REPORT ON

THE EFFECT OF

PHYSICAL AND CHEMICAL VARIABLES

ON REAERATION

by

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Introduction

Unpolluted water maintains in solution the maximum quantity of dissolved oxygen, which is in equilibrium with the partial pressure of oxygen in the atmosphere. When dissolved oxygen is removed from solution, an unbalance is created and the deficiency is made up by oxygen passing into solution through the water surface exposed to the atmosphere. The rate of transfer of oxygen from the atmosphere to water is influenced by physical factors, such as winds and waves, and chemical factors, such as surface active agents and oil films. This phase of the project deals with the effect of surface active agents on the reaeration process.

Review of Previous Work

The rate at which reaeration takes place is proportional to the dissolved oxygen deficit and may be expressed as:

$$\frac{dD}{dt} = -K\left[C_s - C\right] = -K\,D \qquad (1)$$

in which

$\frac{dD}{dt}$ = rate of reaeration

C_s = dissolved oxygen saturation

C = dissolved oxygen concentration

D = dissolved oxygen deficit

K = coefficient of reaeration

Equation (1) is based on the assumption that the concentration of dissolved oxygen is uniform throughout the depth of the water body and, under this condition of uniform concentration, the reaeration equation is simply a re-expression of Fick's Law of Hydro-diffusion. K, the coefficient reaeration, is referred to as the volumetric coefficient. Its physical significance may be appreciated when it is thought of as a unit rate of oxygen transfer - i.e. ppm oxygen transfer per day per unit of dissolved oxygen deficit. A more fundamental measure of the process is expressed by the transfer coefficient, K_L, which is defined as follows:

$$K = K_L \cdot \frac{A}{V} \qquad (2)$$

in which

A = surface area

V = volume of liquid

K_L = oxygen transfer coefficient

In general, the transfer may be classified as either surface or bubble aeration. In the former case, the ratio of the surface area to volume remains constant, as in natural streams and certain mechanical aeration devices. In the latter case, however, this ratio changes during the transfer process. Examples of this type are compressed air and spray aeration. This work is concerned with the surface aeration mechanism and the effect of surface active agents on this type of aeration.

The transfer coefficient was first defined by Lewis and Whitman (1). This model is based on the assumption that there are two films located at the air-water interface, through which the gas must pass by molecular diffusion. For gases of low solubility, such as oxygen and carbon dioxide, the liquid film is the controlling resistance and the transfer coefficient may be written:

$$K_L = \frac{D_L}{Y} \qquad (3)$$

in which

D_L = coefficient of molecular diffusion of oxygen

Y = film thickness

With the present state of our knowledge, it is not possible to express the hypothetical film thickness in terms of physically or chemically measurable parameters.

The theory, however, has provided a means of understanding the mechanism and reporting data.

The most significant development in recent years has been presented by Danckwerts (2) who proposed a theory defining the transfer coefficient as follows:

$$K_L = \left[D_L r\right]^{1/2} \qquad (4)$$

in which r = rate of surface renewal.

The advantage of this concept is that it better lends itself to quantitative evaluation as compared to the two-film model. The renewal rate may be expressed in terms of turbulence parameters and these, in turn, may be related to physically measurable factors, such as the depth and velocity of fluid flow. By contrast, the nature of the film thickness is relatively indefinable. In spite of this short coming, the two-film model has provided a basis for the formulation of an hypothesis to describe the effect of surface active agents on reaeration.

Since the controlling resistance in the process is located in the film at the gas-liquid interface, it follows that substances which alter the characteristics of the interface influence the gas transfer. These substances are the surface active agents, such as detergents and many organic compounds. The effect on these substances has been recognized, measured and reported. No attempt will be made to indicate all of the references in this regard, but it is significant to note that much work is being done in many fields both here and in other countries, notably England. Recent reports on bubble aeration include complete bibliographies and some interesting hypotheses. All the investigators (3), (4), (5) agree that an increase in surface activity as measured by the criterion of the surface tension of the agents decreases the transfer coefficient. The structure and nature of the substance appeared to have a marked effect (3), particularly the number of the carbon atoms and the hydrophilic and the hydrophobic portions. The reduction in the transfer coefficient to a minimum value was assumed to be related to the critical micelle concentration (4). In all of these cases which reported on bubble aeration, the results were difficult to evaluate because of the interference of the substances on the diameter and surface areas of the air bubbles. In general, however, it was reported that the transfer coefficient dropped sharply to minimum value at a relatively low concentration of surface active agent and remained constant with increasing concentration.

Fewer references appear on the effects of surface active agents on surface aeration. Some of these reports (6), (7), (8) are of direct significance in this work. These investigators also agree that the surface activity is a primary factor and that the transfer coefficients drop to a minimum at relatively low concentrations. However, when the concentration of surface active substance was increased, the value of the transfer coefficient also increased and approached that in pure water. The minimum value of the transfer coefficient is associated with that of critical micelle formation, but with very pure substances, no effect was noted on the transfer of carbon dioxide to water (6).

Before proceeding with the theoretical development, it is necessary to review certain aspects of surface chemistry of these substances. The discussion which follows is taken from the standard references (9), (10), (11), (12) in this field.

Surface Chemistry Effects

Surface active substances tend to concentrate at the gas-liquid interface and their surface concentration is greater than that of an equal mass in the bulk of the fluid. This condition is referred to positive adsorption and is characteristic of detergents and many organic substances. On the other hand, inorganic ionized substances are negatively absorbed. They are drawn into the bulk of the solution and the surface layer has a concentration less than that of the bulk. This phenomenon is described by the Gibbs adsorption equation as follows (5):

$$\Gamma = -\frac{c}{RT}\frac{d\chi}{dc} \qquad (5)$$

in which

Γ = excess concentration in the interface

c = concentration in the bulk of solution

χ = surface tension

T = absolute temperature

R = gas constant

Δ c is positive when the differential of surface tension with respect to concentration is negative, i.e., when the surface tension decreases with concentration. This condition is typical of surface active agents. Conversely Δ c is negative, when there is an increase in the surface tension with concentration, as in solutions of inorganic electrolytes.

The verification of the Gibbs equation depends on accurate measurements of the surface excess or degree of adsorption of the solute. The experimental techniques involved in such measurements have proved to be quite difficult. One of the most direct methods consists in actually cutting off a thin layer of solution, including the surface, by means of a travelling knife and is known as the microtome method. The concentration of solute in the removed surface layer is then compared with that in the bulk of the solution. Agreement between experimental and theoretical results has been very good in some cases and poor in others. The widest discrepancies have occurred with solutions of surface active agents. Discrepancies may be due to a difference between the actual molecular condition of the system being measured and our concept of that system. Lack of agreement between theory and experiment may also arise from a neglect to consider other variables (such as electrical variables, etc.) which may affect the system. In any event, the qualitative relationships among surface tension, adsorption, and concentration which are implicit in the Gibbs equation have never been seriously questioned. In effect there is a layer in the surface region which is far richer than the interior in solute molecules. In the case of surface active agents, this adsorbed layer is equivalent to a film of solute molecules in the surface.

Surface films of insoluble substances have received considerable attention and a brief review of the pertinent factors is presented. Some of these considerations may be applicable to this study. Films have been classified as follows: (1) Gaseous films, in which the molecules are separate and move about independently. The lateral adhesion is very small. (2) Condensed films, in which the molecules are closely packed due to strong lateral adhesion. The molecules are usually normally oriented to the surface. (3) Liquid-expanded films, which are still coherent but less so than the condensed films. (4) Vapor-expanded films, which are more coherent than the liquid-expanded, but less coherent than the

gaseous films.

The vapor-expanded and liquid-expanded films represent intermediate degrees of lateral cohesion among the surface molecules. The same spreading substance can sometimes form different types of film at different temperatures. Furthermore, one type of film may be transformed into another type in the same manner that ordinary phase changes take place in three dimensions. Changes in the type of film may often be brought about by adding a second insoluble film-forming component to the material which is already spread.

Condensed films are often characterized by having their molecules oriented normal to the surface plane. In gaseous films, however, most of the evidence indicates that the molecules lie flat in the surface and have random orientation. Studies in the homologous series of straight-chain fatty acids illustrate the transition from gaseous to condensed films as the molecular weight increases. It may be noted at this point that the adsorbed surface layer of solute molecules in solutions of positively adsorbed solutes, including surface active agents, usually exhibits the structure of a gaseous monofilm, i.e., the molecules lie flat in the surface and have random orientation.

The main theoretical relationship between the study of monofilms and surface active agents is established by the high degree of surface adsorption of the latter. The relatively dense adsorbed layer is in effect a monofilm. In most cases of dilute solutions at the air-solution interface, this film is of the gaseous type and it is inadvisable to assume any high degree of orientation or any strong lateral adhesion. The film can and does affect the free surface energy, viscosity, optical properties, and surface potential. Although the adsorbed surface films of most soluble surface active agents are of the gaseous type, condensed films have been observed. In general, gaseous films are characterized by large areas and low pressures, while the condensed film is marked by the large pressures and small areas. The intermediate zone covers the liquid-expanded and vapor-expanded films and the various relations shown in this figure are due to changes in temperature, concentration and molecular structure.

The solutions of surface active agents are characterized by a unique type of colloidal system in which aggregates form by the association molecules and ions. These aggregates or micelles begin to form in significant quantity only when a definite concentration value or range is reached, usually referred to as the critical micelle concentration. Below this concentration, the solution is ionic. Over the relatively short range of micelle formation, changes take place in the physical properties of the solution, such as conductivity, density, freezing point, viscosity and surface tension. The concentration at which this change takes place is dependent upon the chain length of the surface active substance. Experimental data furthermore, indicates that the nature of the micelle changes with increasing concentration.

Surface active agents produce changes in the viscosity of the solution and in particular, in the surface viscosity. It is probable that any change in the viscosity affects the diffusion coefficient of the gas in the liquid. Viscosity relationship are defined for the compressed film but not for the gaseous films. Since most detergent solutions are of this type, there is no general relationship available between the concentration and viscosity or diffusivity.

Theoretical Development

Based on the assumption that the diffusion is molecular in nature through a very thin film at the liquid-air interface, it follows that substances which concentrate at the interface interfere with the transfer of gas from the atmosphere to the liquid.

It is assumed that such substances have a two-fold effect on gas transfer by virtue of their effect on: (1) the diffusion coefficient, which is reduced with increasing concentration because of the change in the surface or bulk viscosity; (2) the film thickness, which varies with the excess surface concentration. Since a defined surface film exists in solutions of surface-active substances, some form of Equation (3) may be assumed as an appropriate model. In accordance with this model and the above assumptions, the reduction in the transfer coefficient varies inversely as the diffusion coefficient and directly as the excess surface concentration:

$$\Delta K \propto \frac{\Gamma}{D_L} \tag{6}$$

It is assumed that the diffusion decreases with concentration of surface active agent as follows:

$$D_L = Fc^{-b} \tag{7}$$

in which F = constant
c = concentration of surface active agent
b = exponent

Substituting for Γ its value from the Gibbs equation (Equation 5) and for D_L its value as given by Equation (7) and combining constants and exponents, the following equation is obtained:

$$\Delta K = - Bc^{m} \frac{d\chi}{dc} \tag{8}$$

in which $\Delta K = K_o - K_c$ = change in transfer coefficient
K_o = coefficient at zero concentration
K_c = coefficient at concentration c
B = constant (for a given temperature)
m = exponent = $b + 1$

Depending on the relationship between the concentration and surface tension, $d\chi/dc$ will have various forms. A relationship between these variables cannot as yet be expressed as a general equation valid for all solutes, although many empirical relationships (12) have been proposed.

