine for several time variable functions: the boundary conditions, loads, extinction coefficients, temperature, light, etc. The present form of the model contains 13 such functions. The total cost of a typical run of the model including printing and line plotting the results is approximately \$10.

## MODEL VERIFICATION

The kinetic and stoichiometric coefficients in the biological production model for Grand Traverse Bay have been obtained by examination of the results of controlled laboratory and field investigations, as well as from results reported in the scientific literature. The derivation of these coefficient values have been discussed in detail in an earlier section. Figure 28 shows the model-predicted seasonal cycle of phytoplankton, zooplankton, and nutrients in cell 3 based on average values of model coefficients and average nutrient loading. All the curves shown in Figure 28 represent the expected depth averaged results except for the primary productivity which has been calculated using model predicted results at depths of 2 and 20 meters. The cycles shown in Figure 28 appear reasonable and are in general agreement with field observations. In order to further evaluate the adequacy of the model to reproduce the seasonal variation of the system variables, the solution of the forty-eight differential equations has been compared to depth-averaged field observations taken over a period of two years. In this case, two model predictions have been made using an upper and lower bound on the measured inputs from the Boardman River and the upper bay. Figures 29-35 show a comparison of the model predictions for chlorophyll a, zooplankton, ammonia, nitrate, silicon, soluble phosphorus, primary productivity, and the field data. In Figure 29 some of the data points were calculated from total cell counts, assuming that 1  $\mu\text{g}$  of chlorophyll a/ $\ell$  is equivalent to 1057 cells/ml. This correlation was derived by comparing data from

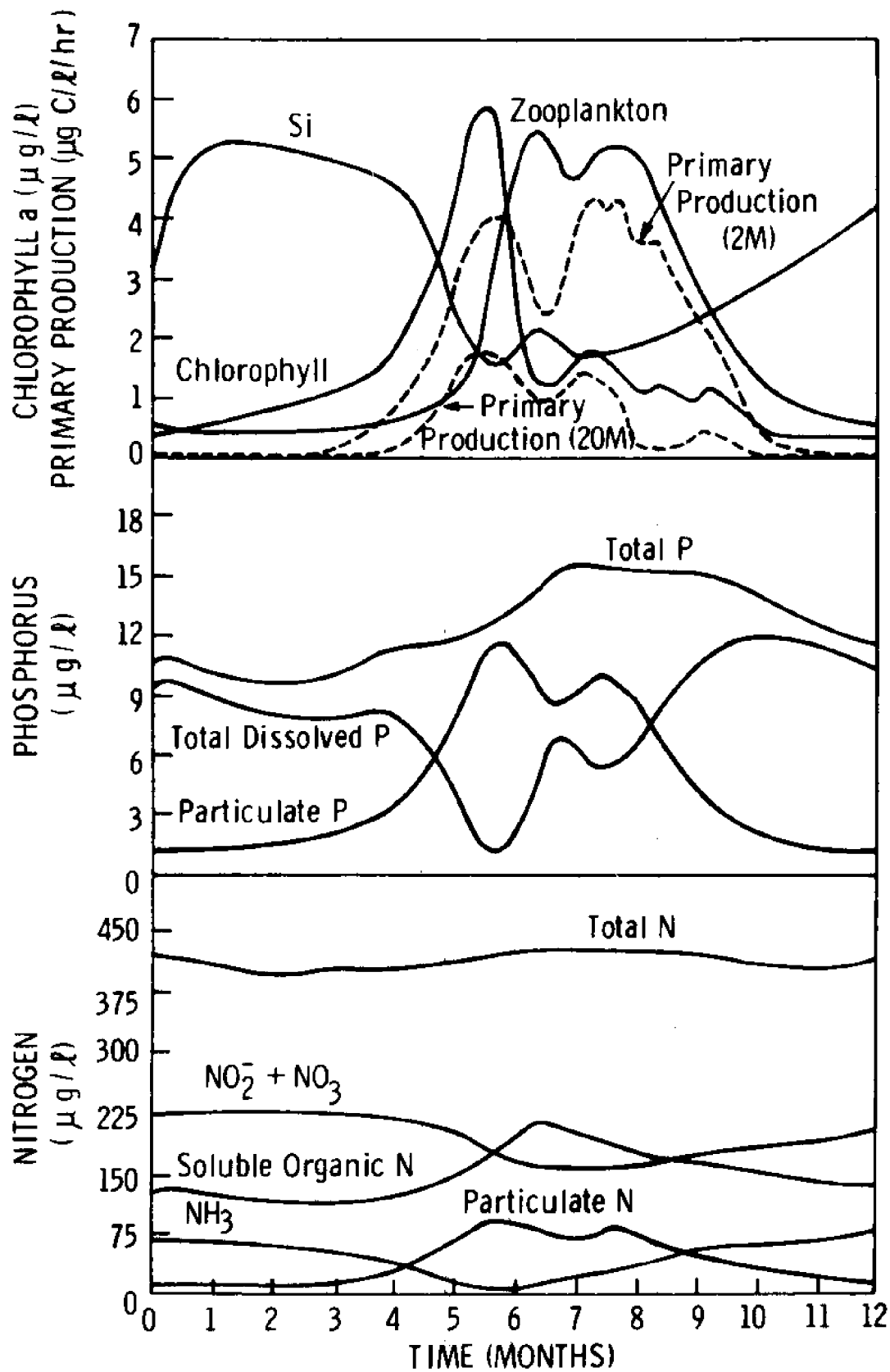


FIGURE 28. MODEL CALCULATION OF AVERAGE CONDITIONS IN CELL 3



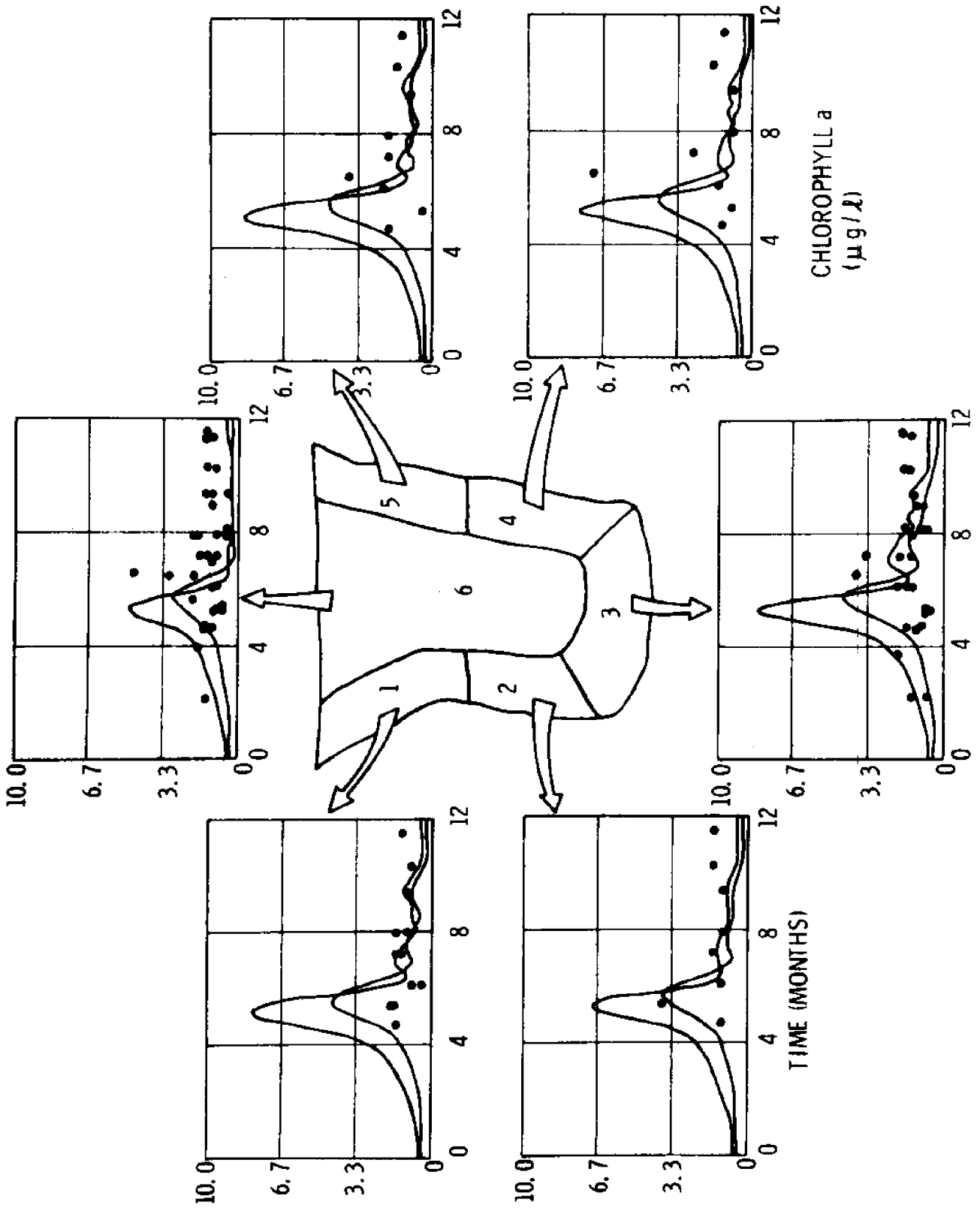


FIGURE 29. MODEL CALCULATIONS FOR CHLOROPHYLL A

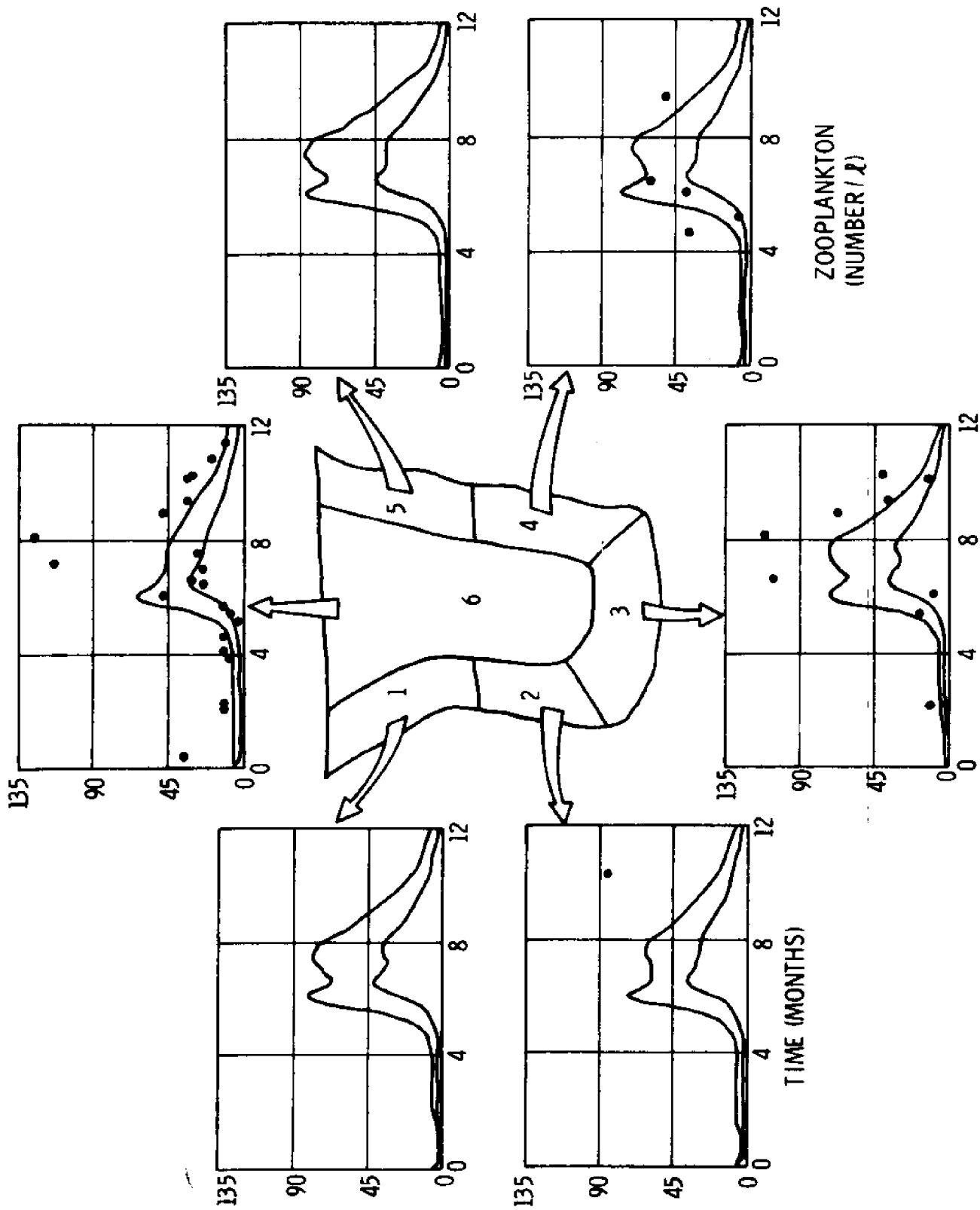


FIGURE 30. MODEL CALCULATIONS FOR ZOOPLANKTON

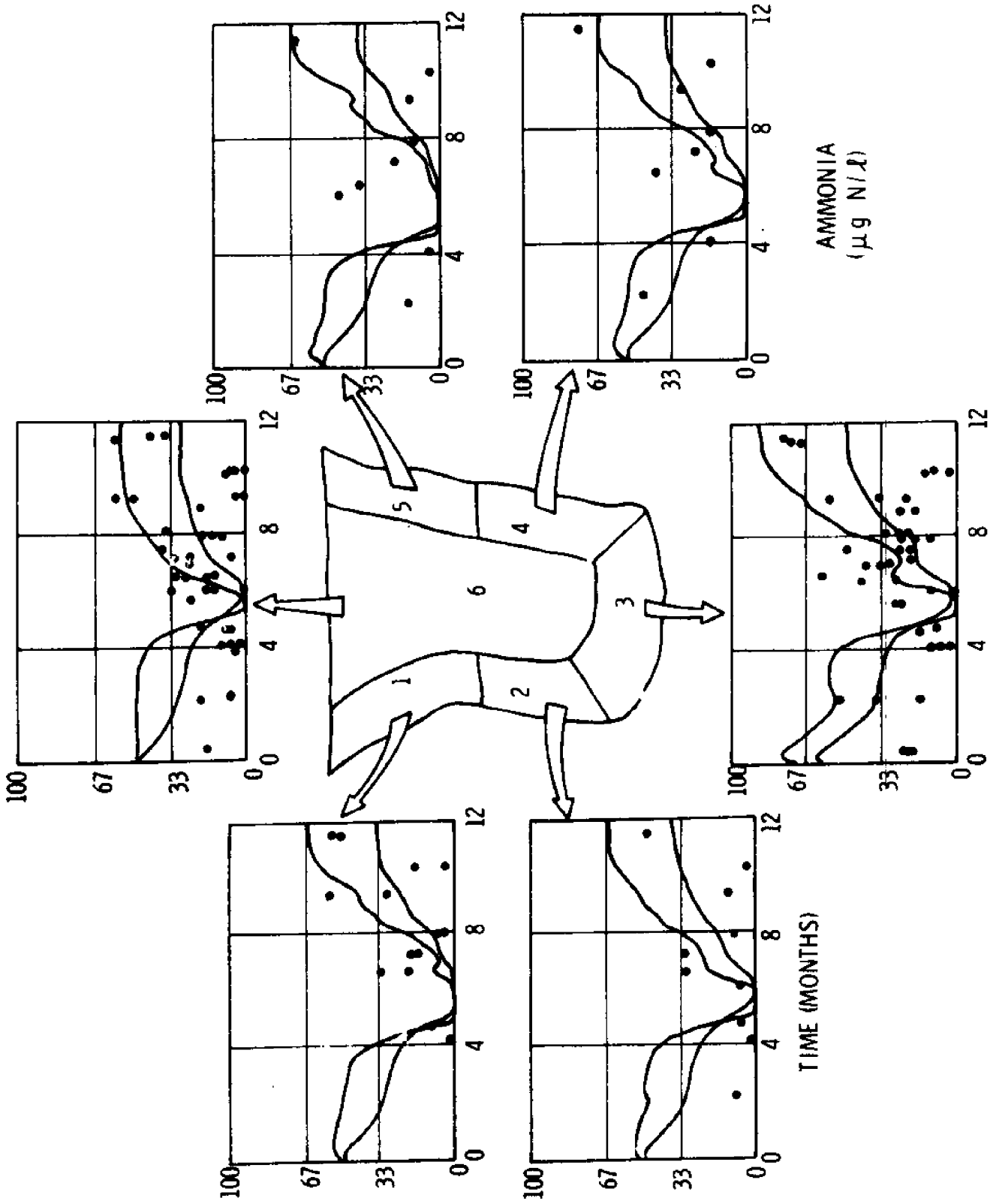


FIGURE 31. MODEL CALCULATIONS FOR AMMONIA

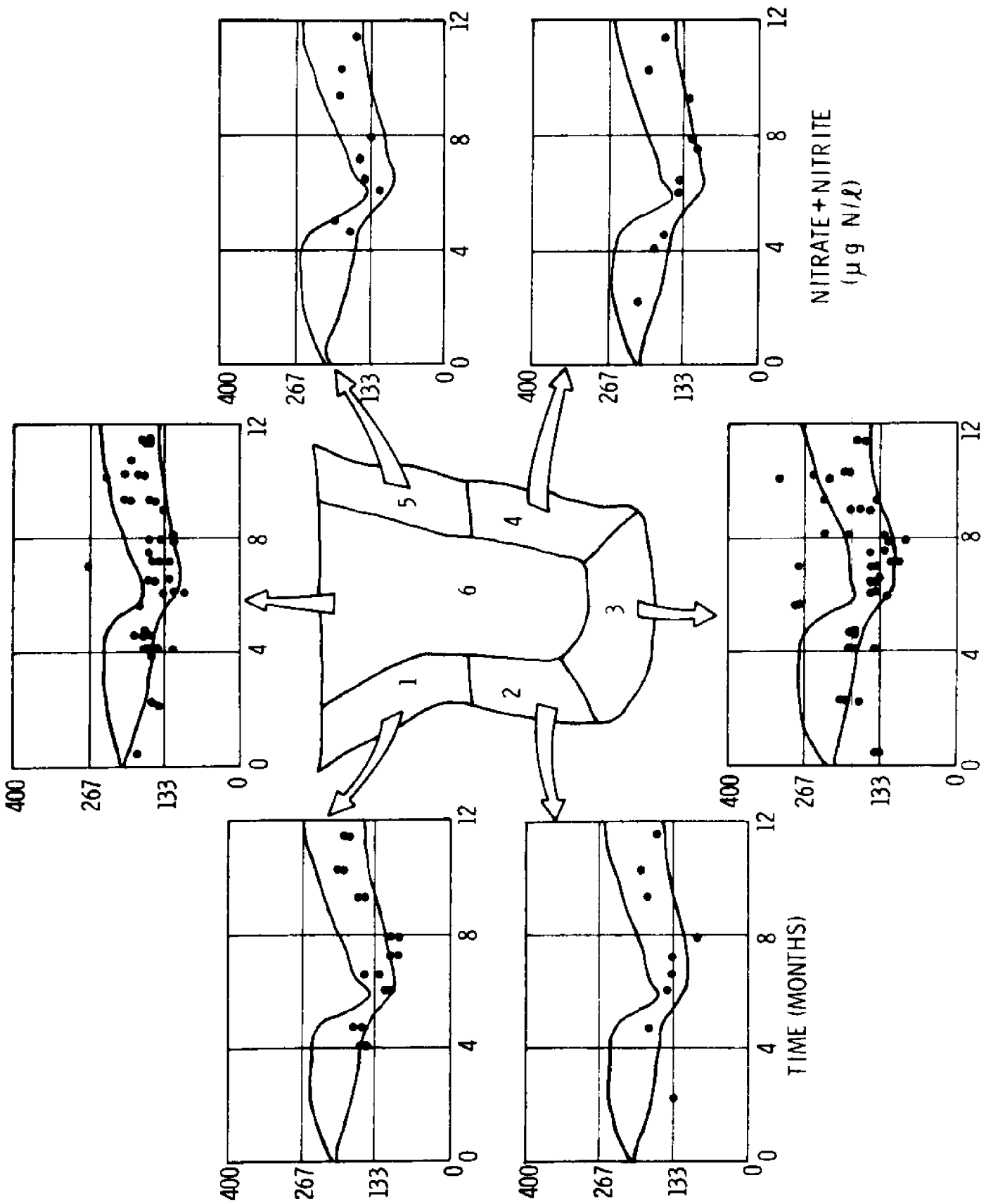


FIGURE 32. MODEL CALCULATIONS FOR NITRATE+NITRITE

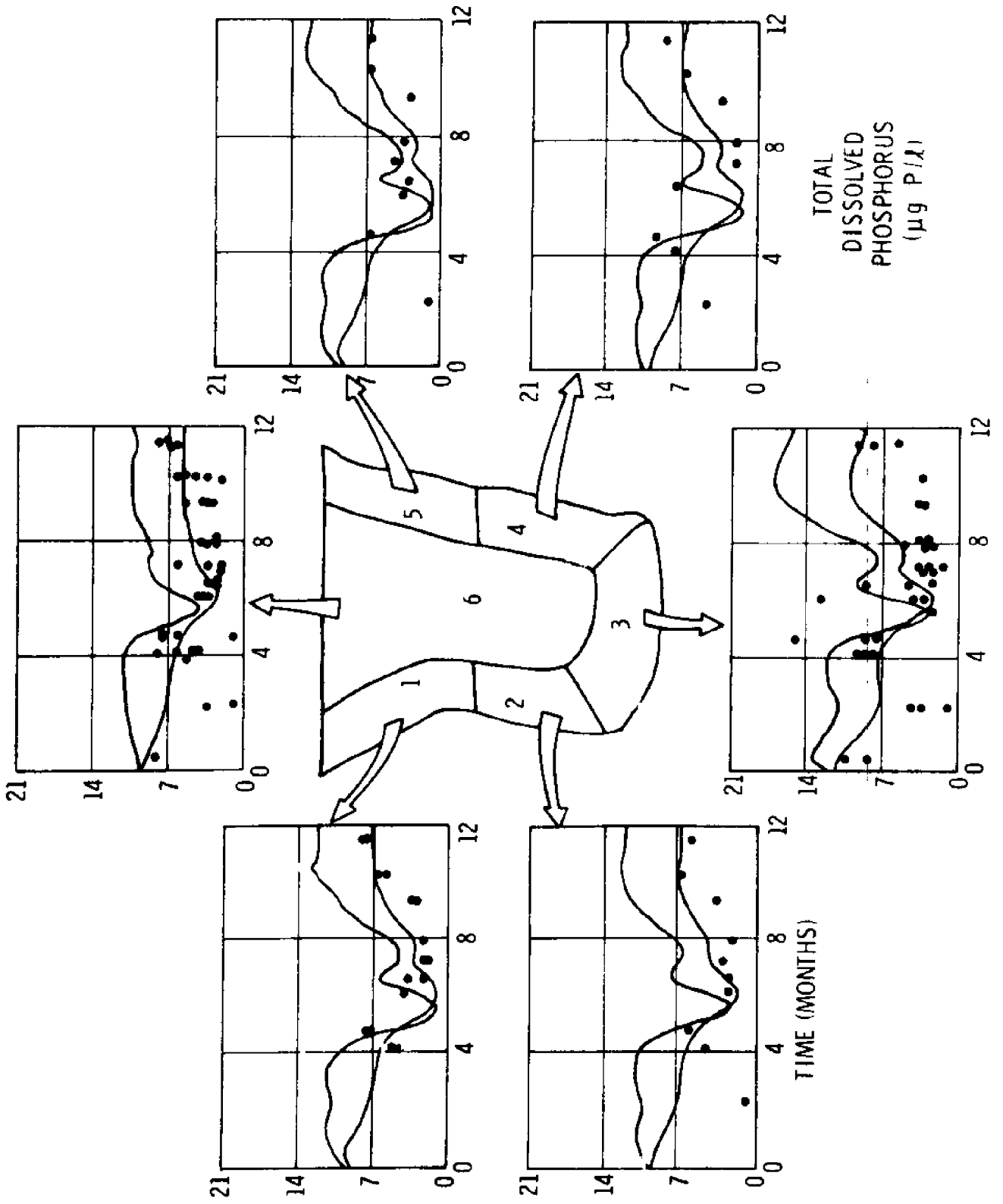


FIGURE 33. MODEL CALCULATIONS FOR DISSOLVED PHOSPHORUS

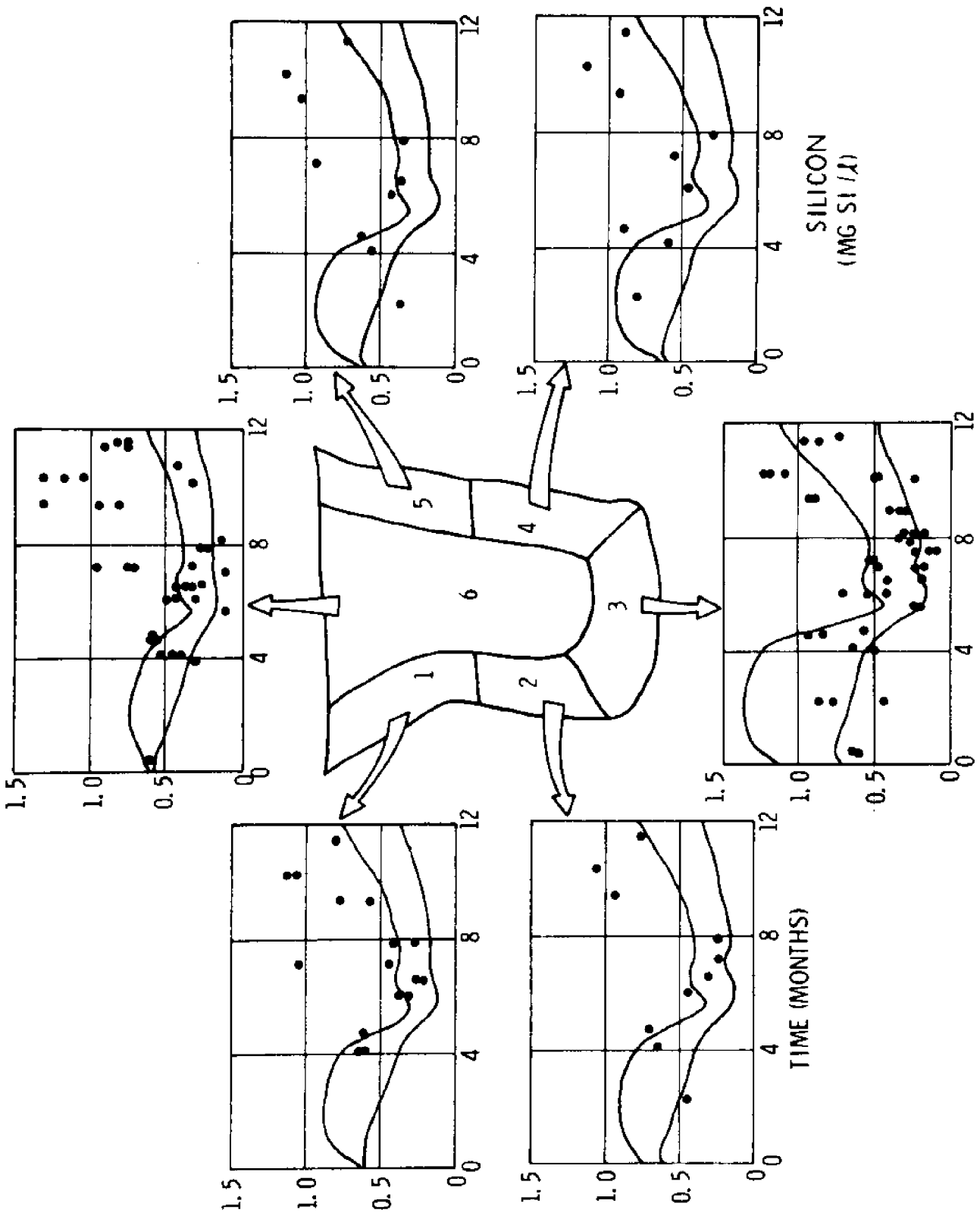


FIGURE 34. MODEL CALCULATIONS FOR SILICON

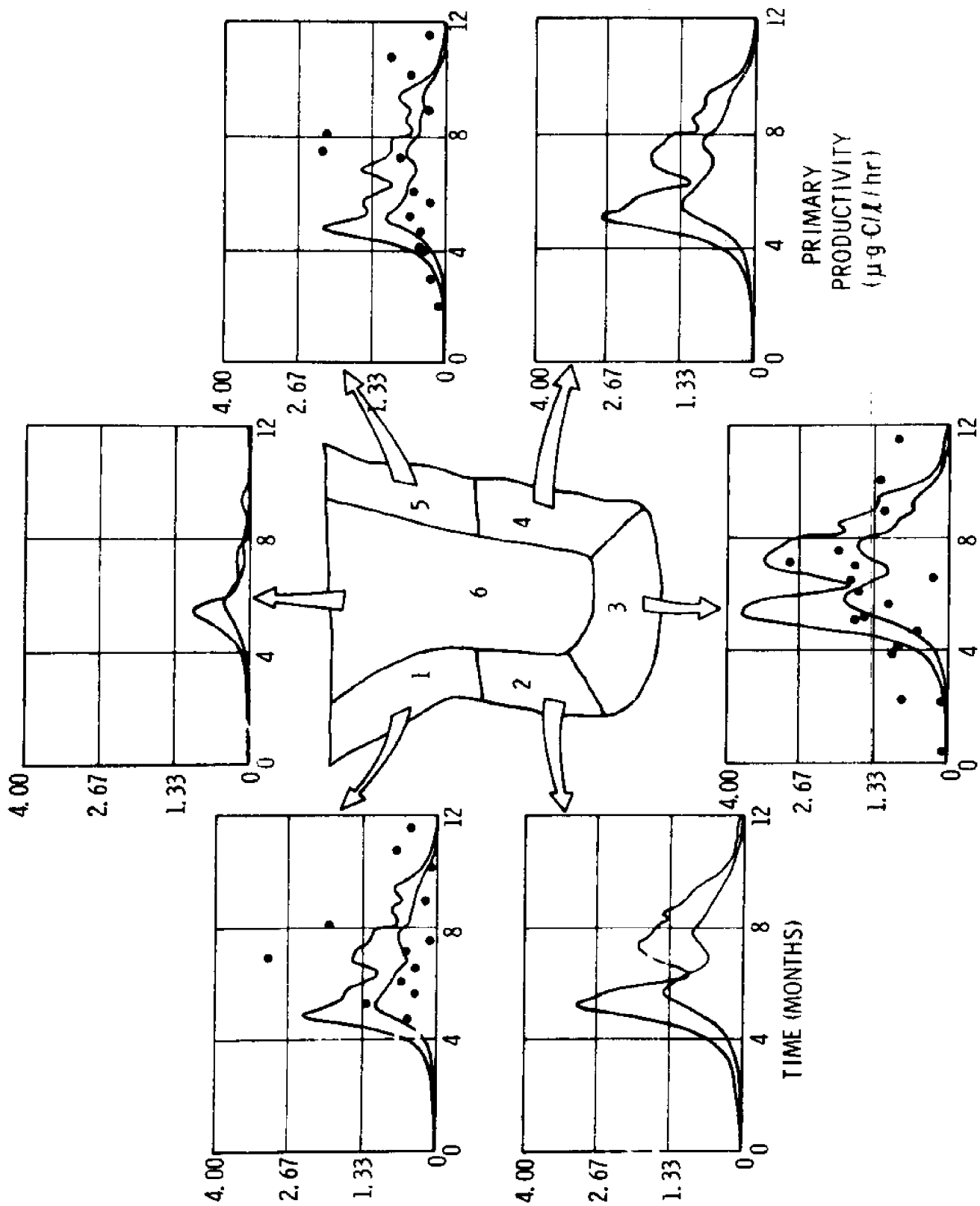


FIGURE 35. MODEL CALCULATIONS FOR DEPTH AVERAGED PRIMARY PRODUCTIVITY

samples where both chlorophyll a and total cell count information were available. In Figure 30 the model calculations are compared with zooplankton numbers by assuming that 188 organisms are equivalent to 