A function which defines the surface tension data of the solutions dealt with in this work is:

$$\frac{d\chi}{dc} = - f_n \left[\chi - \chi_\infty\right]^n = - f_n \sigma^n \tag{9}$$

in which χ = surface tension

χ_∞ = limiting surface tension

$\Gamma = \chi - \chi_\infty$

c = concentration of surface active agent

f_n = constant

n = exponent

From a preliminary analysis of the solutions investigated in this work it appears that the exponent m has a value of either 1 or 2. The vast majority of the substances tested in this work or reported elsewhere are correlated with m = 2. Only this condition, therefore, is considered in the following development.

Equation (9) integrates to for m = 2:

$$\frac{1}{\Gamma} = f_2 c + \frac{1}{\Gamma_o} \tag{10a}$$

Rearranging terms, there results:

$$\Gamma = \frac{\Gamma_o}{f_2 c \Gamma_o + 1} \tag{10b}$$

Substitution of Equation (9) for m = 2 in Equation (8) yields:

$$\Delta K = B_2 f_2 c^m [\chi - \chi_\infty]^2 = B_2 f_2 c^m \Gamma^2 \tag{11}$$

The final form of the equation is obtained by substituting Equation (10b) in Equation (11) and rearranging terms:

$$K_c = K_o - \frac{B_2 f_2 \Gamma_o^2 c^m}{[f_2 c \Gamma_o - 1]^2} \tag{12}$$

in which $\Gamma_o = \chi - \chi_\infty$

χ_o = surface tension of water

The constants A and f are related to the nature and type of surface active substance. The constant f may be determined from published surface tension data or from laboratory measurements and the constant A from the experimental data of the aeration runs.

A graphical interpretation of the mathematical development is shown qualitatively in Figure 1. The first plot shows a typical relationship between the surface tension and the concentration of surface active agent. Assuming a functional relationship as indicated by Equation (9), it follows mathematically that the excess surface concentration takes the form shown in the second plot. It is emphasized that this is strictly a mathematical interpretation of the Gibbs equation. From the viewpoint of the simple surface active agent, this representation may be assumed since most investigators have found that the concentration of the simple agent decreases with increasing total concentration. There is no doubt that the viscosity and particularly the surface viscosity increases with increasing bulk

concentration of surface active agent, which results in a decrease in the value of the oxygen diffusivity. There are many possible mathematical relationships between concentration of agent and diffusivity, and the power form of Equation (7) is one which is assumed to define the relationship shown in this figure.

It follows mathematically from these assumptions that the transfer coefficient varies as shown. It may be observed that the minimum value of this coefficient is displaced from that of the maximum excess concentration. Furthermore, the transfer coefficient does not return to its original value in water at higher concentrations. Both of these effects are due to the assumed variation in diffusion coefficient. As a matter of fact, the transfer coefficient may decrease again with further increase in concentration.

Experimental Apparatus & Procedure

The experimental procedure consisted in determining the reaeration coefficient in pure water and in solutions of various concentrations of detergents. The apparatus consisted of a lattice work oscillating vertically in simple harmonic motion, which caused a uniform degree of turbulence throughout the solution. The lattice work consisted of two layers of screening placed one on top of the other such that the openings of one was bisected by the wiring of the other. The screening was 1/4" in diameter with 4 3/4" of water depth, containing 1600 ml of solution. An operating speed of 82 strokes per minute was employed, which was induced by a gear-reduced motor. The motor speed of 1750 rpm was reduced to approximately 200 rpm, which in turn was further decreased to 82 rpm by means of a pulley and belt arrangement. The amplitude of the oscillating grid was approximately equal to the depth of the water, which insured a uniform concentration of dissolved oxygen throughout the depth. A volume of solution was used such that a cover of 1/4 inch of fluid above the uppermost position of the grid was effected. With this condition no air bubbles were introduced and oxygen was transferred only through the water surface exposed to the atmosphere. The test temperature was held constant at 25°C $\pm$ 0.5°C by a constant-temperature bath in which the cylinders were immersed.

A second experimental apparatus was also employed in which agitation was induced by means of a propeller which was attached to a shaft of a variable speed motor. The test cylinder contained about 1600 ml. The submergence of the liquid over the propeller at rest was 4 inches and approximately 1 inch during rotation. The speed of rotation was 750 rpm.

The reaeration coefficient was determined by means of the non-steady condition, as indicated in Equation (1). The values of dissolved oxygen concentration required for this calculation were measured polarographically. The following surface - active substances were used in solutions of various concentrations for which the reaeration coefficient was measured: sodium lauryl sulfate, peptone, caproic and heptanoic acids. Solutions of potassium chloride and magnesium carbonate were also tested. The selected substances were dissolved in distilled water to obtain stock solutions of high concentration. Appropriate amounts of the stock solution were then added to deaerated distilled water to obtain the desired concentrations. The procedure of adding the solute to the deaerated water was found necessary since with most surface active substances, foaming resulted when the solution was subjected to a nitrogen purge. The test cylinder with this solution was placed in the experimental apparatus. The initial sample was then taken. After the polarographic scale reading was recorded, the sample was returned to the test cylinder. Careful technique in the removal and the return of the sample was observed, so as not to introduce oxygen into the solution. After return of the initial sample, the grid or the propeller was placed in operation. At specified time intervals, usually between 5 and 10 minutes, the grid was stopped and a sample was removed. After the reading, the sample was returned and the procedure repeated. The time required to obtain a reading is so short that the amount of oxygen absorbed by the solution or the sample is negligible. The length of the test run was usually in the order of 30 to 40 minutes, which resulted in approximately 60% replacement of the dissolved oxygen.

This procedure was modified in cased where either low concentrations or non-ionizable materials required the addition of electrolyte to the sample. Replenishment of the test volume was then made by means of a fresh sample of the estimated mean dissolved oxygen concentration. Polarograms for each solution were measured

and appropriate voltage values used. A 0.6 voltage was suitable for most solutions.

Knowledge of the saturation values is required in the calculation of the reaeration coefficient. The procedure for the laboratory determination of the saturation values is as follows:

1. A large volume of distilled water was aerated for a period of 12 to 24 hours.
2. Three samples were siphoned from the volume into 300 ml DO bottles and allowed to stand for 10 to 15 minutes.
3. An appropriate amount of solute was added in highly concentrated form to obtain the desired concentration to two of the bottles. The bottles were stoppered and shaken to insure complete mixing.
4. The bottles were opened and allowed to stand for 10 to 15 minutes.
5. The dissolved oxygen concentration was measured in each of the 3 bottles, employing the Winkler procedure. These values indicated the effect the substance has on the saturation value at the given concentration.
6. The above testing was performed over the range of concentrations expected in the laboratory runs.

In order to measure dissolved oxygen values accurately, it is necessary to calibrate the polarograph daily for each solution employed. This procedure is as follows:

1. Three to five samples of distilled water were prepared, approximately 2000 ml in volume, each sample having a concentration of dissolved oxygen between 1 and 2 ppm apart. A nitrogen purge of varying duration was used to obtain this range of DO concentration.
2. A water sample from each 2000 ml flask was placed into 3-300 ml DO bottles.
3. The solute was added to obtain the desired concentration to all the bottles, which were stoppered and shaken.
4. For each series of 3 bottles, the DO in one sample was measured polarographically and the Winkler method was employed on the other two.
5. The Winkler DO values were plotted against the polarographic scale readings, which points defined a straight line.
6. Saturation values were also determined polarographically in saturated samples.

Values of surface tension were determined by means of a Cenco du Nouy Tensiometer. Surface tension measurements were made on the solutions which were tested. A period of a few minutes was allowed before measurements were made in order to achieve equilibrium. These values were then checked after a period of approximately 30 minutes.

Discussion of Results and Procedures

The experimental apparatus which was first employed proved to be unsatisfactory because reproducible results were difficult to achieve. The second device, simpler in concept, proved to be more consistent in this regard. Consequently most of the test work was performed with the propeller apparatus. The advantage of the first apparatus is that the fluid turbulence parameters could be more directly correlated to geometric and dynamic characteristics of the mechanism and grid. For this reason, consideration is still being given to this apparatus and it is hoped that future work may be done with it. For the present, the propeller device will be used and one of the next steps is to investigate the effect of varying speeds on the reduction of the transfer coefficient.

It was noted above that the values of static surface tensions were employed in the correlation of the data in accordance with the equations which were developed. It appears that the dynamic surface tension is a more representative characteristic of a fluid system which is subjected to agitation. There is little evidence of the existence of thick oriented films at surfaces which are in rapid motion. Films subjected to motion or agitation are swept away and thinned to relatively fine layers. Therefore, it appears that films which may be regarded as condensed in the static sense could be gaseous in the dynamic state provided the fluid agitation is sufficient. This condition also has a bearing on the time required for static equilibrium of the surface. In some cases, this time is in the order of hours. In most cases, however, the order of magnitude is seconds or minutes. It is pertinent to observe that average times of renewal in the transfer equation is the same order of magnitude. A comparison of these time periods and the associated effect on the transfer process should be very informative.

A further difficulty encountered was in the measurement of surface tension. The values given in the literature for such substances as heptanoic and caproic acids could not be checked by the methods employed in this work. It was concluded that the values reported in the literature were for highly purified compound, while those used in this work were laboratory reagent grade, not necessarily of the same degree of purity. Furthermore, certain substances such as peptone were eliminated because of their erratic composition and surface tension values.

Analysis of Data

The reaeration coefficient was determined by means of Equation (1). The laboratory data of dissolved oxygen concentrations with the associated times of aeration and the saturation values of oxygen in the various solutions are employed in this calculation. The DO deficits were plotted on a logarithmic scale versus an arithmetic scale of time. The experimental points define a straight line, which was drawn by eye. The slope of this line is a direct measure of the reaeration coefficient as follows:

$$K = \frac{1}{t} \log \frac{D_o}{D_t}$$

in which K = reaeration coefficient

t = elapsed time

D = DO deficit at zero time

D_t = DO deficit after time, t.

For each substance tested, there was available the reaeration coefficient and the surface tension at various concentrations. The analysis proceeded as follows:

1. It is first necessary to assume a value of the limiting surface tension, if This is not available from the laboratory data. This value is then subtracted from each of the measured surface tensions. The reciprocal of this difference is plotted against its associated concentration, in accordance with the Equation (10a). The linearity of this plot confirms the use of this equation to define the surface tension - concentration relationship. The value of the constant, f_2, is measured from the slope of this line. With the exception of caproic acid, all of the substances tested in this work were correlated by means of equation.