1 milligram of dry weight. This conversion was obtained by direct measurements and confirmed through knowledge of the weight of individual species and the composition of the community. Figures 36 and 37 show predicted values of organic and particulate nitrogen. Comparison with actual data is not possible since the parameters are not being measured in the field program.

Although the model does not exactly fit all the data presented in Figures 29-35, the general agreement between the level and trend of the data and the model is encouraging. It is not possible to completely explain the deviation between the model and certain data points. Some of the deviation is undoubtedly due to analytical errors or the natural heterogeneity of the system, since in some cases several nearby stations were compared with the same model output. Some deviation between the model and the data could result from the adaption of inappropriate parameter values. However, no attempt was made to use formal search techniques for optimum parameter values. Differences between the model and the data arise as a consequence of the need to time average inputs on a seasonal basis. Thus, short-term fluctuations due to phenomena such as variable cloud cover, rainfalls, and circulation transients are not accounted for in the model.

Although an initial verification of the model has been achieved, it seems obvious that more careful testing of the



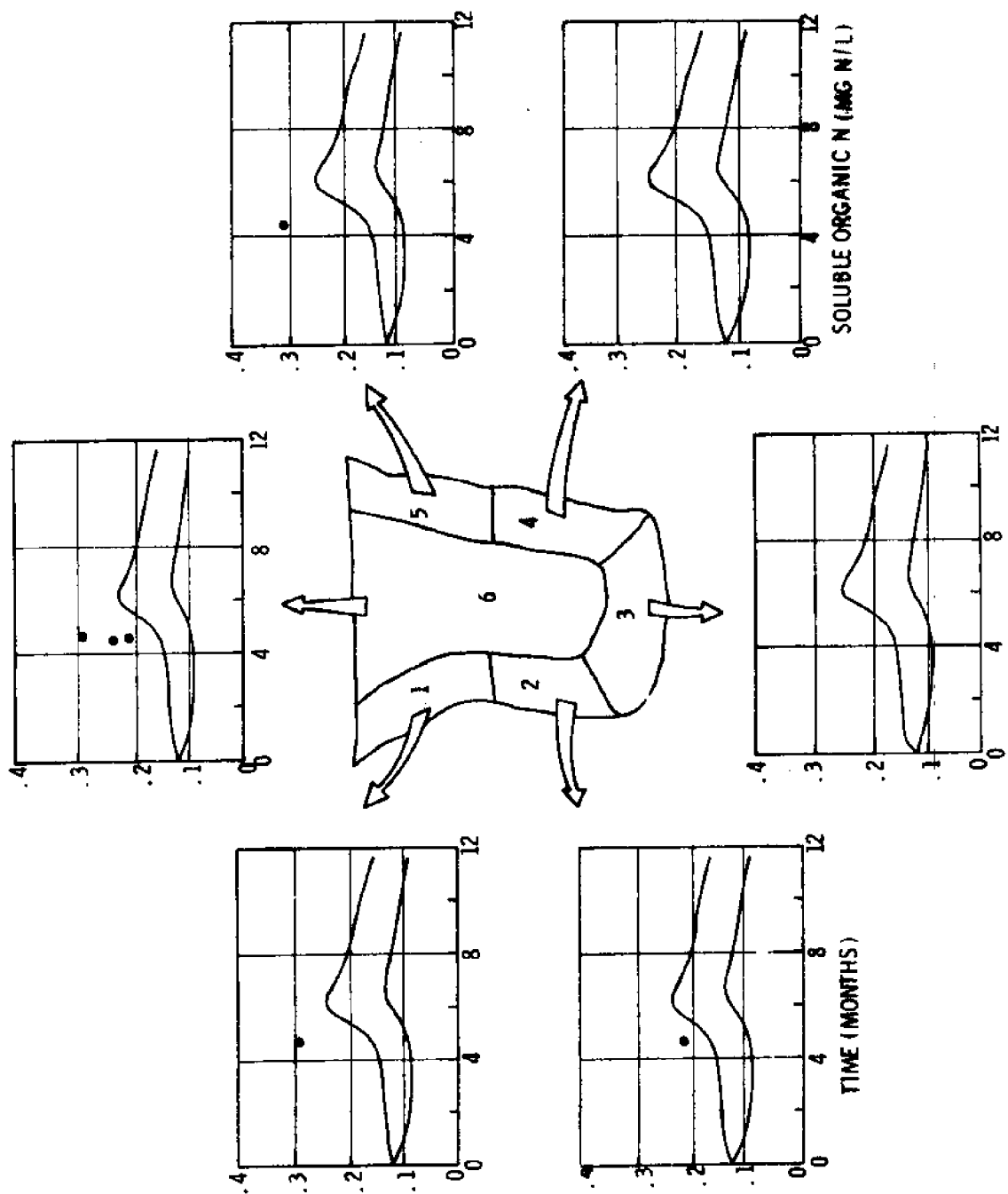


FIGURE 36. MODEL CALCULATIONS FOR PARTICULATE NITROGEN

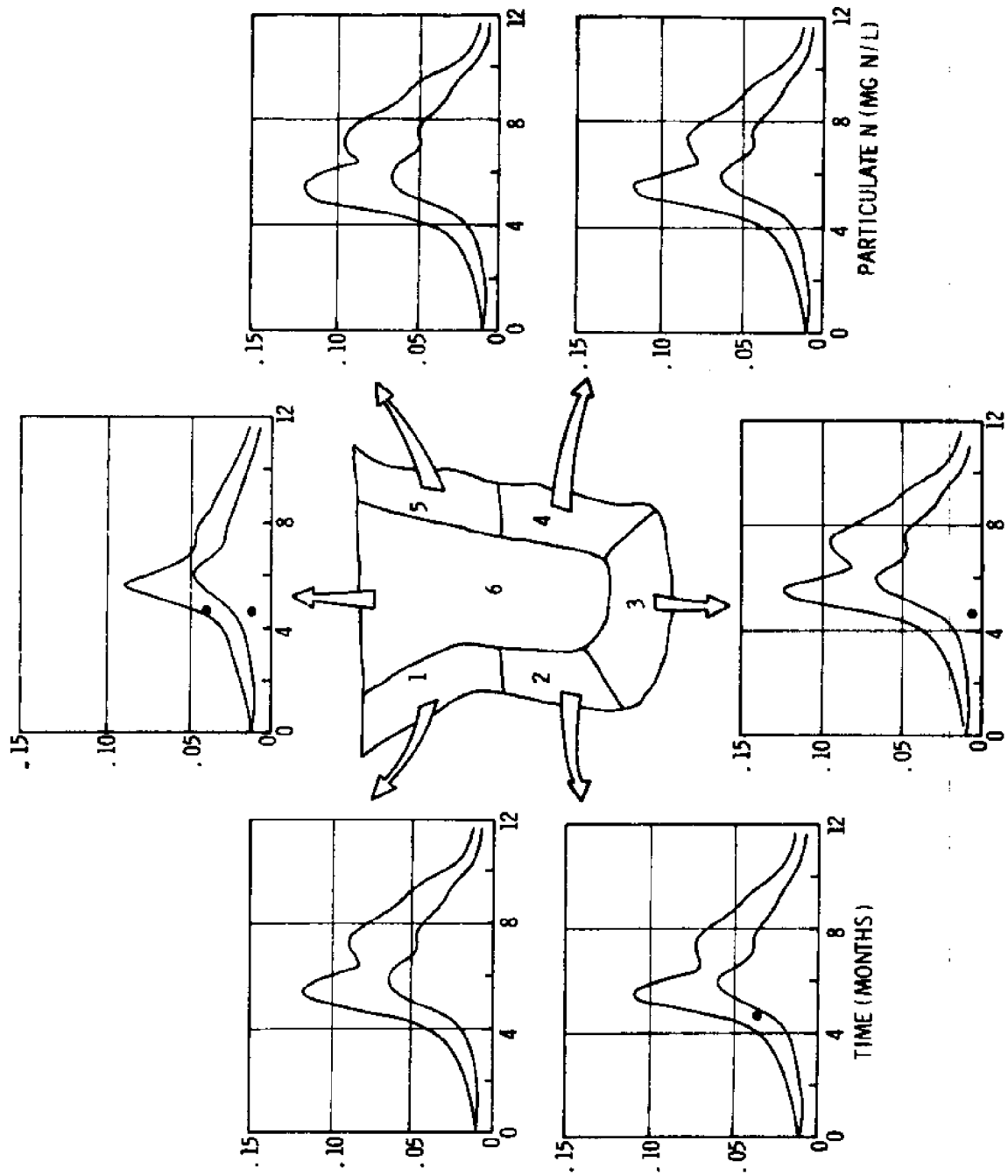


FIGURE 37. MODEL CALCULATIONS FOR SOLUBLE ORGANIC NITROGEN

mathematical predictions will require a more extensive field observation program. During the spring and summer of 1973, it is planned to sample eight bay water stations and the input to the bay every three to four days. This expanded field program should guide the addition of further refinements to the model.