2. Based on the relationship, as determined in step 1, the surface tensions are calculated for each concentration. The ratio of ΔK over $(\gamma_o - \gamma_\infty)^2$ is plotted against its associated concentration on log-log paper in accordance with Equation (11). A line is fit by eye, from which the power, m, of the concentration and the combined constant $B_2 f_2$ are determined. An example of this correlation is shown in Figure 2.

3. Equation (12) may now be used directly to calculate the transfer coefficient for various concentrations of surface active agent. These results are compared to observed data and this comparison is shown graphically in Figure 3. Also indicated are the observed surface tension data and the calculated line from Equation (10b).

Extensive work was conducted on various concentrations of sodium lauryl sulfate. Since these experiments were performed with the first test apparatus, reproducibility was difficult to achieve. To indicate the variation of the transfer at one specific concentration Figure 4 is presented. All concentrations showed comparable variations. In spite of this condition, the average value of the transfer coefficient at each concentration indicated the trend of a reduction and a subsequent rise in the value of the coefficient, as shown in Figure 5.

The data collected on caproic acid also showed the general pattern of changing coefficient, as shown in Figure 6. Since these were preliminary tests, the data on both caproic acid and sodium lauryl sulfate were not analyzed as described above, but the data presented to indicate the order of magnitude of the reduction in transfer.

The data for peptone showed a constant value for the reaeration coefficient at low concentrations up to 200 ppm and evidenced a slow decrease after this point. At a concentration of 2500 ppm, no rise in the curve was evident. The reaeration data for the solutions of potassium chloride and magnesium carbonate indicated slight changes. The differences, however, were not sufficiently significant to draw any conclusions.

Data from another source (6) were also available to test the proposed hypothesis. These experiments were conducted in order to determine the effects that surface active agents have on the carbon dioxide transfer coefficient. Since carbon dioxide is a sparingly soluble gas, like oxygen, the hypothesis may be assumed to apply. The data were analyzed as described in steps 1, 2 and 3. The comparison between the calculated and observed values of the transfer coefficient and surface tension for different flow conditions is shown in Figure 7 for various concentrations of the commercial detergent, Teepol.

Conclusions and Future Work

From the results of this and other studies, the following conclusions may be drawn:

1. The addition of surface active agents causes a reduction in the oxygen transfer coefficient in surface aeration to a minimum value. Further addition causes a rise in curve to a value which approaches that of pure water.

2. This phenomenon may be related to the excess surface concentration as defined by the Gibbs absorption equation and to the variation of the oxygen diffusion coefficient, each of which may be expressed as functions of bulk concentration of surface active agent.

3. The proposed hypothesis provides some insight into the nature of this interference. The equations, which are developed from the hypothesis, agree reasonably well with the experimental data.

4. Further work should be conducted covering a wide range of substances to verify the hypothesis proposed in this work.

In the future, it is planned to investigate:

1. A series of substances, which are of the basic components of commercial detergents.

2. A homologous series of organic compounds, which are surface active.

3. The effect of various degrees of agitation on the process in conjunction with 1 and 2.

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References

1. Lewis, W. K. and Whitman, W. G., "Principles of Gas Absorption", Ind. & Eng. Chemistry, 16, 1215 (1924).

2. Danckwerts, P. V. "Significance of Liquid Film Coefficients in Gas Absorption", Ind. & Eng. Chemistry, 43, No. 6 (June 1951).

3. Lynch, W. O. and Sawyer, C. N., "Effects of Detergents on Oxygen Transfer in Bubble Aeration", Journal, Water Pollution Control, 32, No. 1 (January 1960).

4. Mancy, K. H. and Okun, D. A., "Effects of Surface Active Agents on Bubble Aeration", Journal, Water Pollution Control, 32, No. 4 (April 1960).

5. Eckenfelder, Jr. W. W., "Absorption of Oxygen from Air Bubbles in Water", Journal, Sanitary Engineering, Proceedings ASCE, (July 1959).

6. Cullen, E. J. and Davidson, J. F., "The Effect of Surface Active Agents on the Rate of Absorption of Carbon Dioxide by Water", Chemical Engineering Science, 6, No. 2, (November 1956).

7. Holroyd, A. and Parker, H. A., "Investigations on the Dynamics of Aeration - The Effects of Some Surface Contaminants", Journal Institute of Sewage Purification, 280 (1952).

8. Downing, A. L., Melbourne, K. V. and Bruce, A. M., "The Effect of Contaminants on the Rate of Aeration in Water", Journal of Applied Chemistry 7, (1957).

9. Adam, N. K., "Physics and Chemistry of Surfaces", 3rd Edition, Oxford University Press, London, 1941.

10. Harkins, W. D., "The Physical Chemistry of Surface Films", Reinhold Publishing Corporation, New York, 1957.

11. Schwarz, A. M. and Perry, J. W., "Surface Active Agents", Volume I, Interscience Publishers, Inc., New York, 1949.

12. Bikerman, J. J., "Surface Chemistry", Academic Press Inc., New York, 1958.

List of Notations

A	=	surface area
B	=	constant in Equations (8) and (11)
b	=	exponent in Equation (7)
C	=	concentration of dissolved oxygen
C_s	=	saturation value of dissolved oxygen
c	=	concentration of surface active agent
D	=	dissolved oxygen deficit
D_L	=	diffusion coefficient
F	=	constant in Equation (7)
f	=	constant in Equations (9) and (11)
K	=	aeration coefficient
K_L	=	transfer coefficient
K_o	=	coefficient in water
K_c	=	coefficient in solution of concentration, C
ΔK	=	change in coefficient
m	=	exponent in Equation (8)
n	=	exponent in Equation (9)
R	=	gas constant
Γ	=	surface renewal rate
T	=	absolute temperature
V	=	volume
Y	=	film thickness
χ	=	surface tension
χ_o	=	surface tension of water
χ_∞	=	limiting surface tension
Γ	=	excess surface concentration
∇	=	$\chi - \chi_\infty$