#### APPLICATION

The verified model has been used to predict the effects of population growth and phosphorus removal on the quality of water in the bay. Five cases have been compared with present conditions. The first example assumes stable population, industrial and agricultural activity, and a 90% decrease in phosphorus inputs due to more stringent control. The next case assumes that cultural activities result in a doubling of the nutrient loading to the bay. Example 3 assumes no phosphorus removal, while case 4 assumes 80% phosphorus removal. The fourth and fifth examples assume an increase in residential population from 22,000 to 88,000, a twofold increase in the recreational and industrial activity, and a stable agricultural production. The pollutional effects of these expansions are examined under conditions with 80% phosphorus removal and without phosphorus input controls. The loadings associated with these cases, as used in the calculations, are illustrated in Figures 38-41.<sup>2</sup>

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<sup>2</sup>Personal Communication, Professor R.L. Patterson, School of Natural Resources, University of Michigan

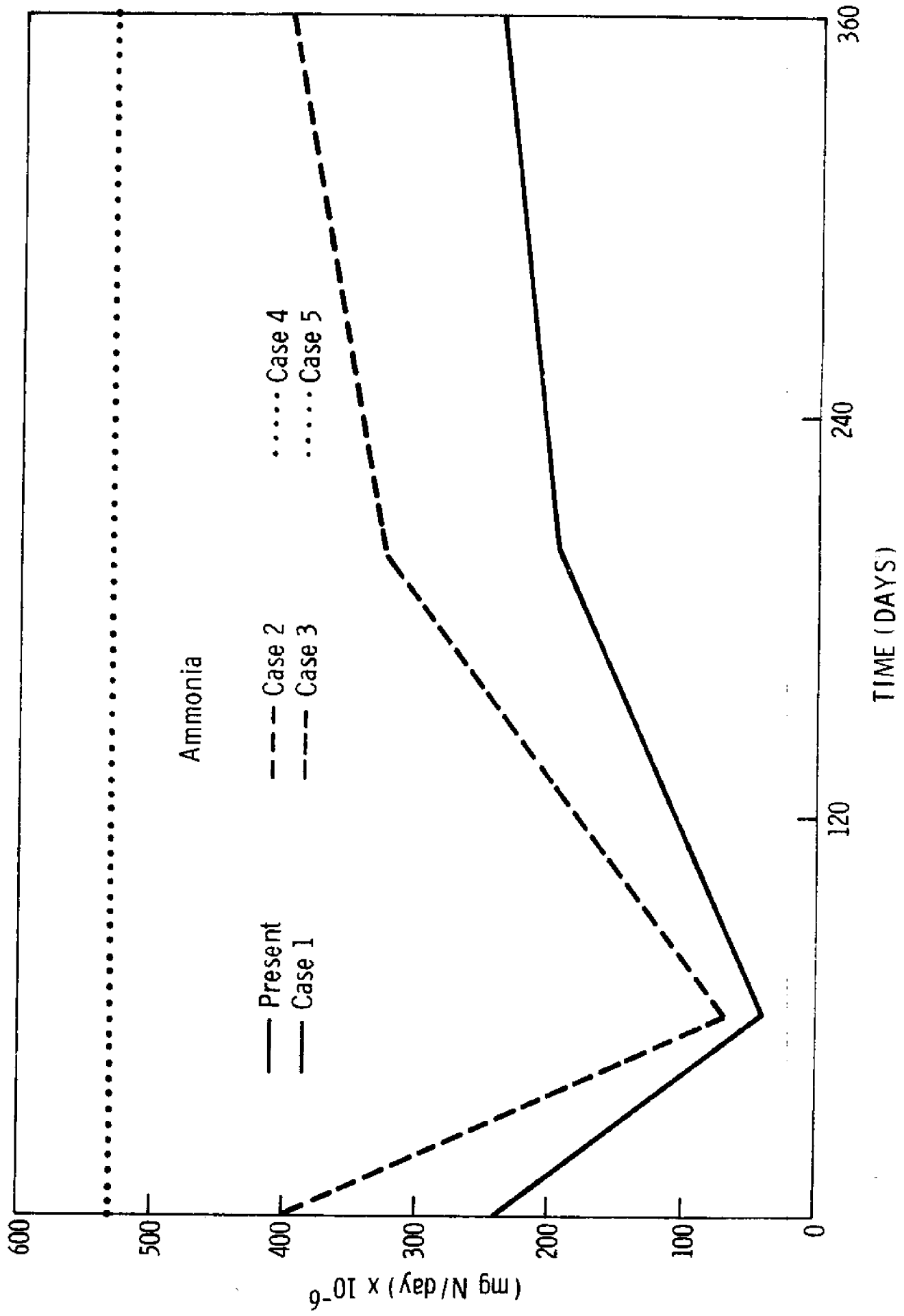


FIGURE 38. PROJECTED AMMONIA LOADING

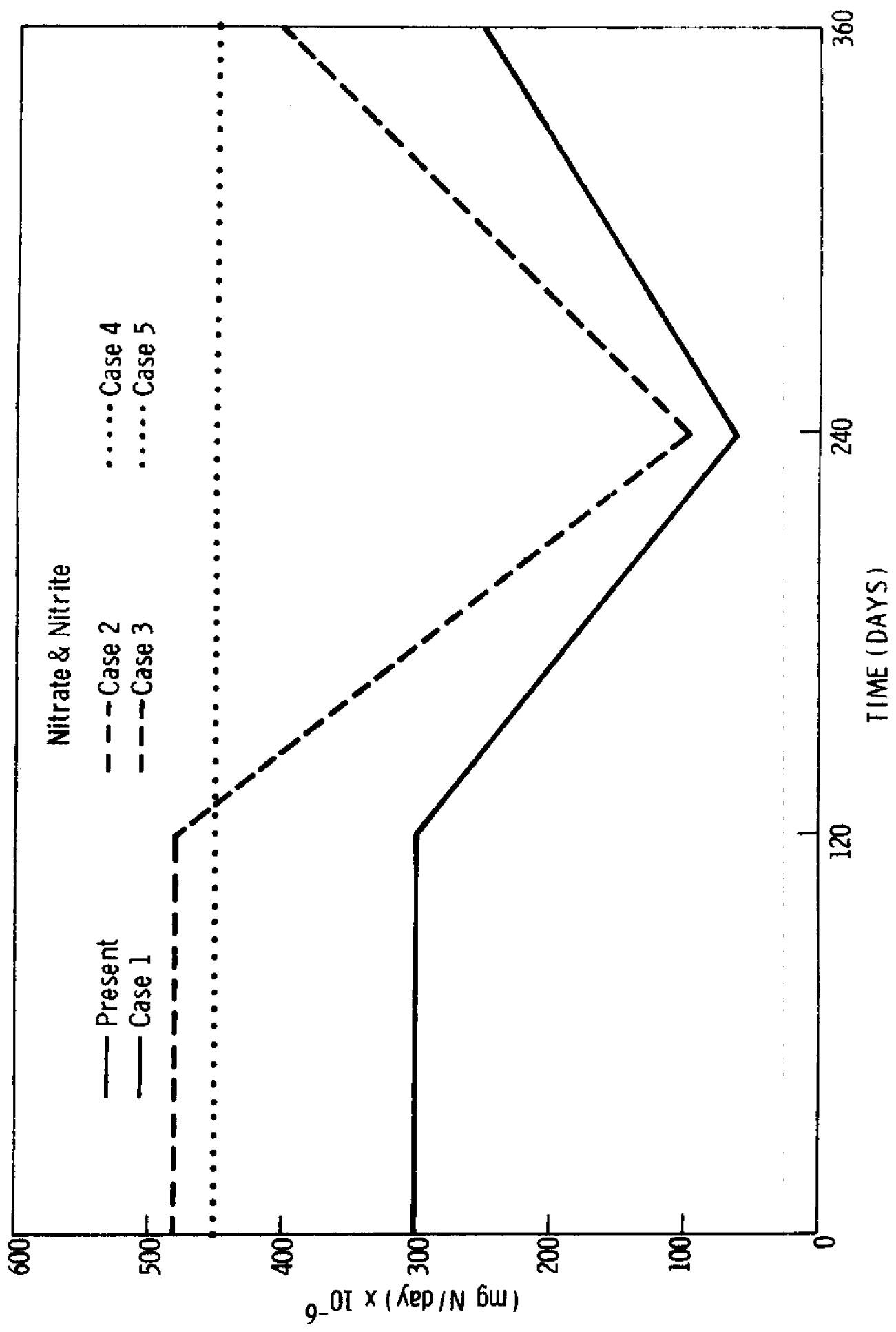


FIGURE 39. PROJECTED NITRATE + NITRITE LOADING

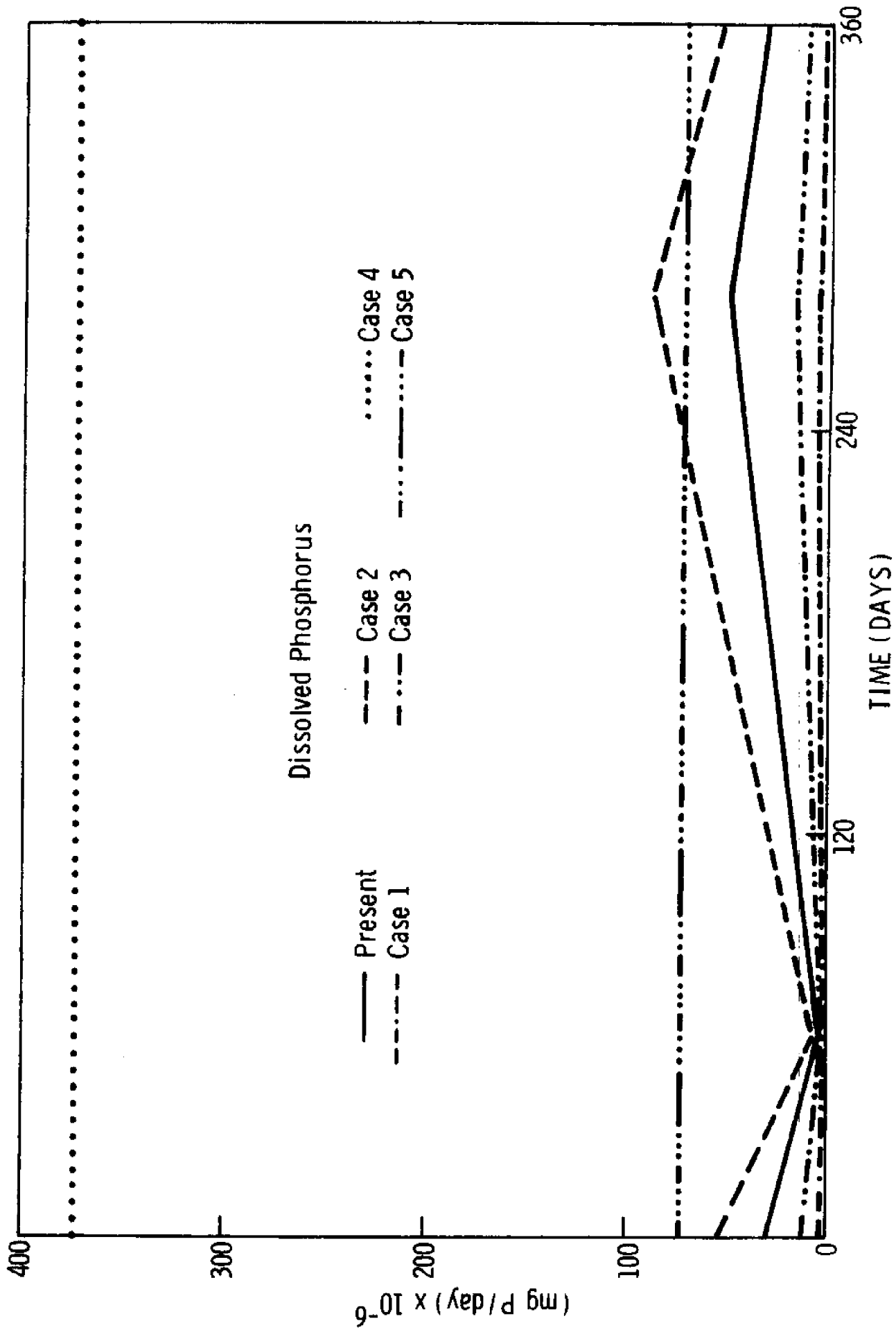


FIGURE 40. PROJECTED DISSOLVED PHOSPHORUS LOADING

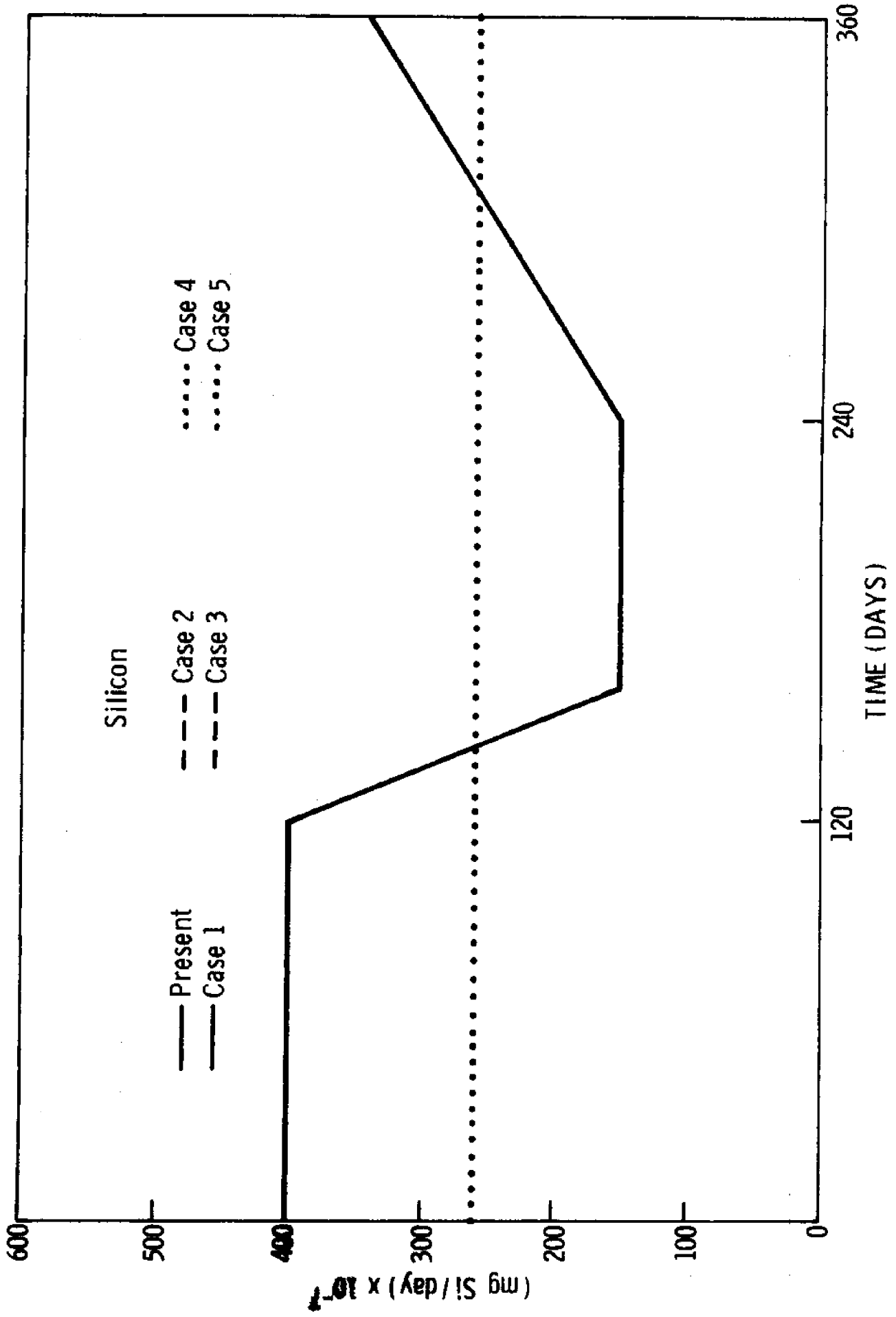


FIGURE 41. PROJECTED SILICON LOADING

The predicted populations of phytoplankton and zooplankton expected after 90% phosphorus removal are only slightly lower than the populations observed in the bay. These results reflect the fact that the major source of nutrients to the lower part of the west arm of the bay is the upper bay rather than the Boardman River. The calculations, assuming case 3 and case 4, gave results similar to present conditions without treatment. However, as the river loads increase approximately fourfold, these inputs become more significant, resulting in approximately twofold increases in the peak plankton populations. This effect is illustrated in Figures 42-46. The nonlinear relation between cultural nutrient inputs and plankton populations is an unanticipated result as suggested by the model and is expected to be a unique characteristic for a given natural water body. All five cases assume that conditions outside the system, as represented by the boundary concentrations, do not change. Thus the plankton results predicted could be higher if the other parts of Lake Michigan were to become more contaminated.

Figure 43 shows the expected seasonal patterns of soluble phosphorus and silicon. It is interesting to note that at the highest loading the silicon becomes growth limiting for diatoms, resulting in high residual phosphorus levels. This situation, of course, would not persist in the Bay. Rather, the silicon limitation would lead to a shift in the species composition of the phytoplankton from diatoms to greens and blue-greens. Similar species changes due to silicon limitation have been reported by Schelske and Stoermer (1972) in lower Lake Michigan. This species shift would result in more complete utilization of