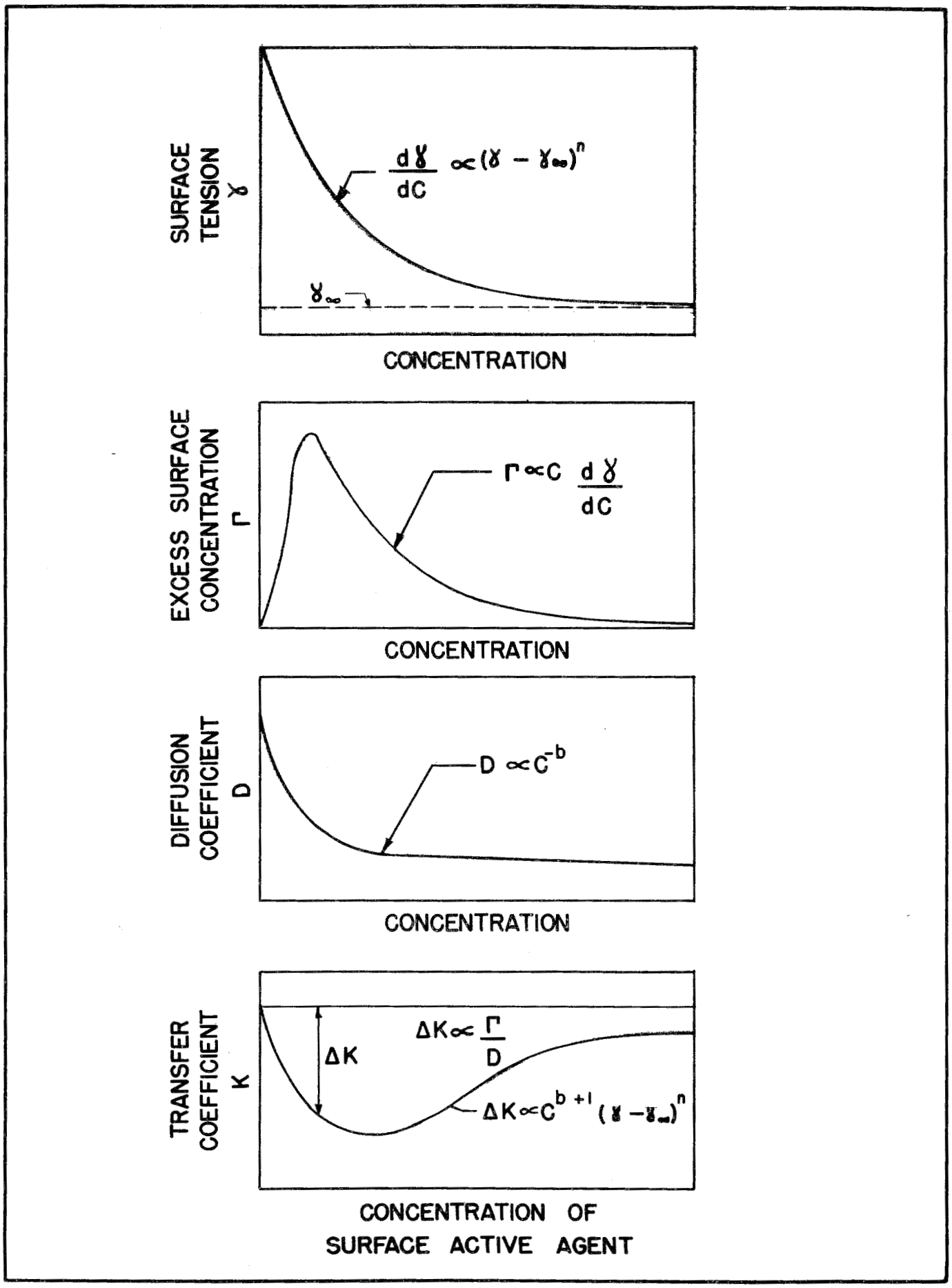


Fig. 1 - General Graphical Relationships

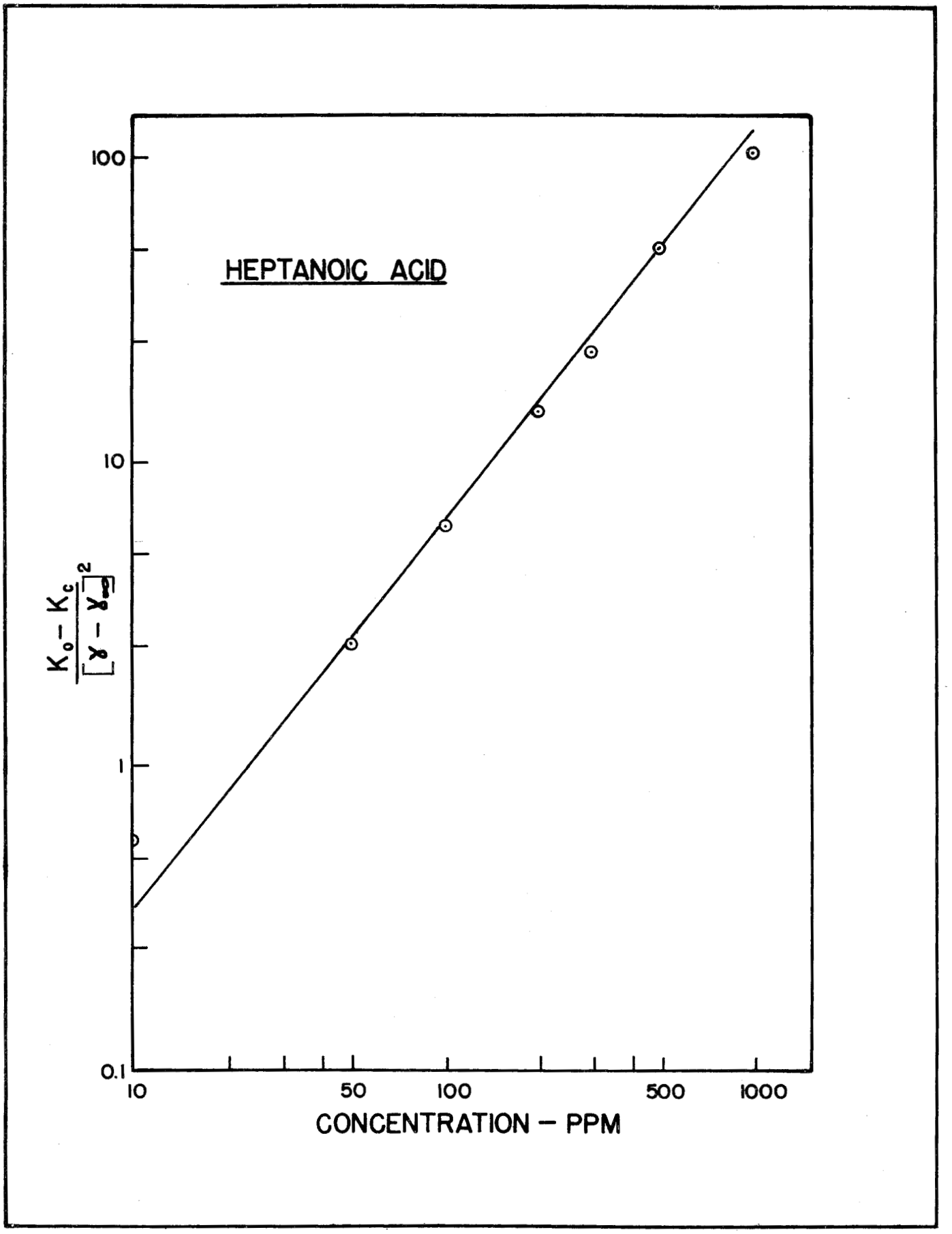


Fig 2 – Heptanoic Acid - Graphical Correlation of Data

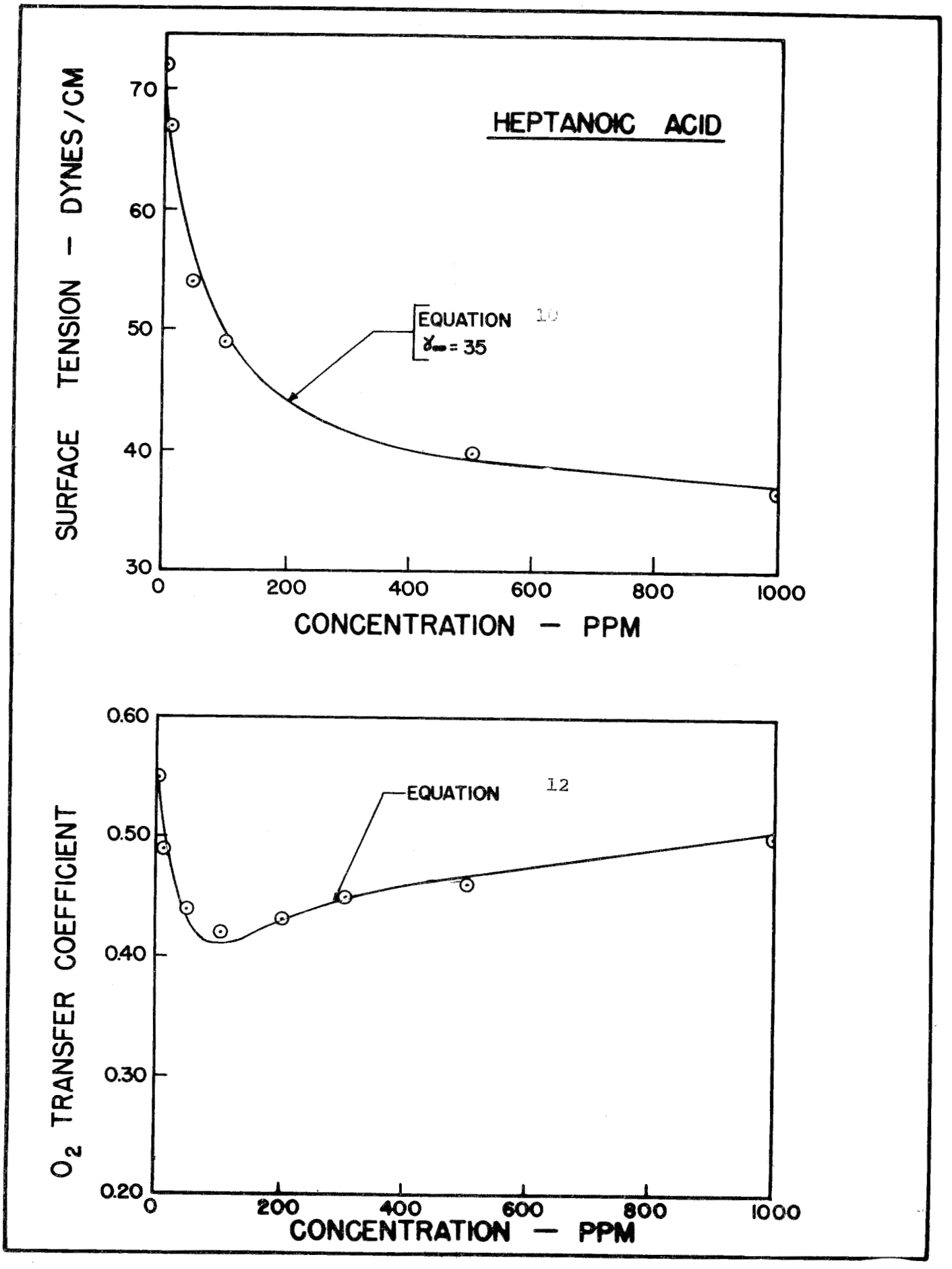
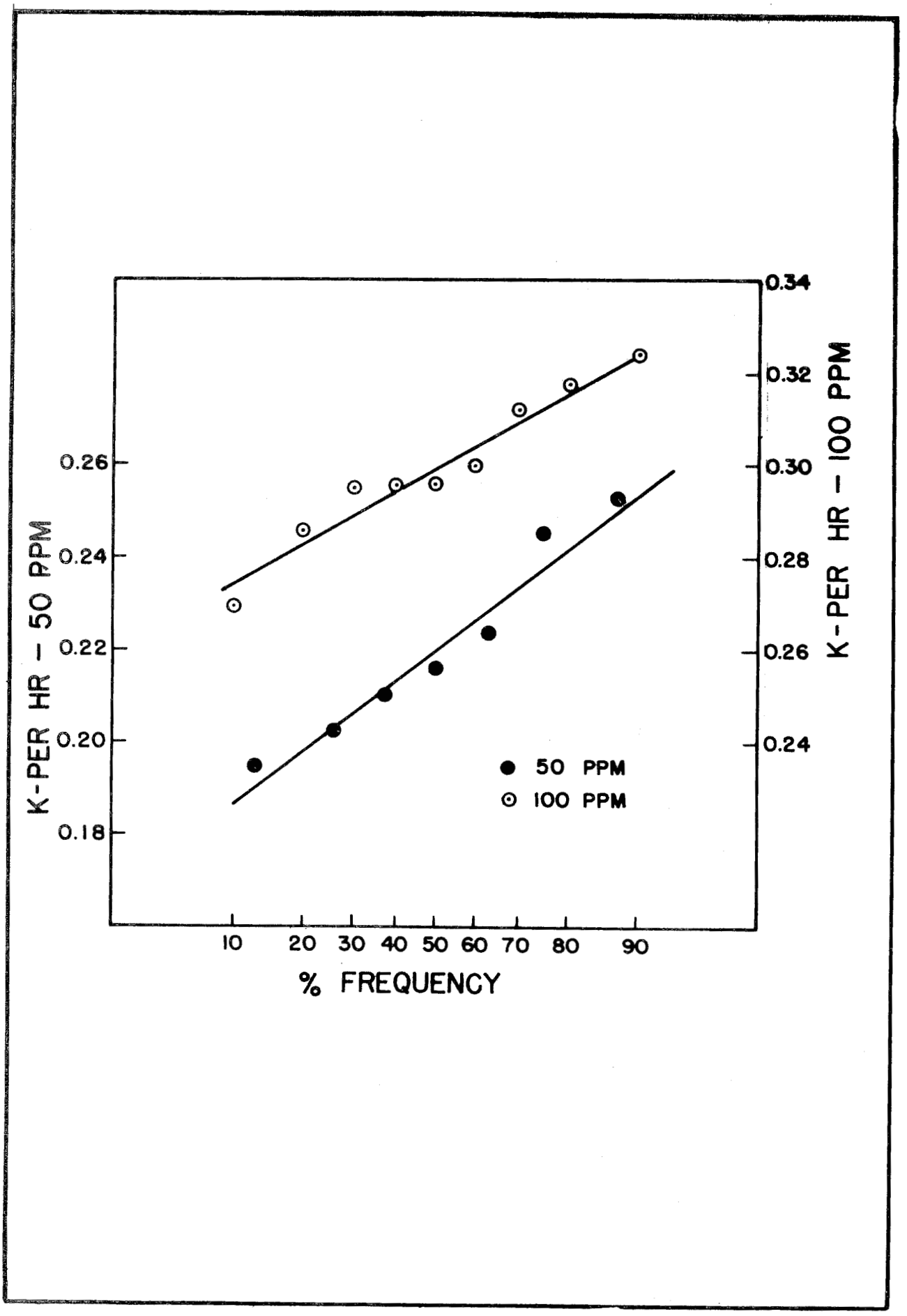


Fig. 3. - Heptanoic Acid - Surface Tensions & Reaeration Coefficients



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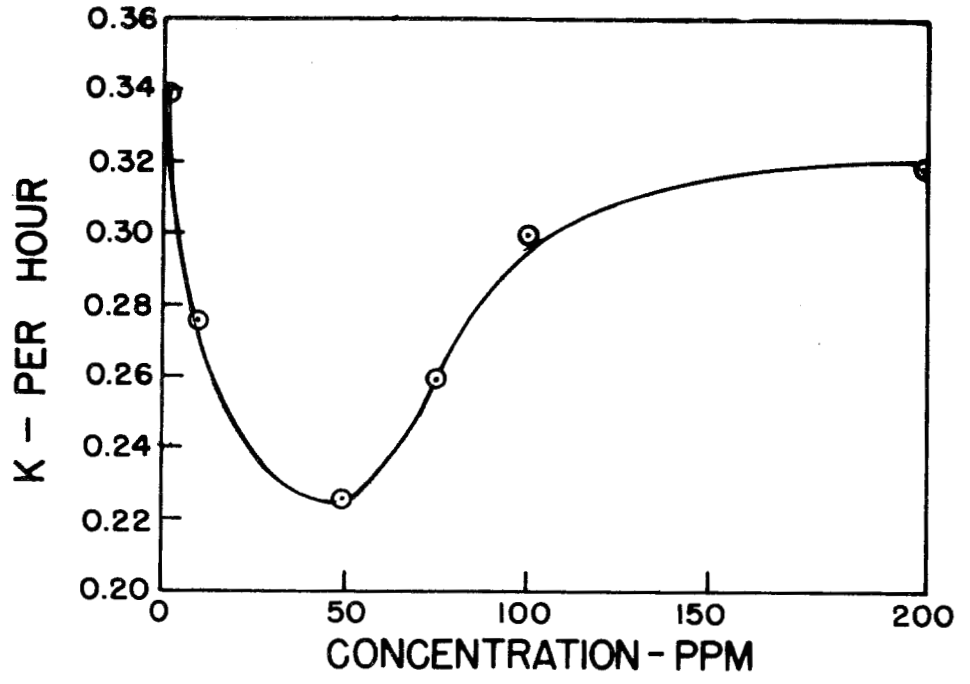


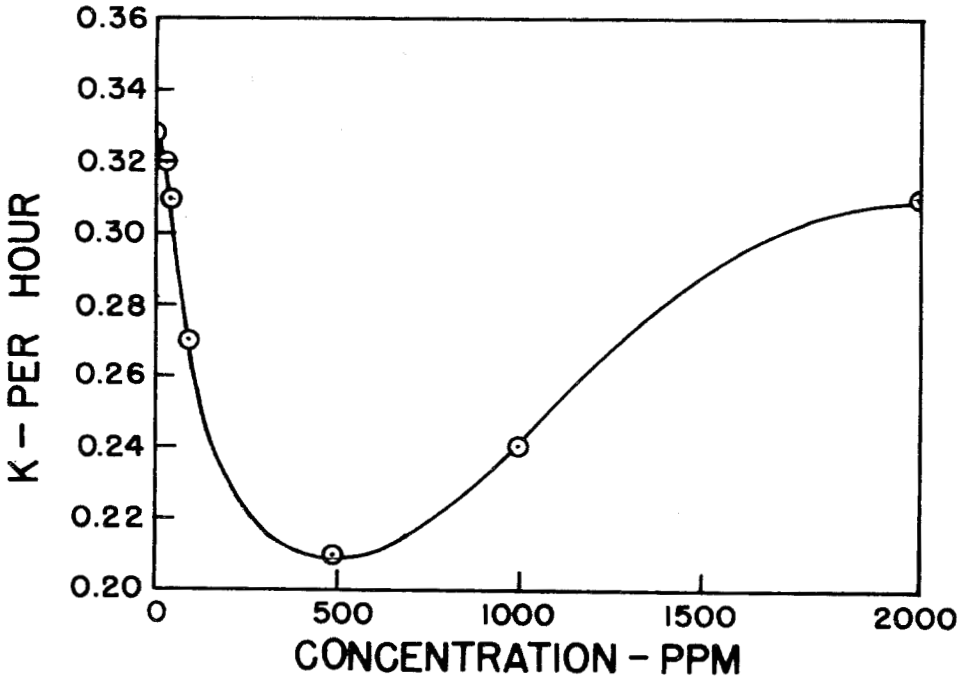
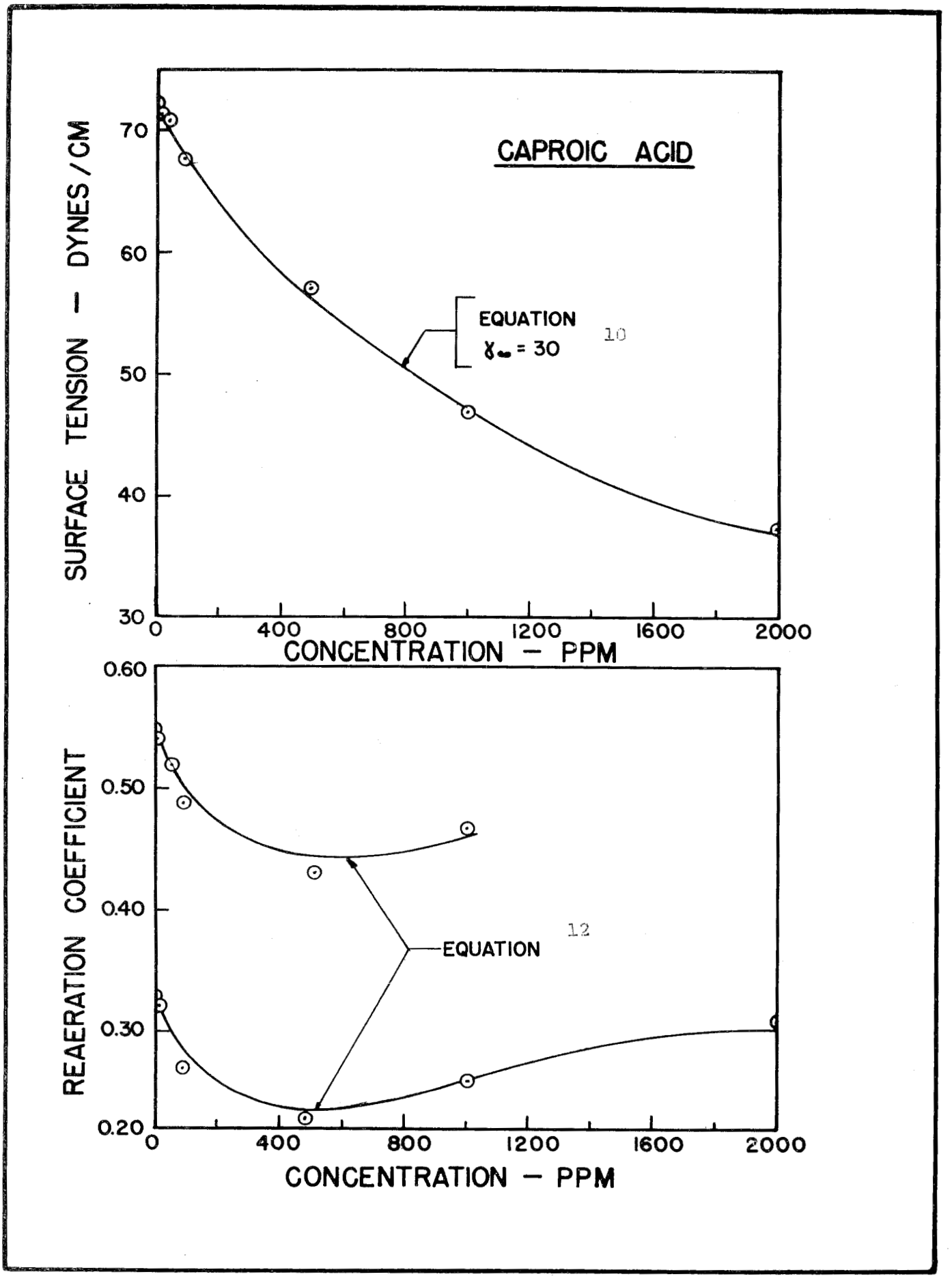


Fig. 9 - Sodium Lauryl Sulfate - Surface Tensions & Reaeration Coefficients



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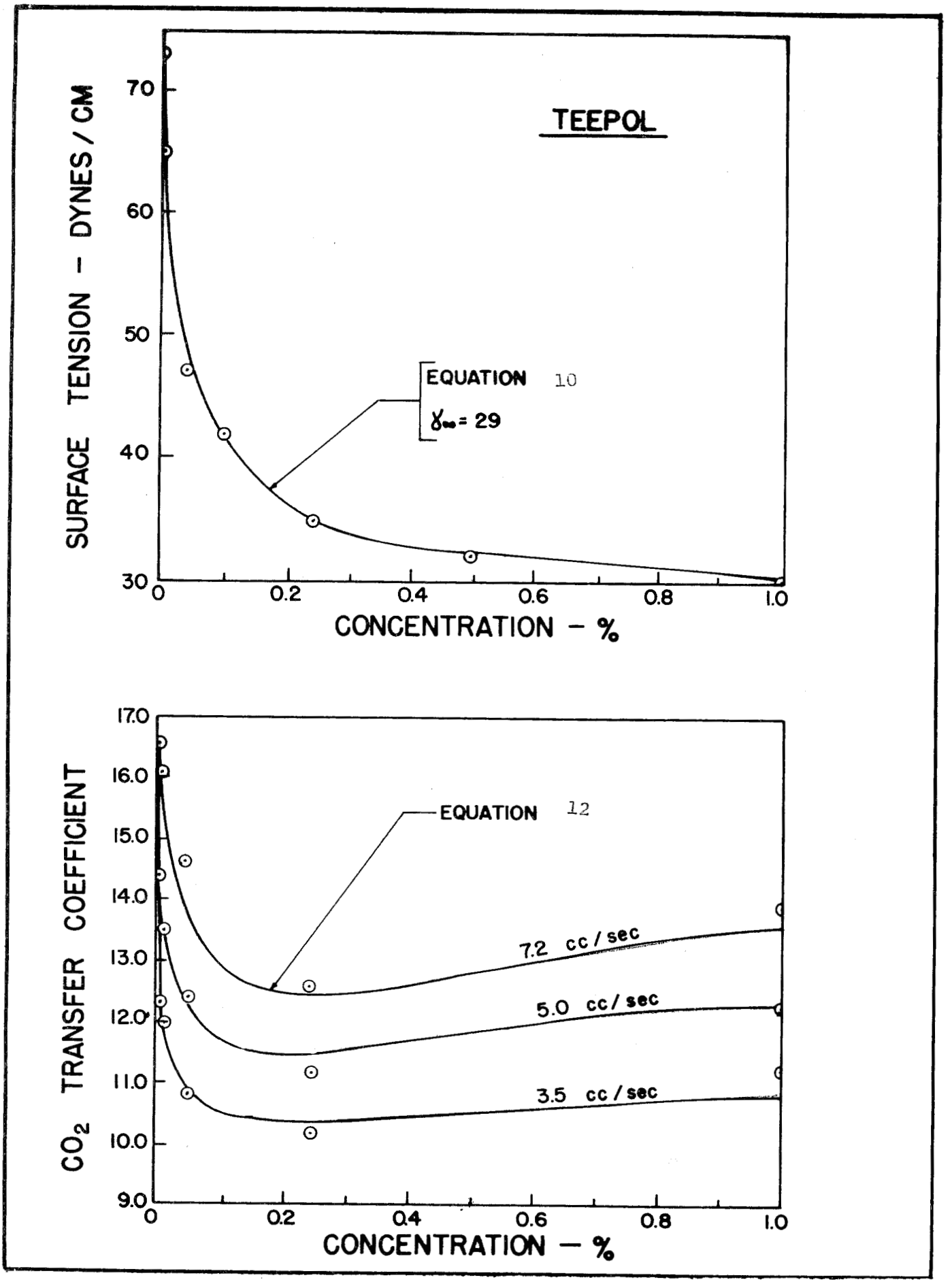

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THE DEVELOPMENT AND CALIBRATION OF A SPATIALLY SIMPLIFIED MULTI-CLASS PHYTOPLANKTON MODEL FOR SAGINAW BAY, LAKE HURON

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FOREWORD

As part of the Great Lakes Basin Commission's Great Lakes Environmental Planning Study (GLEPS), a variety of alternate control strategies for reducing pollutant inputs to the Great Lakes have been studied and their cost-effectiveness compared. Further, the probable response of the Great Lakes system to these alternative strategies has been sought. An effective way of assessing this response is through mathematical models. Therefore, a detailed evaluation of models that have been developed for understanding or managing Great Lakes waters was conducted early in the GLEPS study. Since then, additional reports on specific models either have been or will be prepared.