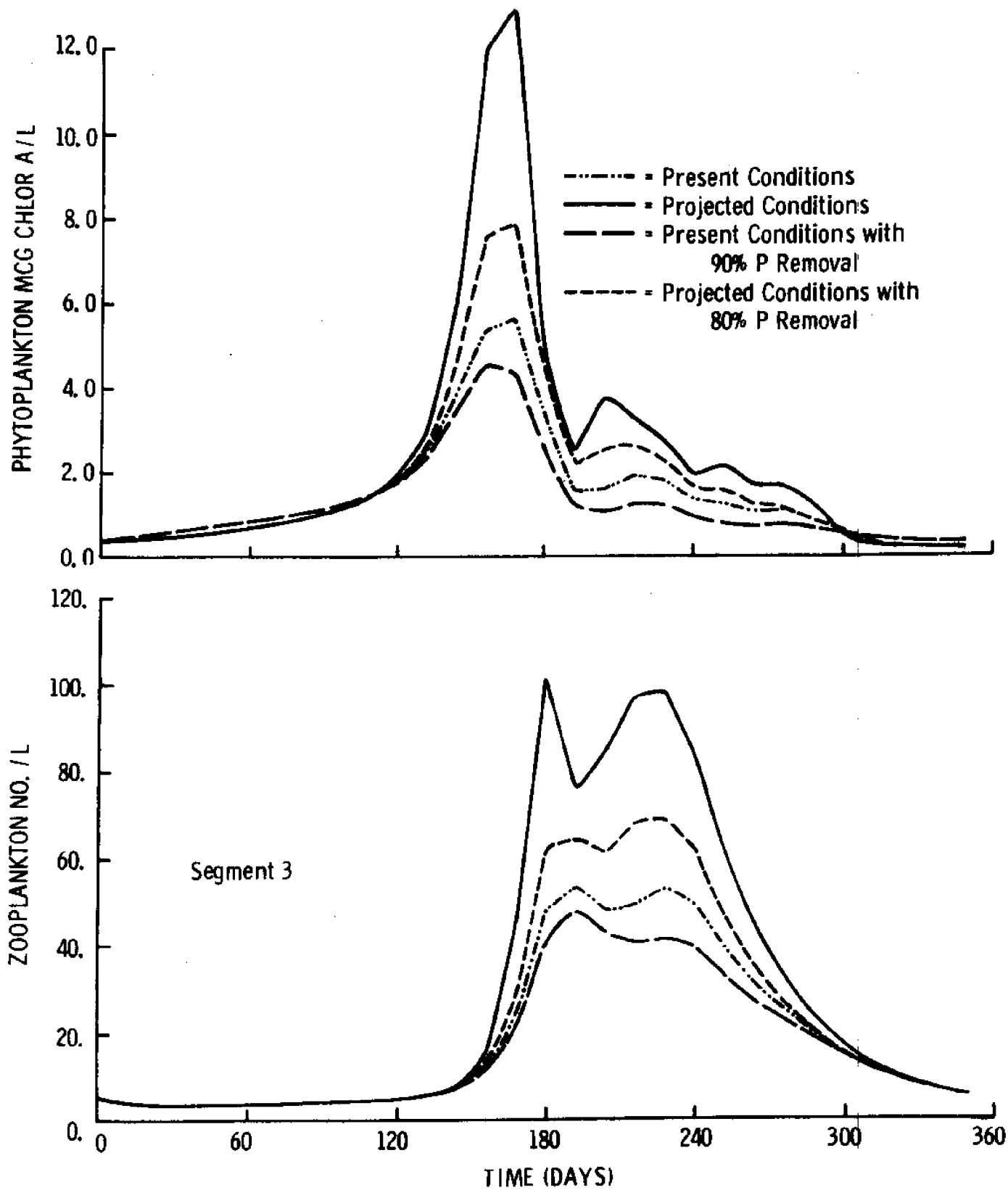


FIGURE 42. MODEL CALCULATIONS FOR PHYTOPLANKTON AND ZOOPLANKTON

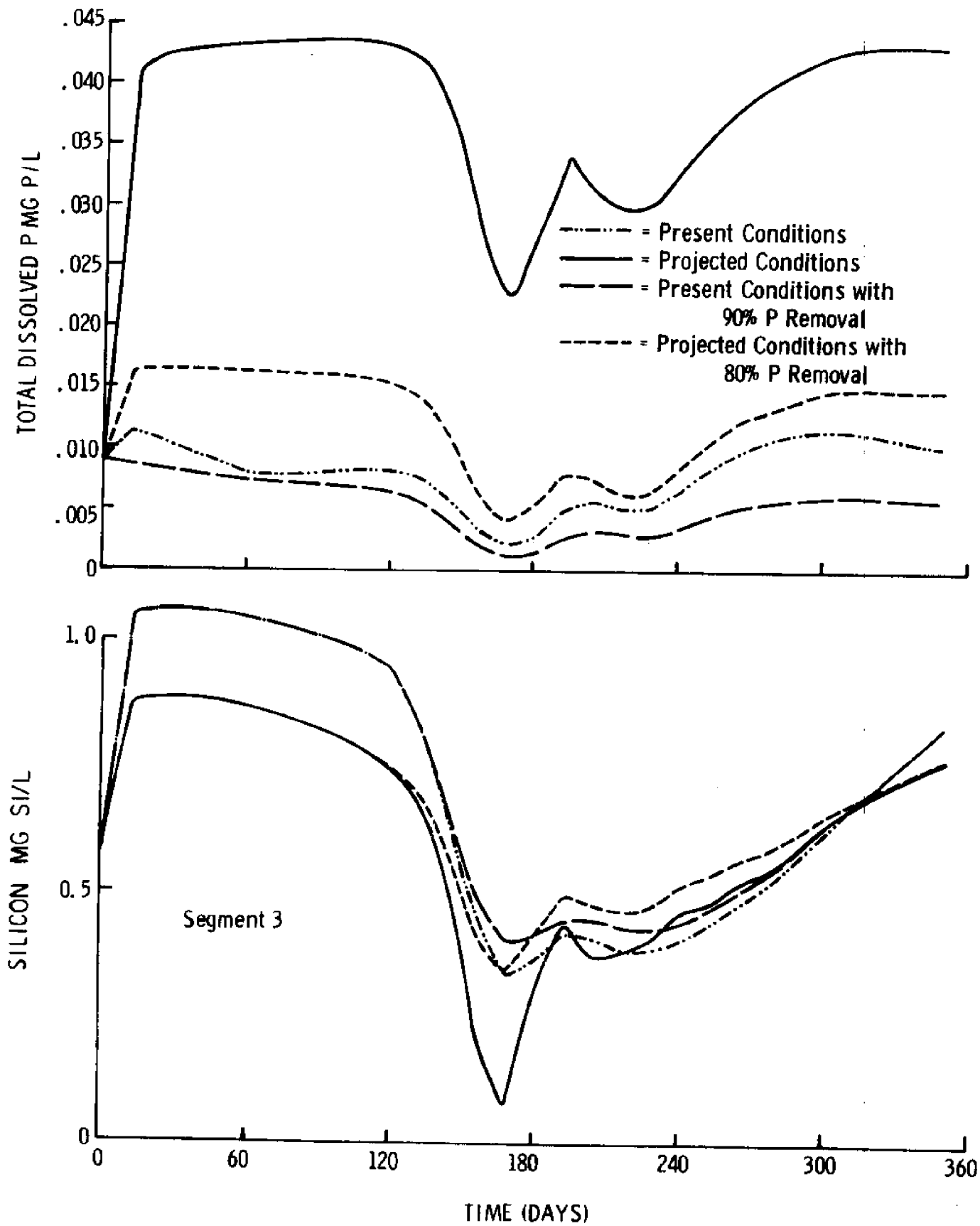


FIGURE 43. MODEL CALCULATIONS FOR DISSOLVED PHOSPHORUS AND SILICON

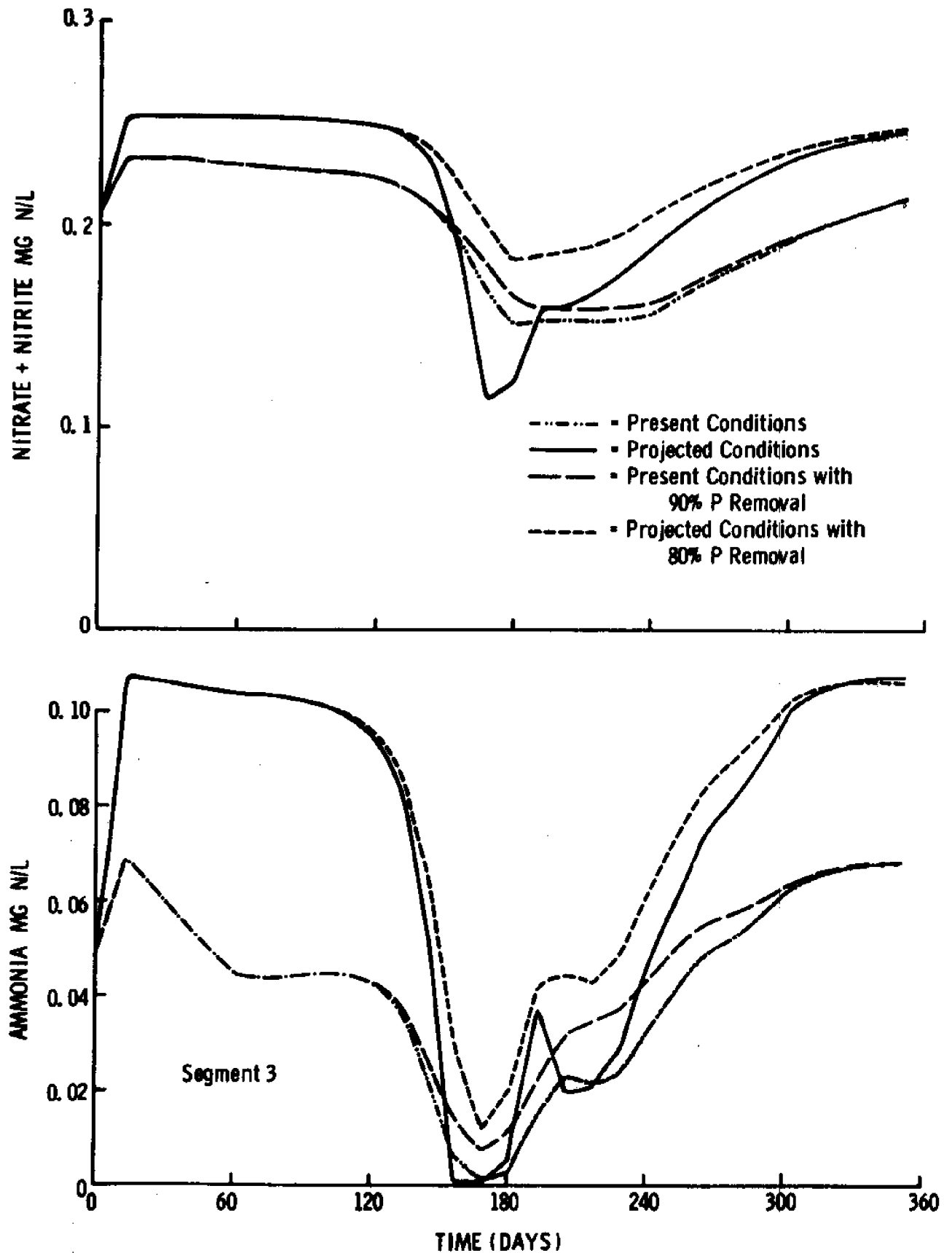


FIGURE 44. MODEL CALCULATIONS FOR NITRATE + NITRITE AND AMMONIA

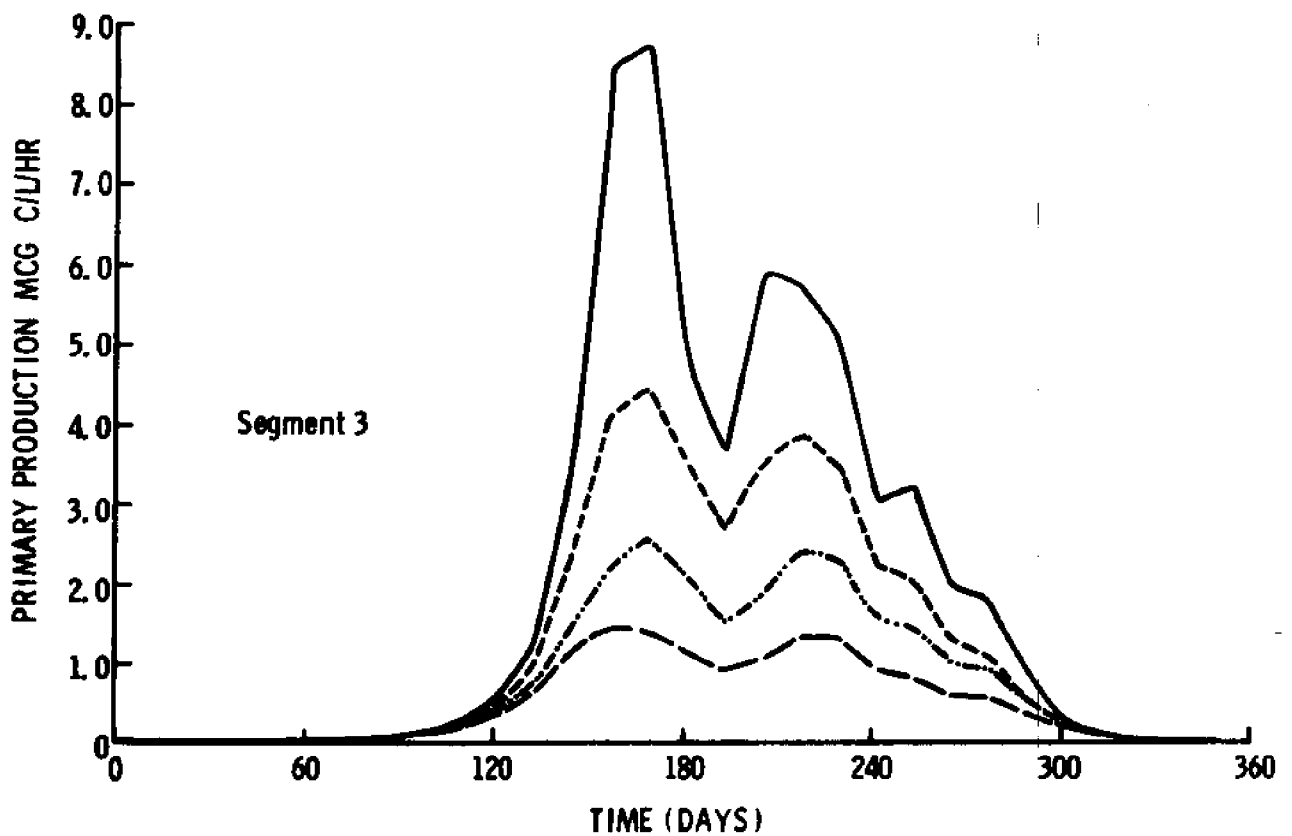
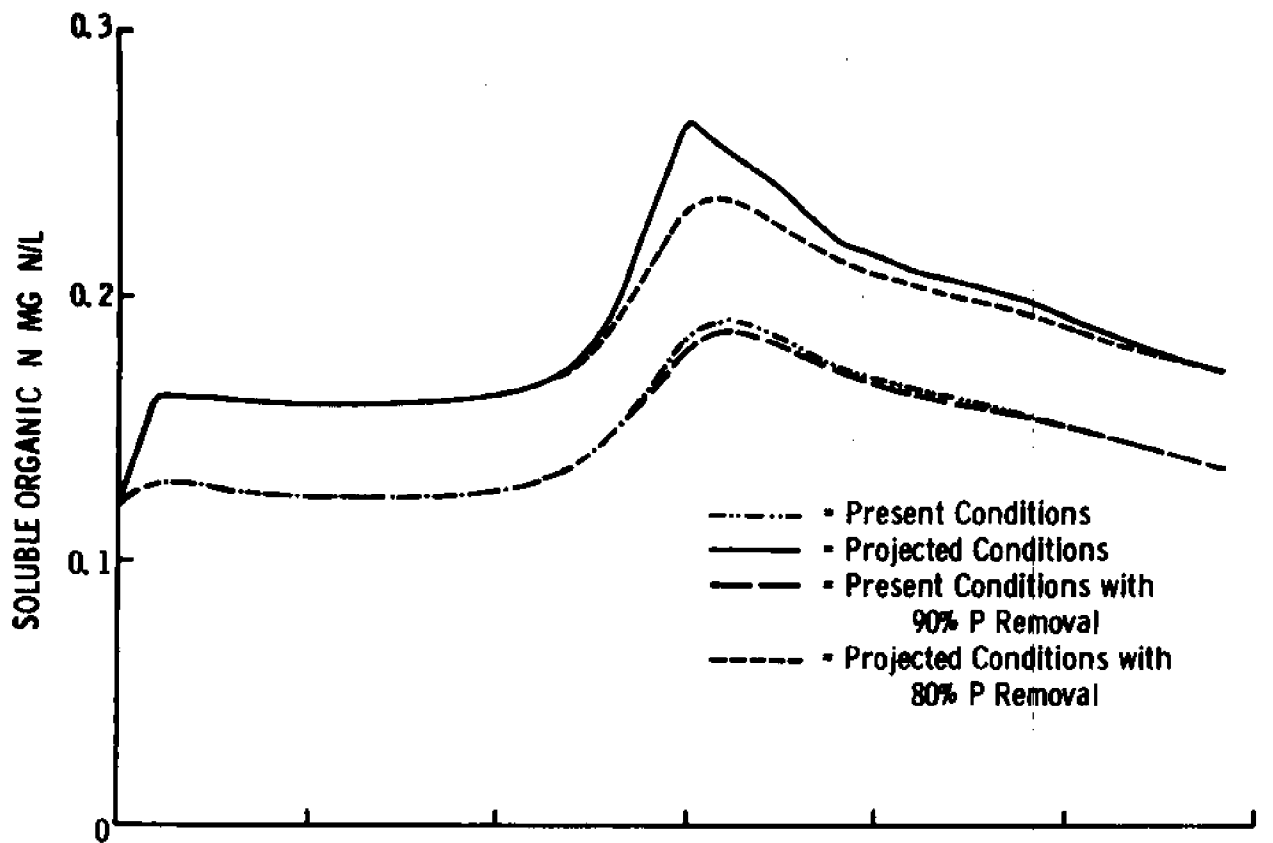


FIGURE 45. MODEL CALCULATIONS FOR SOLUBLE ORGANIC NITROGEN AND PRIMARY PRODUCTIVITY

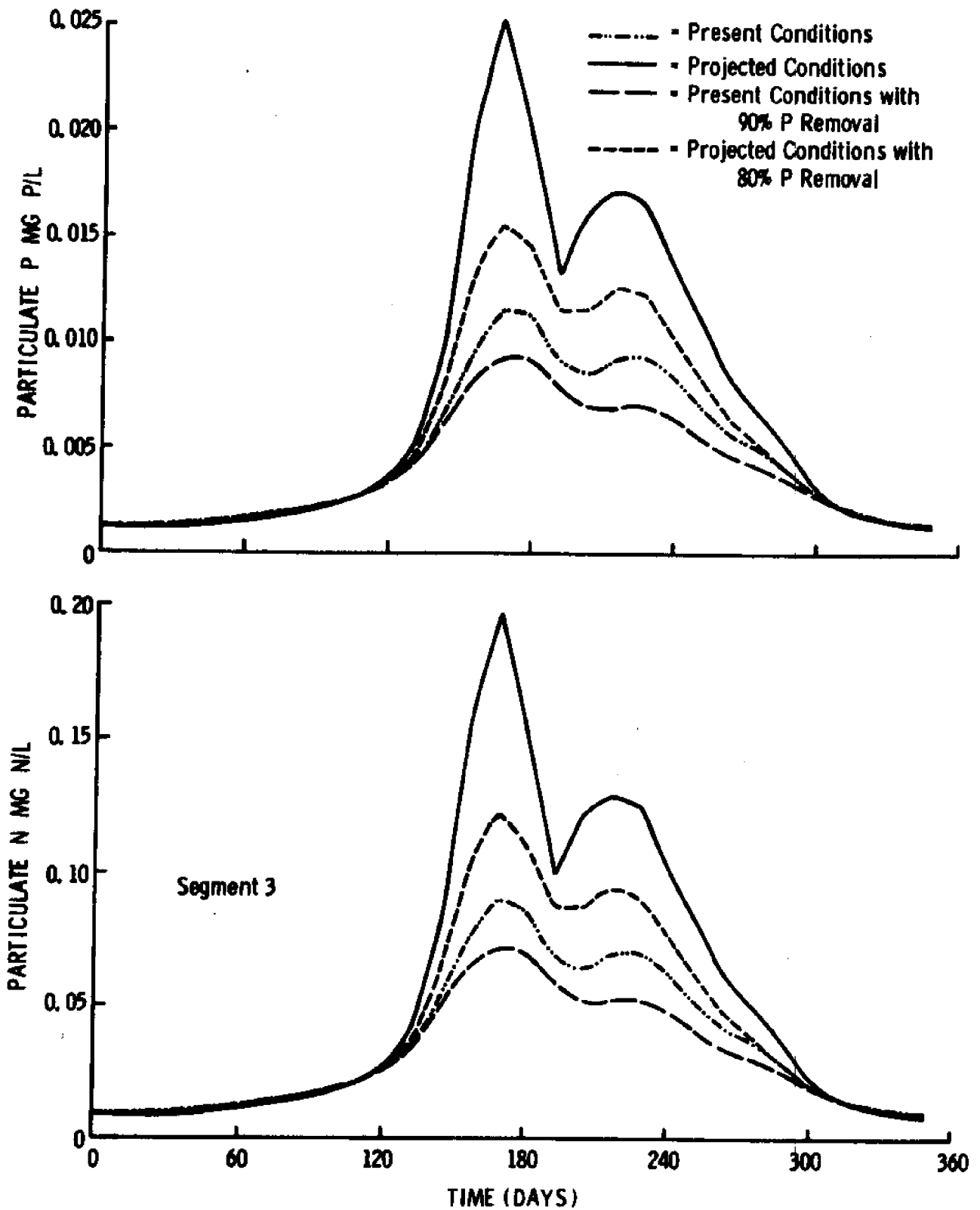


FIGURE 46. MODEL CALCULATIONS FOR PARTICULATE NITROGEN AND PHOSPHORUS

available nutrients and, subsequently, higher plankton population. Thus, the chlorophyll a estimates projected in Figure 42 may be considered a lower bound.

The model has been used to calculate the effects of the cultural activities assuming a complete shift of the phytoplankton to a group having minimal silicon requirements. Figures 47, 48 and 49 show projected levels of chlorophyll a, zooplankton, soluble phosphorus, organic nitrogen, nitrate, and ammonia as expected under case five loading conditions assuming the plankton require no silicon. It is seen that the resultant phytoplankton level is approximately 50% higher and the phosphorus and nitrogen utilization more complete. The results in these figures may be considered an upper bound on the predictions.

These results clearly indicate the need for a more sophisticated approach to modeling biological production in natural waters. A more comprehensive field data program should be associated with more complex models. Current modeling work on Lake Michigan, geared to simulating the fishery ecosystem, is based on a more detailed specification of the phytoplankton and zooplankton communities.