This report constitutes a contribution to the subregional model section of GLEPS. It documents the development and calibration of what is probably the most sophisticated model of any Great Lakes embayment. The model addresses the relationship between nutrient input reductions and biological changes, particularly the change in phytoplankton biomass. The model has already found practical application in the negotiations of the 1978 Water Quality Agreement between the U.S. and Canada where it was used to estimate phosphorus loads necessary to achieve alternate water quality objectives for Saginaw Bay. It is hoped that publication of this report will assist in the wise management of Saginaw Bay and the Great Lakes ecosystem in general, as well as provide scientific insight on processes affecting phytoplankton dynamics.

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ABSTRACT

A multi-class, internal nutrient pool, phytoplankton simulation model was developed and applied to an extensive set of field data acquired in 1974 on Saginaw Bay, Lake Huron. Phytoplankton biomass was partitioned into five functional groups: diatoms, greens, heterocystous blue-greens, non-heterocystous blue-greens, and "others". The nutrients included in the model were phosphorus, nitrogen, and silicon. The model was applied to a single spatial segment encompassing the inner portion of Saginaw Bay.

To supplement the results of traditional chemical and biological measurements, an extensive series of phytoplankton cell volume measurements and zooplankton dry weight measurements were conducted at the species level to provide data for comparison with model output. These data provided additional insight into the biological dynamics of Saginaw Bay, quite apart from their use in the model calibration.

Component analyses were conducted to determine the relative importance of temperature, light, and nutrients in controlling phytoplankton growth rates. Results indicated that temperature and light were relatively more growth rate limiting than nutrients. In an average sense, results indicated that nitrogen was relatively more growth rate limiting than phosphorus over the annual cycle. Further analysis indicated that there were important differences among individual phytoplankton groups. At various times, and for various phytoplankton groups, phosphorus, nitrogen, and silicon were all important in limiting either the rate of growth and/or the maximum sizes of the phytoplankton crops.

Component analyses were conducted to determine the relative importance of phytoplankton loss processes. The results indicated that non-predatory death processes were very important, especially for blue-greens. Grazing was the most important loss process for diatoms and green algae during the July-August period.

Model results confirmed the soundness of pursuing a strategy of phosphorus control to reduce excessive phytoplankton growth in Saginaw Bay. Results were consistent with the hypothesis that while nitrogen and silicon were important in phytoplankton-nutrient dynamics, the supply of phosphorus will ultimately determine the size of the nuisance blue-green component of the total crop because N_2-fixing blue-greens do not have absolute requirements for dissolved nitrogen and silicon.

An analysis of phytoplankton-phosphorus dynamics indicated that phosphorus requirements of spring and fall diatom crops were satisfied primarily

by external loading; phosphorus requirements of summer blue-green crops were satisfied primarily by recycle processes within the water column. Upon cell death, direct nutrient recycle to the available compartments in the water column from excess internal phytoplankton stores was extremely important for both phosphorus and nitrogen.

An extensive series of sensitivity analyses was conducted with the calibrated model. These analyses included systematic variations to external forcing functions, phytoplankton growth rates, and other rate coefficients in the model. Results were expressed in terms of percent changes in phytoplankton peak concentrations and annual integrated gross productions, relative to the final calibration.

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ABBREVIATIONS AND SYMBOLS

ABBREVIATIONS

A	--phytoplankton concentration in mg dry wt/l
$ADUM_{k\ell}$	--minimum concentration of phytoplankton ℓ necessary for zooplankton k to begin grazing
ASINK	--phytoplankton sinking rate in meters/day
$AZMIN_k$	--refuge concentration of phytoplankton below which zooplankton k can not graze
BDETH	--maximum zooplankton death rate in day^{-1}
CIS	--Cranbrook Institute of Science
CONCP, CONCN	--internal concentration factors for phosphorus and nitrogen, respectively (dimensionless)
FACT	--phytoplankton cell size in mg dry wt/cell
f(L)	--phytoplankton light reduction factor (dimensionless)
f(T)	--phytoplankton temperature reduction factor (dimensionless)
GLRD	--Great Lakes Research Division, University of Michigan
IIASA	--International Institute for Applied Systems Analysis
IFYGL	--International Field Year for the Great Lakes
IJC	--International Joint Commission
Ke	--light extinction coefficient in $meter^{-1}$
KNCELL	--intracellular half-saturation constant for nitrogen-dependent growth in moles N/cell
KPCELL	--intracellular half-saturation constant for phosphorus-dependent growth in moles P/cell

ABBREVIATIONS

KSCM	--half-saturation constant for silicon-dependent growth of diatoms in moles Si/l
$KZSAT_k$	--half-saturation concentration for grazing by zooplankton k
LLRS	--Large Lakes Research Station
MDNR	--Michigan Department of Natural Resources
P, N	--actual moles of phosphorus (nitrogen) per phytoplankton cell
PCA, NCA	--intracellular available phosphorus (nitrogen) concentrations in moles/liter cell volume
PCAMIN, NCAMIN	--minimum intracellular concentrations, corresponding to PSAMIN and NSAMIN, respectively, for available phosphorus (nitrogen) in moles/liter cell volume
PCM, NCM, SCM	--concentrations of available nutrients (phosphorus, nitrogen, silicon) in water column in moles/l
PDETH	--maximum predatory death rate for zooplankton in liter/mg-day
PHOTO	--photoperiod (dimensionless)
PK1, NK1	--affinity coefficient for phosphorus (nitrogen) uptake mechanism in liter/mole
PO, NO	--minimum cell quota of phosphorus (nitrogen) per phytoplankton cell in moles/cell
PSA, NSA	--actual total phosphorus (nitrogen) in phytoplankton cells in moles/mg dry wt
PSAMIN, NSAMIN	--minimum quota of phosphorus (nitrogen) in phytoplankton cells in moles/mg dry wt
$PSAT_k$	--saturation concentration of zooplankton k above which predatory death rate remains constant
Q	--water circulation rate in volume/day
R1PM, R1NM	--maximum phosphorus (nitrogen) uptake rate in day^{-1}
RADINC	--incident solar radiation in langleys/day

ABBREVIATIONS

RADSAT	--saturation light intensity for phytoplankton growth in langleys/day
$RAGRZD_{\ell}$	--rate at which a phytoplankton ℓ is ingested (grazed) by zooplankton in mg A/liter day
RAMAX	--phytoplankton maximum growth rate at 20°C in day^{-1}
RLYS	--phytoplankton decomposition rate in liter/mg day
RRESP	--phytoplankton respiration rate in day^{-1}
RTOP, RTON, RTOS	--rates of transformation from unavailable nutrient forms (phosphorus, nitrogen, silicon) to available forms in day^{-1}
RZ	--zooplankton specific growth rate in day^{-1}
RZMAX	--zooplankton maximum ingestion rate in day^{-1}
$RZPEX_k$, $RZNEX_k$, $RZSEX_k$	--nutrient (phosphorus, nitrogen, silicon) excretion by zooplankton k to unavailable nutrient pool in moles/mg zooplankter-day
SPGR	--phytoplankton specific growth rate in day^{-1}
SSA	--silicon composition of diatoms in moles/mg dry wt
T	--temperature in °C
TCROP	--total phytoplankton concentration in mg dry wt/l
TOP, TON, TOS	--concentration of unavailable nutrients (phosphorus, nitrogen, silicon) in moles/l
TOPSNK, TONSNK, TOSSNK	--sinking rates of unavailable nutrient forms (phosphorus, nitrogen, silicon) in meters/day
ULRS	--Upper Lakes Reference Study
UMBS	--University of Michigan Biological Station - Pellston
USEPA	--United States Environmental Protection Agency
USGS	--United States Geological Survey
V	--system volume
WPCM, WNCM, WSCM	--external loading rates of available nutrients (phosphorus, nitrogen, silicon) in moles/day

ABBREVIATIONS

WTOP, WTON, WTOS	--external loading rates of unavailable nutrients (phosphorus, nitrogen, silicon) in moles/day
Z	--zooplankton concentration in mg dry wt/l
ZASSIM	--zooplankton assimilation efficiency (dimensionless)
$ZEFF_{k\ell}$	--ingestion efficiency of zooplankton k for phytoplankton ℓ (dimensionless)
ZDETH	--specific zooplankton death rate in day^{-1}
$ZKDUM_k$	--effective half-saturation concentration of total phytoplankton for grazing by zooplankton k
$ZSAFE_k$	--refuge concentration of zooplankton k below which zooplankton k is not subject to predatory grazing

Note: The addition of the suffix "BD" to a variable refers to the boundary value of the variable.

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THE DEVELOPMENT AND CALIBRATION OF A SPATIALLY SIMPLIFIED MULTI-CLASS PHYTOPLANKTON MODEL FOR SAGINAW BAY, LAKE HURON

SECTION 1

INTRODUCTION

This project was initiated as part of the Upper Lakes Reference Study (ULRS) sponsored by the International Joint Commission (IJC). The principal goal of the ULRS was to acquire baseline data on water quality conditions in Lake Superior and Lake Huron. Saginaw Bay is an important component of the Lake Huron system and is one of the most highly enriched bodies of water in the Laurentian Great Lakes. The development of water quality models on Saginaw Bay was closely coordinated with comprehensive field and laboratory experimental studies.

The principal issue addressed in the model development effort was cultural eutrophication, defined as overproduction of phytoplankton biomass due to increased nutrient loadings as a result of man's activities in the watershed. The purpose of the modeling effort was to develop a deterministic phytoplankton simulation model that could describe the cause-effect connection between external nutrient loading and phytoplankton growth in Saginaw Bay. The objectives were twofold: first, to gain insight into the relevant physical, chemical, and biological processes affecting phytoplankton growth; and second, to use the model as a tool for comparing future effects of various wastewater management strategies.

This report constitutes a documentation of the model development and calibration phase of the project using a spatially simplified version of the model. The model was calibrated to a comprehensive set of field data acquired during 1974 on Saginaw Bay. Ongoing efforts involve the calibration and verification of a spatially segmented version of the model to two independent sets of data acquired on Saginaw Bay during 1974 and 1975. This more advanced version of the model will be used to generate a set of revised predictions corresponding to expected reductions in external phosphorus loads. Subsequently, these *a priori* results will be compared to the outcome of a follow-up field survey to be conducted in 1980 on the Lake Huron-Saginaw Bay system.

The emphasis in the present report is on the research aspects of the model development and calibration. In this context, model development is seen as providing a quantitative framework for organizing and interpreting experimental data. The calibrated model is seen as providing a tool for testing different hypotheses on a whole-system scale.