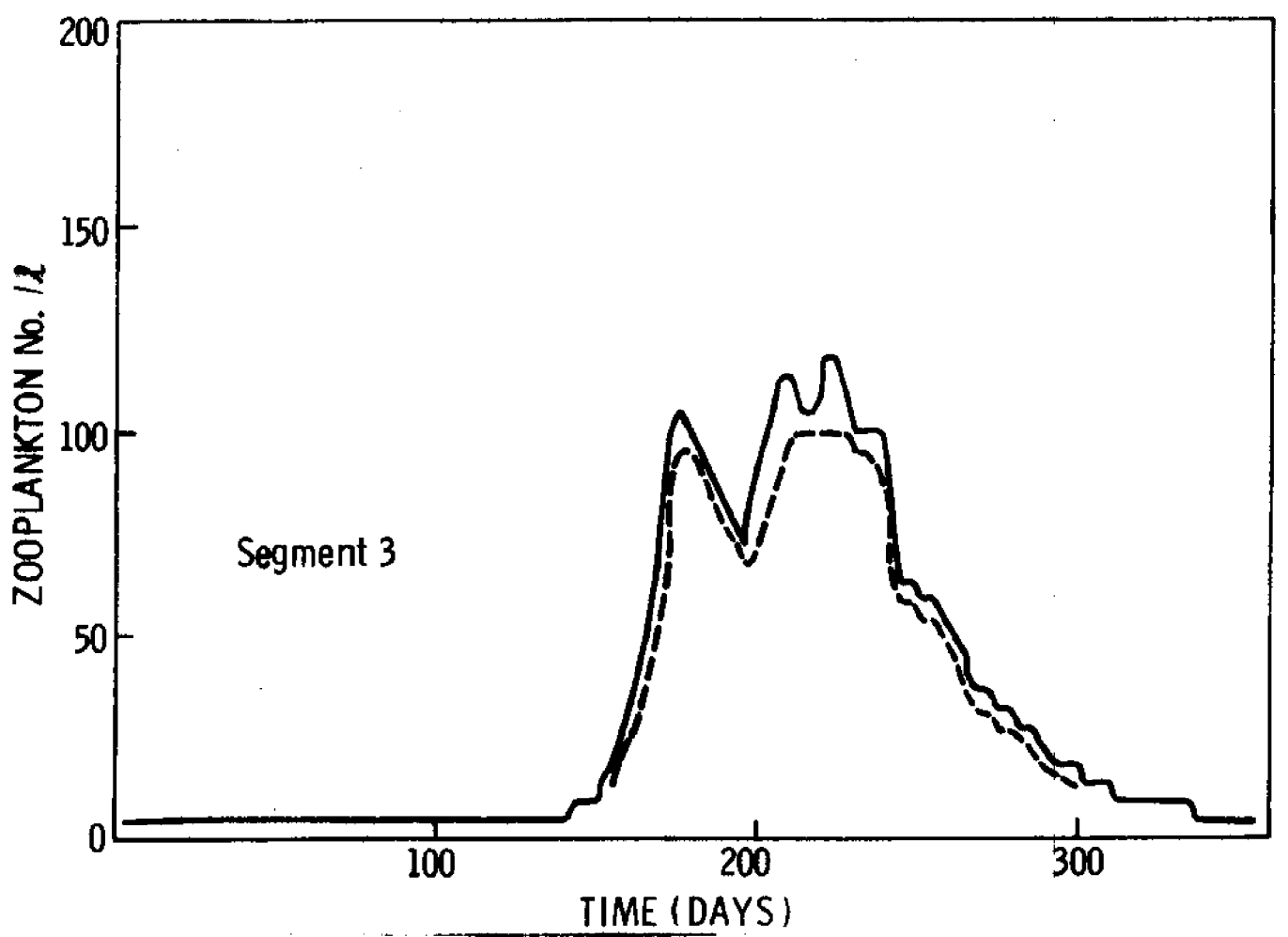
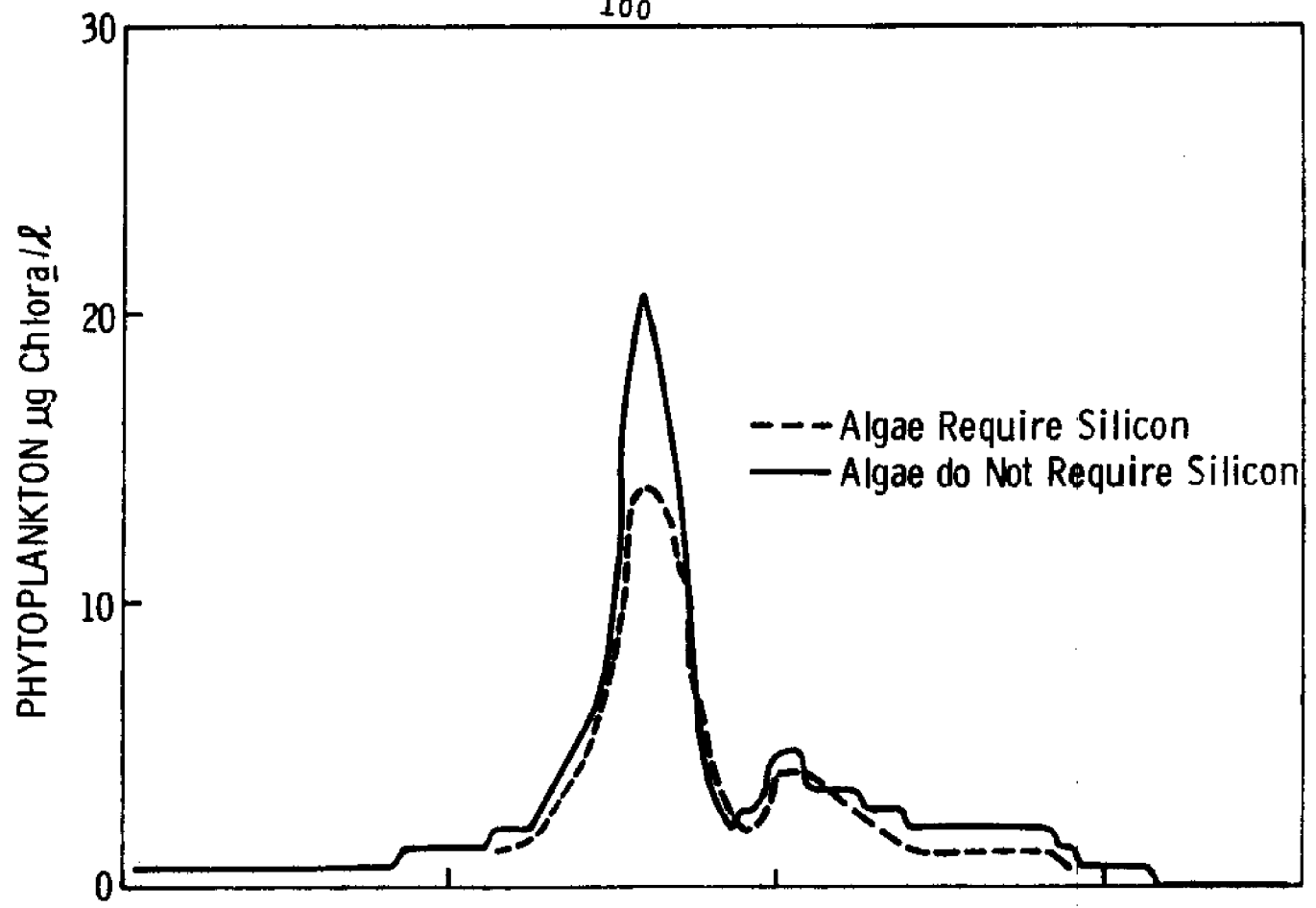


FIGURE 17. MODEL CALCULATIONS FOR PHYTOPLANKTON AND ZOOPLANKTON

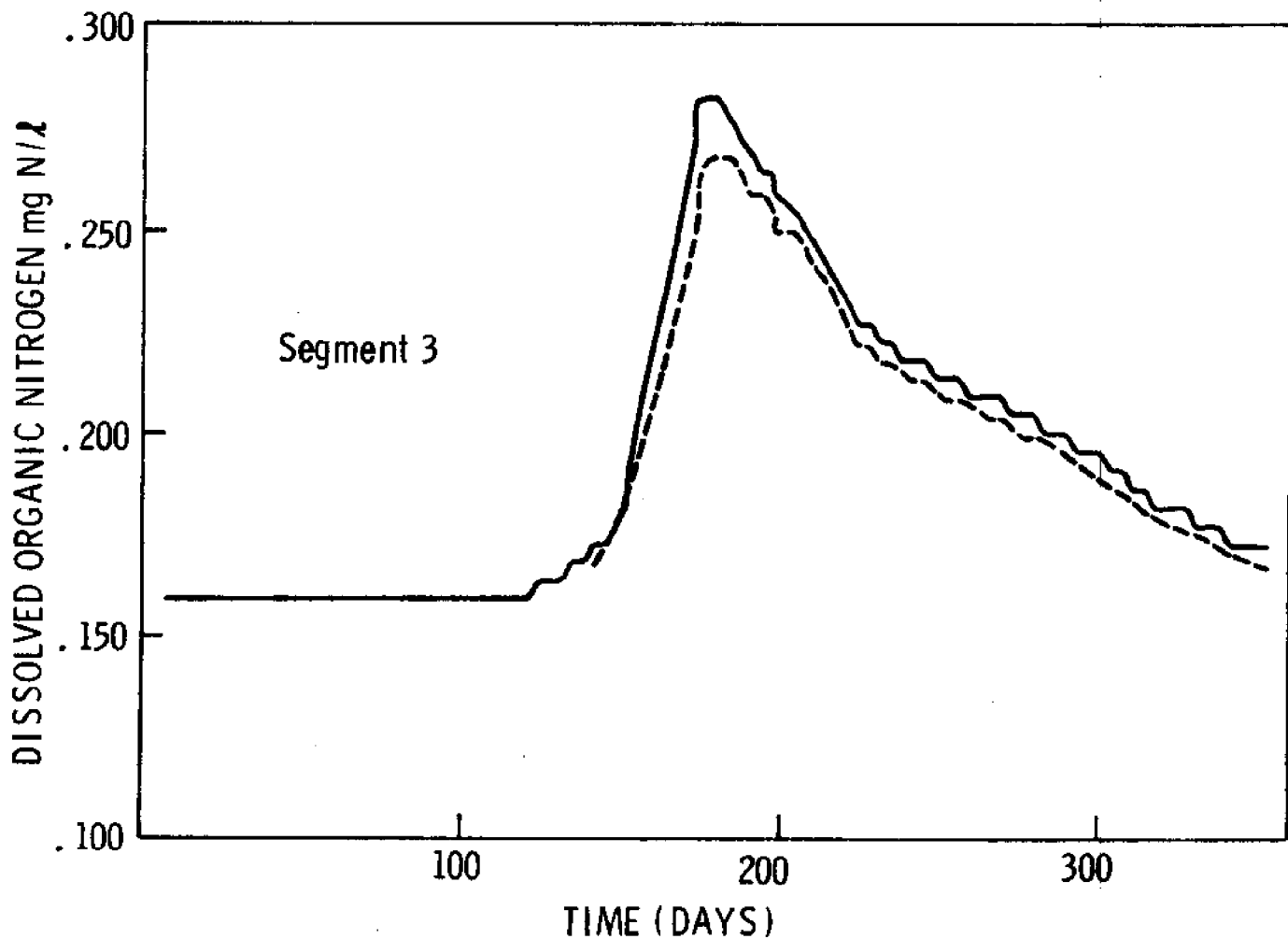
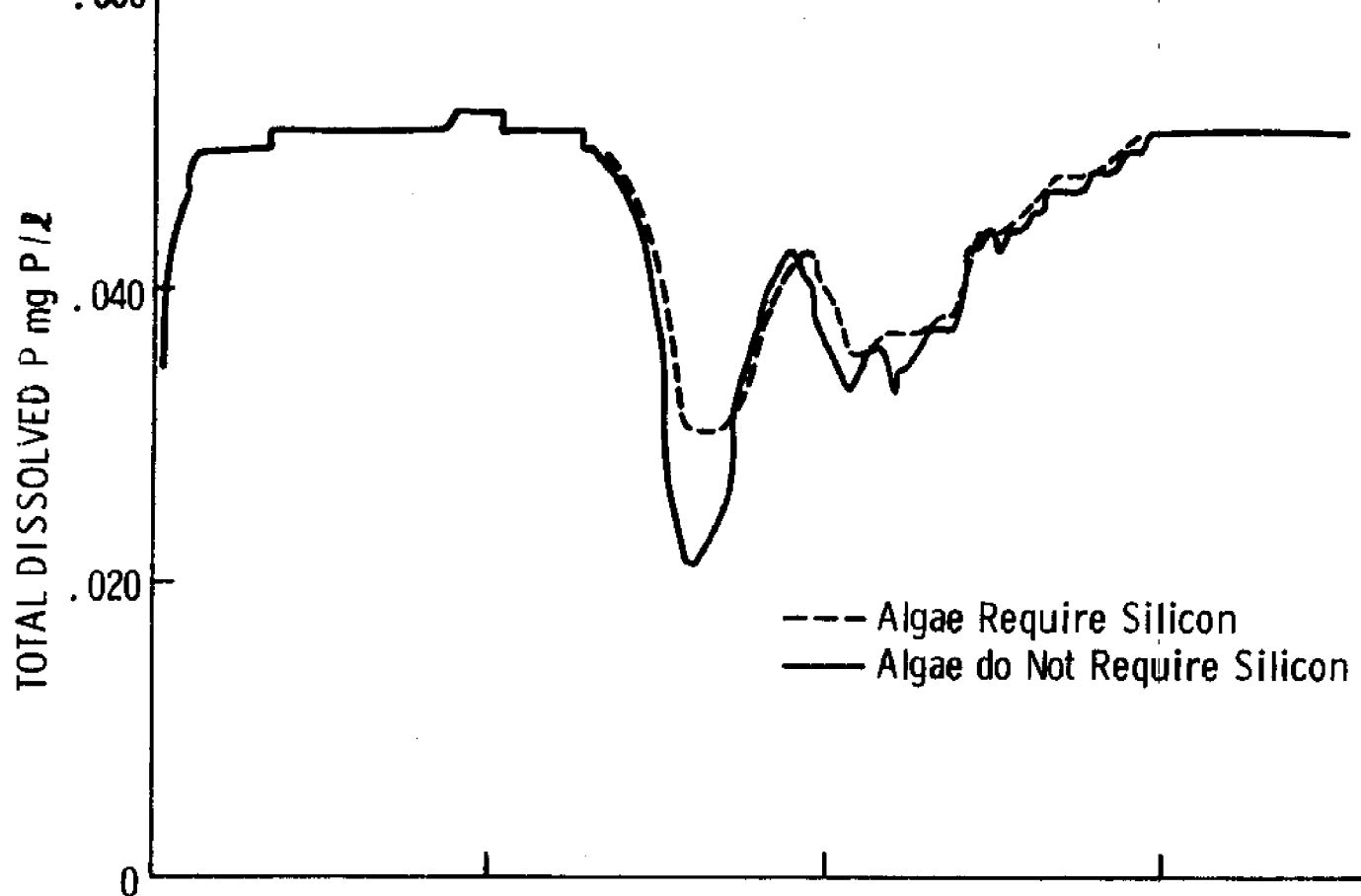