SECTION 2

CONCLUSIONS

As a result of this phytoplankton modeling study of Saginaw Bay, the following conclusions were drawn:

1. The feasibility of applying a sophisticated, multi-class, internal nutrient pool kinetic model to an actual physical system has been demonstrated.

2. The model development effort was responsible for stimulating several important by-products as a result of model requirements for experimental data. Chief among these by-products was an extensive set of phytoplankton cell volume measurements at the species level which was required to provide calibration data for model output. These data constitute an independent set of measurements for phytoplankton abundance in Saginaw Bay, in supplement to traditional measurements of chlorophyll concentrations. Valuable new insights were gained by comparing and contrasting these two data sets.

3. Model results indicated that temperature and light were the dominant factors controlling phytoplankton growth rates in Saginaw Bay. Most of the difference between maximum theoretical growth rates and actual specific growth rates was due to non-optimal temperatures and vertically-averaged, non-optimal light intensities that usually existed in the water column.

4. Results indicated that grazing was the most significant loss process for diatoms and greens during the July-August period. Grazing accounted for 25 to 70 percent of total losses for diatoms, and 40 to 70 percent of total losses for greens during this period.

5. Results of component analyses for phytoplankton loss processes indicated that non-predatory death processes were important, especially for blue-green algae. Respiration, defined as population losses due to self-maintenance requirements, accounted for 15 to 50 percent of total losses for diatoms and greens, respectively, and 20 to 65 percent of total losses for blue-greens. Decomposition, assumed to be principally mediated by bacteria, accounted for 25 percent of total losses for diatoms and greens, and 40 percent of total losses for blue-greens during periods of peak biomass.

6. In an average sense, model results indicated that nitrogen was relatively more growth rate limiting than phosphorus over the annual cycle. Further analysis of results indicated that important differences occurred among individual phytoplankton groups. Results for diatoms indicated that nitrogen was rate limiting for most of the year; however, phosphorus, nitrogen, and silicon were equally rate limiting in mid-May, and extreme silicon limitation occurred from mid-May to the end of June. Results for greens and non-N_2-fixing blue-greens indicated that nitrogen was relatively more rate limiting than phosphorus for the entire year. Results for N_2-fixing blue-greens indicated a shift from nitrogen limitation to phosphorus limitation during the period of minimum dissolved available nutrient concentrations in the water column.

7. Results of sensitivity analyses for nutrient recycle, and results of nutrient load reduction simulations, confirmed the soundness of pursuing a strategy of phosphorus control to reduce excessive phytoplankton growth in Saginaw Bay, especially the nuisance blue-green component of the total crop. Results of the load reduction simulations indicated that blue-green production responded to a much greater degree than diatom production for a given change in phosphorus load. Results of the sensitivity analyses indicated that nitrogen control in the absence of phosphorus control would increase the production of N_2-fixing blue-green phytoplankton.

8. Results of an analysis of phytoplankton-phosphorus dynamics indicated that external nutrient loads satisfy most of the phytoplankton growth requirements during the early and latter parts of the year, and that nutrient recycle satisfied most of the phytoplankton growth requirements during the third quarter of the year. The most important recycle mechanism for phosphorus and nitrogen was direct recycle from the excess intracellular pools upon cell losses due to grazing, respiration, and decomposition. Recycle as a result of respiration and decomposition losses alone contributed 70 percent of the nutrient requirements for growth of blue-green algae during the month of August.

9. An extensive series of sensitivity analyses was conducted with the calibrated model. One of the most significant results was the extreme sensitivity of the phytoplankton to variations in the light extinction coefficient in the water column, and the relative insensitivity to variations in incident solar radiation. In general, the phytoplankton were sensitive to variations in maximum growth and ingestion rates for the phytoplankton and zooplankton, respectively, and to variations in the associated half-saturation concentrations. The phytoplankton were more sensitive to variations in zooplankton assimilation efficiency and phytoplankton respiration rate than to variations in any other loss-related parameters. It was significant that the phytoplankton were relatively insensitive to variations in the conversion rates from unavailable to available nutrient forms in the water column. This result was most probably due to the relatively short hydraulic detention time of the bay.

SECTION 3

RECOMMENDATIONS

Based on the results and conclusions of this phytoplankton modeling study of Saginaw Bay, the following recommendations are made:

1. Measurements of phytoplankton cell biovolumes at the species level, and quantum measurements of underwater light intensities should be conducted on a routine basis as part of the Great Lakes surveillance program.

2. Research is needed on phytoplankton-nutrient kinetic interactions at non-optimal temperature and light levels. Temperature and light are usually the principal factors controlling phytoplankton growth rates in natural systems; however, most present phytoplankton-nutrient kinetics research is conducted at optimal temperature and light levels.

3. Research is needed to better understand and quantify non-predatory death processes for phytoplankton.

4. Research should be continued with a spatially segmented version of the model. The field data show that there are strong horizontal gradients within the inner portion of Saginaw Bay. The present spatially simplified model does not describe any of these variations, nor does it describe any of the strong horizontal gradients between the inner and outer portions of the bay.

5. The Saginaw Bay system should be used as a case study for intercomparisons of different types of phytoplankton models. Saginaw Bay is a highly complicated system, but is of manageable proportions. The existing data base is sufficiently comprehensive to provide calibration data for any existing phytoplankton simulation model.

SECTION 4

BACKGROUND

This section contains a brief summary of those background aspects of Saginaw Bay that are germane to the model development effort. Refer to Freedman (1974) and Bratzel et al. (1977) for more comprehensive information on existing conditions and historical trends. Detailed results of the field surveys that were conducted on Saginaw Bay as part of the ULRS are contained in separate project reports by Smith et al. (1977), Stoermer et al. (1979), and Gannon and Bricker (1979).

Saginaw Bay is a broad, shallow extension of the western shore of Lake Huron (Figure 1). The bay is oriented in a southwestward direction and is approximately 82 km long and 42 km wide. For convenience, Saginaw Bay is usually divided into the indicated inner and outer portions. These portions are approximately equal in surface area; however, only 30 percent of the total water volume is contained in the inner portion. Average depths of the inner and outer portions are approximately 6 m and 15 m, respectively.

The total area of the Saginaw Bay watershed is approximately 21,000 km^2. The Saginaw River is the major tributary, accounting for over 90 percent of total tributary inflow to the bay. The principal land use categories in the watershed are agriculture and forest. The total population of the watershed is slightly over 1.2 million. Most of the population is concentrated into four major urban-industrial centers in the State of Michigan: Bay City, Midland, Saginaw, and Flint. These centers are all situated along the Saginaw River or its major tributaries.

The principal water uses in Saginaw Bay include municipal and industrial water supply, waterborne transportation, recreation, commercial fishing, and waste assimilation. These uses are severely impacted by considerable quantities of waste discharges and runoff to the bay as a result of human activities in the watershed. Saginaw Bay has been identified by the IJC as one of 44 Great Lakes "Problem Areas" (Great Lakes Water Quality Fifth Annual Report - Appendix B 1977).

Taste and odor and filter-clogging problems experienced by municipal water treatment plants on Saginaw Bay are of principal importance to the present study. Measurements of threshold odor and phytoplankton cell numbers were conducted on a daily basis at the Saginaw-Midland Water Supply System intake from November 1973 to October 1974 (Chartrand 1973). This intake, located in the outer portion of the bay, accounts for over 80 percent of the total municipal water supply. Forty-two percent of threshold

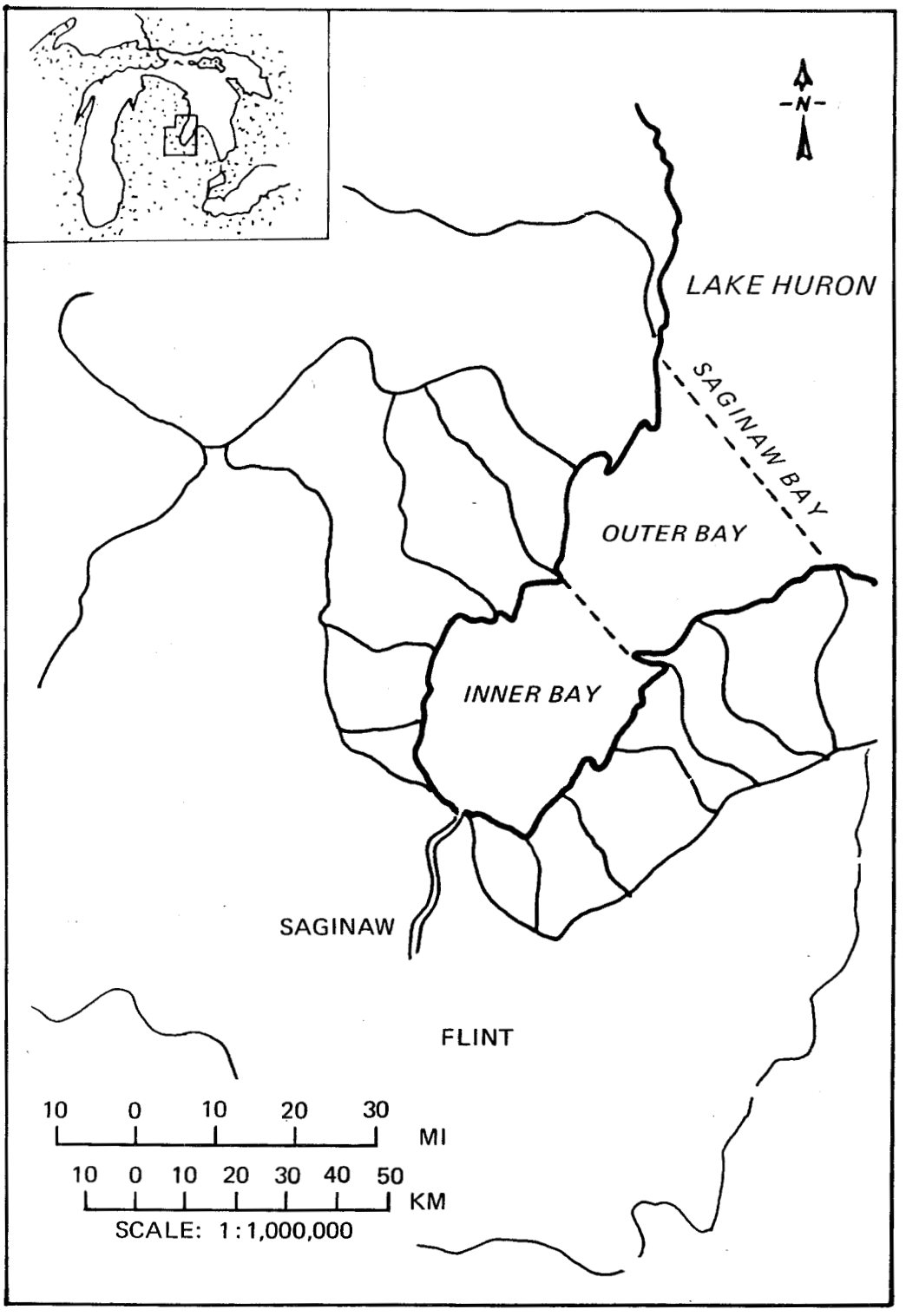


Figure 1. Saginaw Bay and its watershed.

odor numbers were found to be equal to or greater than the U.S. Public Health Service standard of 3. Statistical analyses of these data revealed a strong correlation between threshold odor number and phytoplankton cell number concentration, particularly for the blue-green component of the total crop as represented by the alga Aphanizomenon at the intake site (Figures 2-3). Bratzel et al. (1977) suggested that high threshold odor numbers appear to be due to the products of decomposition of algal biomass by Actinomycetes (aquatic fungi) and by the Aphanizomenon themselves.