FIGURE 48. MODEL CALCULATIONS FOR SOLUBLE PHOSPHORUS AND ORGANIC NITROGEN



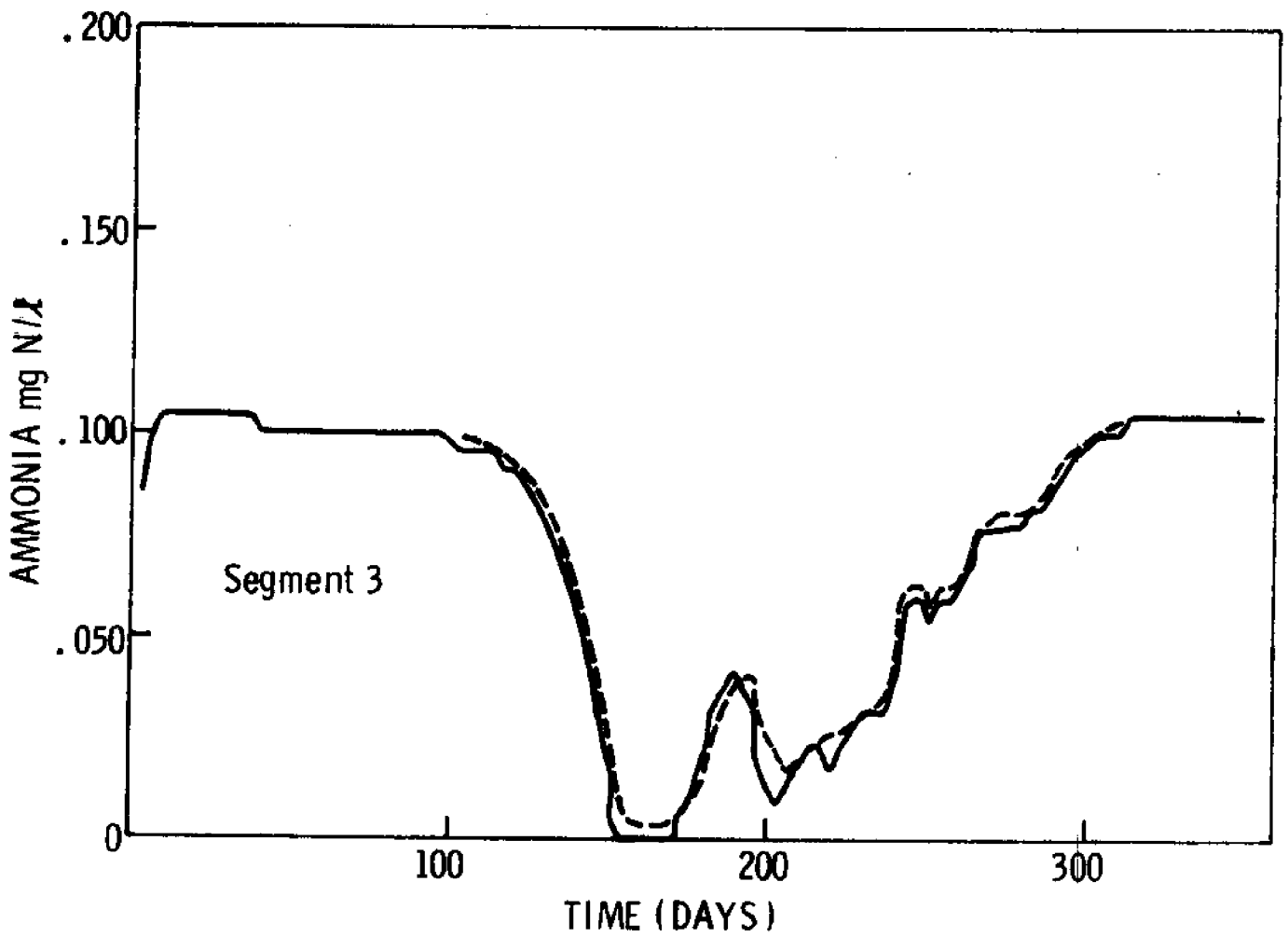
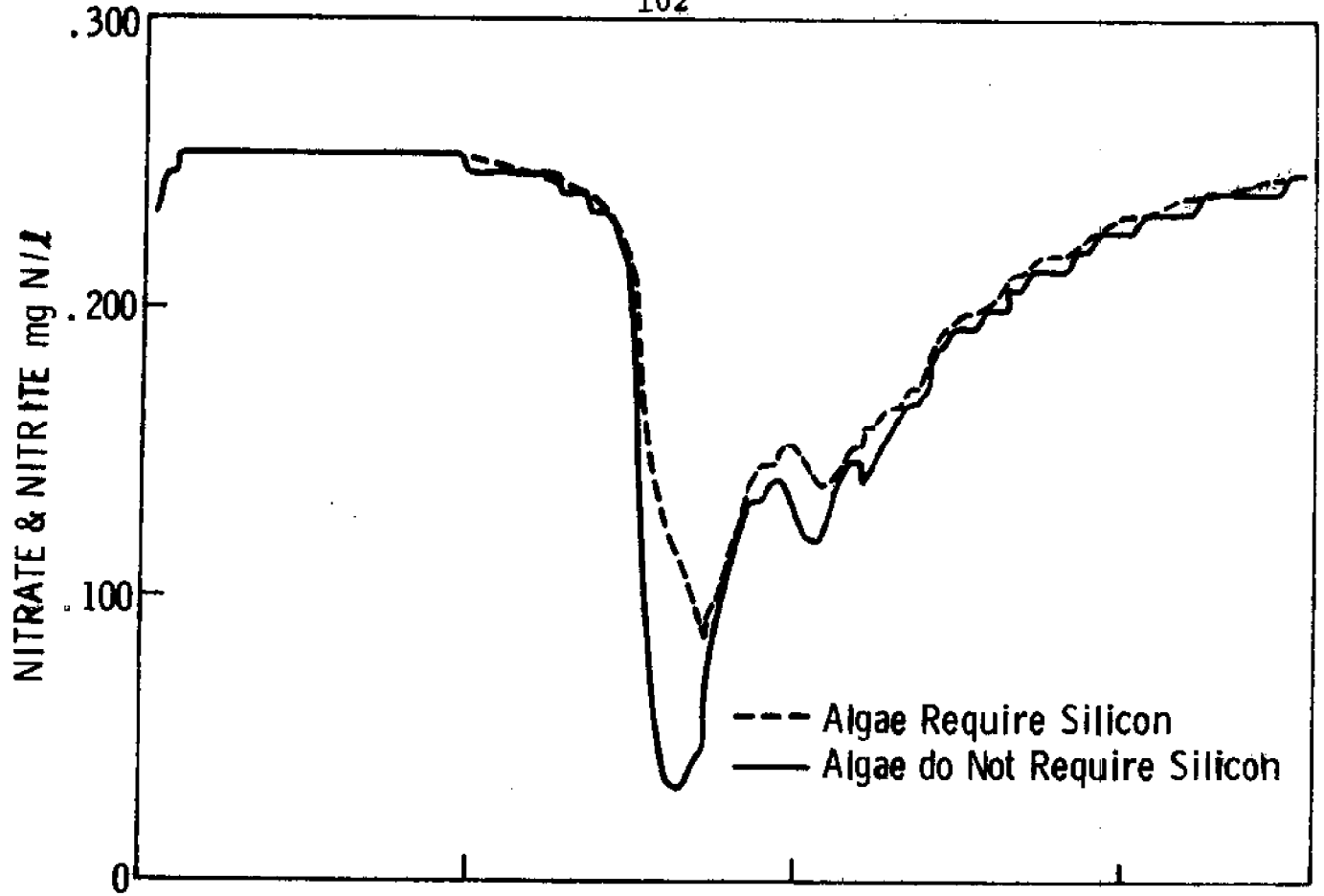


FIGURE 10. MODEL CALCULATIONS FOR NITRATE, NITRITE AND AMMONIA

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## APPENDIX I

## LIST OF SYMBOLS

$A_j$	interfacial area of the $j^{\text{th}}$ segment
$a_1$	kinetic or stoichiometric constant
$a_2$	kinetic or stoichiometric constant
$a_3$	kinetic or stoichiometric constant
$a_4$	kinetic or stoichiometric constant
$a_5$	kinetic or stoichiometric constant
$a_6$	fraction of the maximum grazing rate at high phytoplankton levels
$a_7$	kinetic or stoichiometric constant
$a_8$	kinetic or stoichiometric constant
$a_9$	kinetic or stoichiometric constant
$a_{10}$	kinetic or stoichiometric constant
$a_{11}$	kinetic or stoichiometric constant
$a_{12}$	kinetic or stoichiometric constant
$a_{13}$	kinetic or stoichiometric constant
$a_{14}$	kinetic or stoichiometric constant
$a_{15}$	kinetic or stoichiometric constant
$a_{16}$	kinetic or stiochiometric constant
$C_g$	grazing rate
$C_{g,\text{max}}$	maximum grazing rate
$C_{ij}$	concentration of species $i$ in segment $j$
$D_{\text{ON}}$	conversion rate of organic forms to inorganic forms
$D_{Pj}$	overall death coefficient of phytoplankton
$D_{Zj}$	overall death coefficient of zooplankton
$E_j$	rate of organic nutrient recycle
$e$	base of the natural logarithm system

f	photoperiod
$G_{Pj}$	overall growth rate coefficient for phytoplankton
$G_{Zj}$	overall growth rate coefficient for zooplankton
H	depth of the water segment
I	sunlight intensity
$I_0$	surface light intensity
$I_S$	optimum light intensity
$J_{ij}$	net flux of species i into segment j
$J_{Nj}$	inorganic nutrient flux
$J_{ONj}$	organic nutrient flux
$J_{Pj}$	phytoplankton flux
$J_{Zj}$	zooplankton flux
K	half-saturation or Michaelis constant
$K_N$	Michaelis constant for inorganic nitrogen
$K_{pe}$	Michaelis constant for algae
$K_{Ph}$	Michaelis constant for total dissolved phosphorus
$K_{Si}$	Michaelis constant for silicon
$k_e$	extinction coefficient
$k'_e$	extinction coefficient due to causes other than plankton
N	limiting nutrient concentration
$N_a$	concentration of ammonia
$N_i$	concentration of nitrate
Nit	concentration of total inorganic nitrogen
$N_j$	nutrient concentration
$N_O$	concentration of organic nitrogen
$ON_j$	concentration of the soluble organic form of a nutrient
Ph	concentration of total dissolved phosphorus
$P_j$	phytoplankton population as chlorophyll <u>a</u>

$\text{PNH}_3$	algal preference for ammonia
R	algal respiration rate coefficient
$r(I)$	reduction factor of the phytoplankton growth rate due to light
$r(N)$	reduction factor of the phytoplankton growth rate due to nutrients
$S_i$	concentration of silicon
$S_{ij}$	summation of sources and sinks of species $i$ in segment $j$ which are associated with various biological, chemical, and physical reactions
T	temperature
t	time
$V_j$	volume of segment $j$
$v_s$	sinking velocity
$W_{ij}$	direct input of species $i$ into segment $j$
$W_{Nj}$	input of inorganic nutrients
$W_{ONj}$	input of organic nutrients
$W_{Pj}$	input of phytoplankton
$W_{Zj}$	input of zooplankton
X	depth
$Y_{NP}$	weight of nutrient required per weight of new phytoplankton
$Y_1$	ratio of the dry weight of zooplankton in mg to chlorophyll <u>a</u> of the phytoplankton in $\mu\text{g}$
$Y_2$	nitrogen dry weight ratio in the zooplankton
$Y_3$	nitrogen to chlorophyll <u>a</u> ratio in the phytoplankton
$Y_4$	phosphorus to nitrogen ratio in the zooplankton
$Y_5$	phosphorus to chlorophyll <u>a</u> ratio in the phytoplankton
$Y_6$	phosphorus to nitrogen ratio in phytoplankton
$Y_7$	silicon to chlorophyll <u>a</u> ratio in the phytoplankton
$Y_8$	carbon to chlorophyll <u>a</u> ratio in the phytoplankton

$Z_j$	concentration of zooplankton
$\epsilon$	assimilation efficiency of the zooplankton
$\theta$	percentage of silicon which is regenerated

APPENDIX II  
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