One of the principal reasons for pursuing the development of a multiclass phytoplankton model on Saginaw Bay, as opposed to a conventional chlorophyll-based model, was to directly address water use interferences caused by the blue-green component of the total phytoplankton crop. Dolan (1977) showed that there was a statistically significant correlation between measurements of blue-green algae concentrations in the inner bay, and measurements of threshold odor at the Whitestone Point intake in the outer bay. Even though the Saginaw-Midland intake is located in the outer bay, Paul (1977) showed that blue-green algae produced in the inner bay and transported by water movements to the outer bay are responsible for taste and odor problems at this intake.

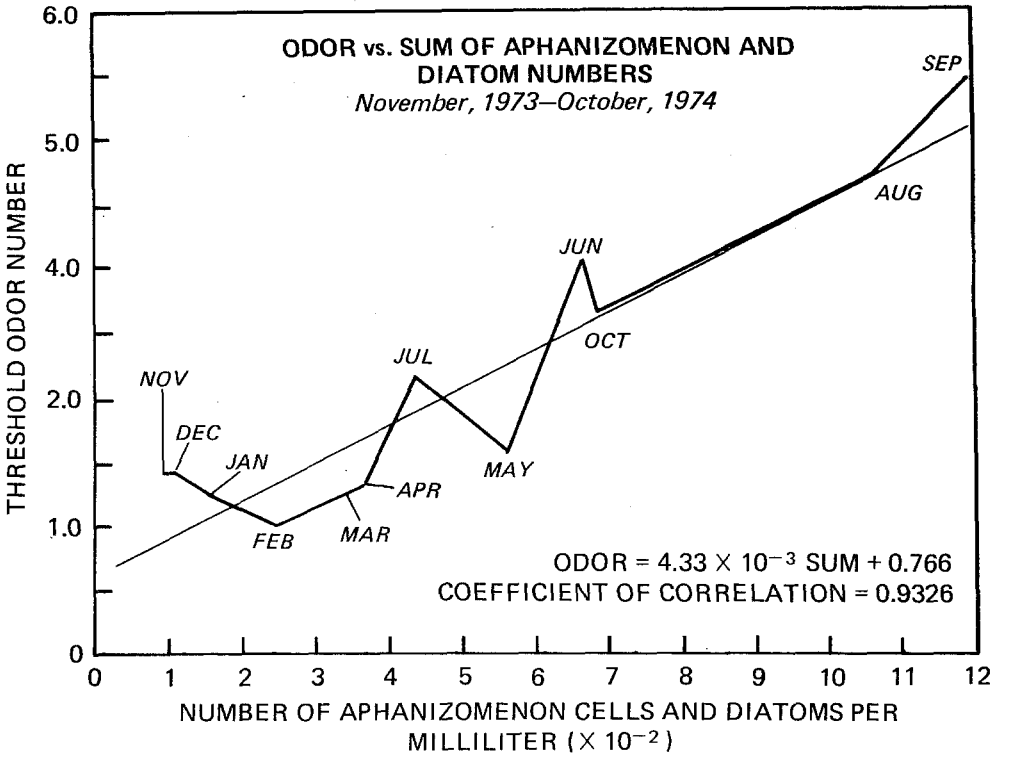
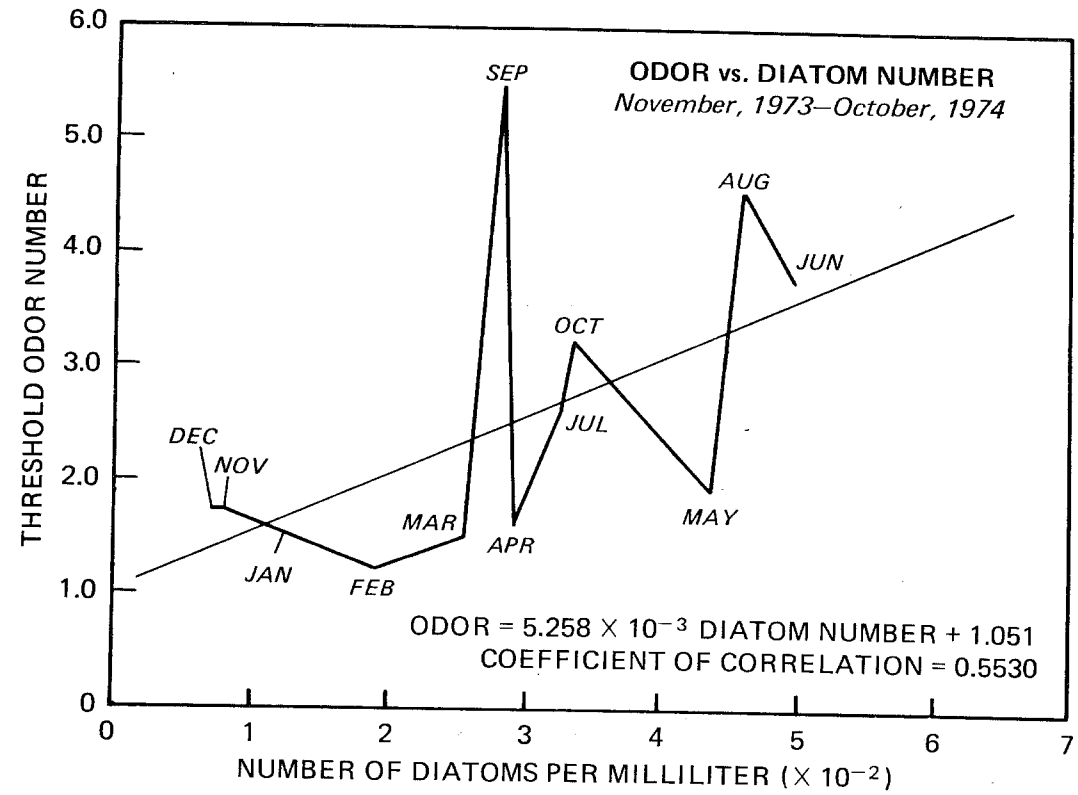


Figure 2. Statistical correlation between threshold odor and phytoplankton cell number concentration at the Whitestone Point water intake.



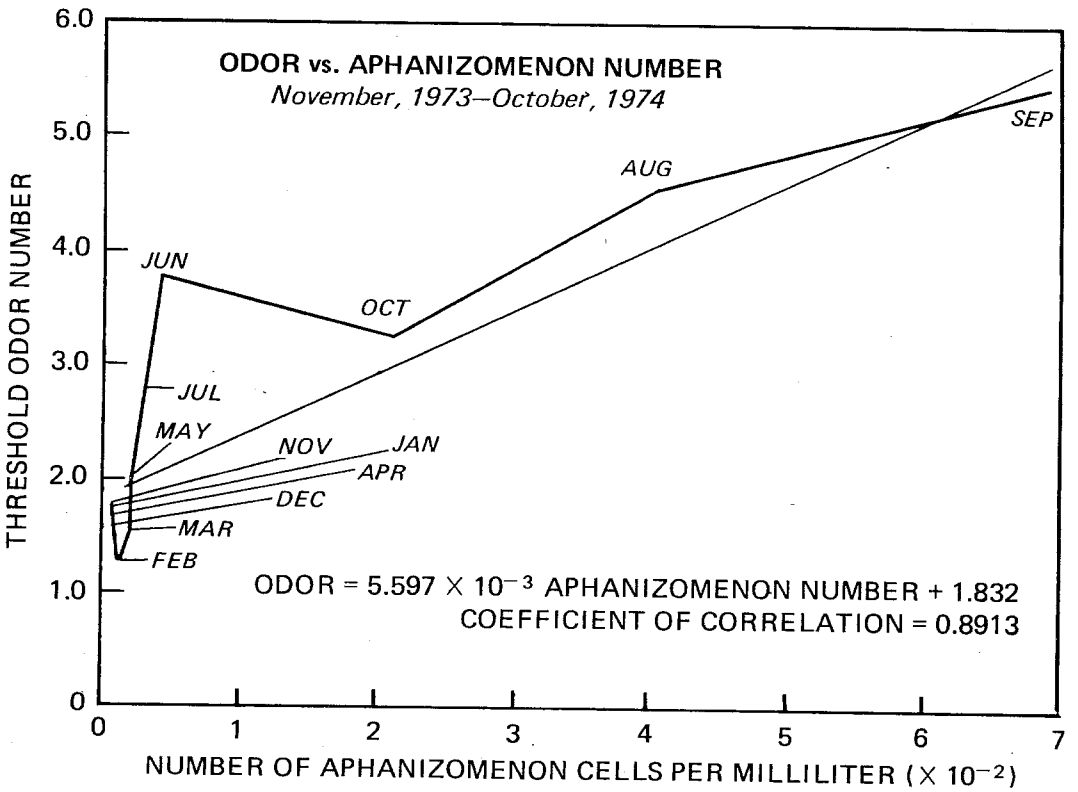


Figure 3. Statistical correlations between threshold odor, and diatom and Aphanizomenon cell numbers at the Whitestone Point water intake.

SECTION 5

MODEL DEVELOPMENT

INTRODUCTION

This section contains a description of the various processes and mechanisms included in the model. Emphasis is placed on conceptual development. The actual equations for all state variables are contained in Appendix A. References to these equations are made throughout the text, as appropriate. Appendices B through D contain tabulations of model coefficients, initial conditions, and forcing functions. The information contained in the appendices is sufficient to reproduce any of the results in the report.

RATIONALE AND APPROACH

Phytoplankton dynamics is a function of temperature, light, nutrients, zooplankton grazing, system morphometry, and hydrography. It is not possible to simulate all of these dynamic processes to their ultimate level of detail. An intractable computational problem would result and, assuming solutions could be obtained, the output of such a simulation would be in such complex terms that the desired information would be impossible to understand. Judgements must be made regarding the level of resolution of phytoplankton biomass, the principal nutrients, and the space and time scales to be simulated. These judgements must be made within the context of the purposes for which the model is being developed, and within the state of our knowledge of the processes to be simulated.

Although the present model was developed for Saginaw Bay, an attempt was made to structure its mechanisms in a general fashion so that it could be applied to other physical systems, particularly Great Lakes systems. A preliminary application of the model has been made to data from the International Field Year for the Great Lakes (IFYGL) on Lake Ontario (Bierman, unpublished results).

Phytoplankton

Phytoplankton biomass, on the basis of dry weight, was resolved into five functional groups: diatoms, greens, heterocystous blue-greens, non-heterocystous blue-greens, and "others" (Figure 4). The latter category includes primarily dinoflagellates and cryptomonads. Heterocystous blue-greens consist of those species capable of fixing atmospheric nitrogen, as well as using dissolved combined nitrogen. Non-heterocystous blue-greens

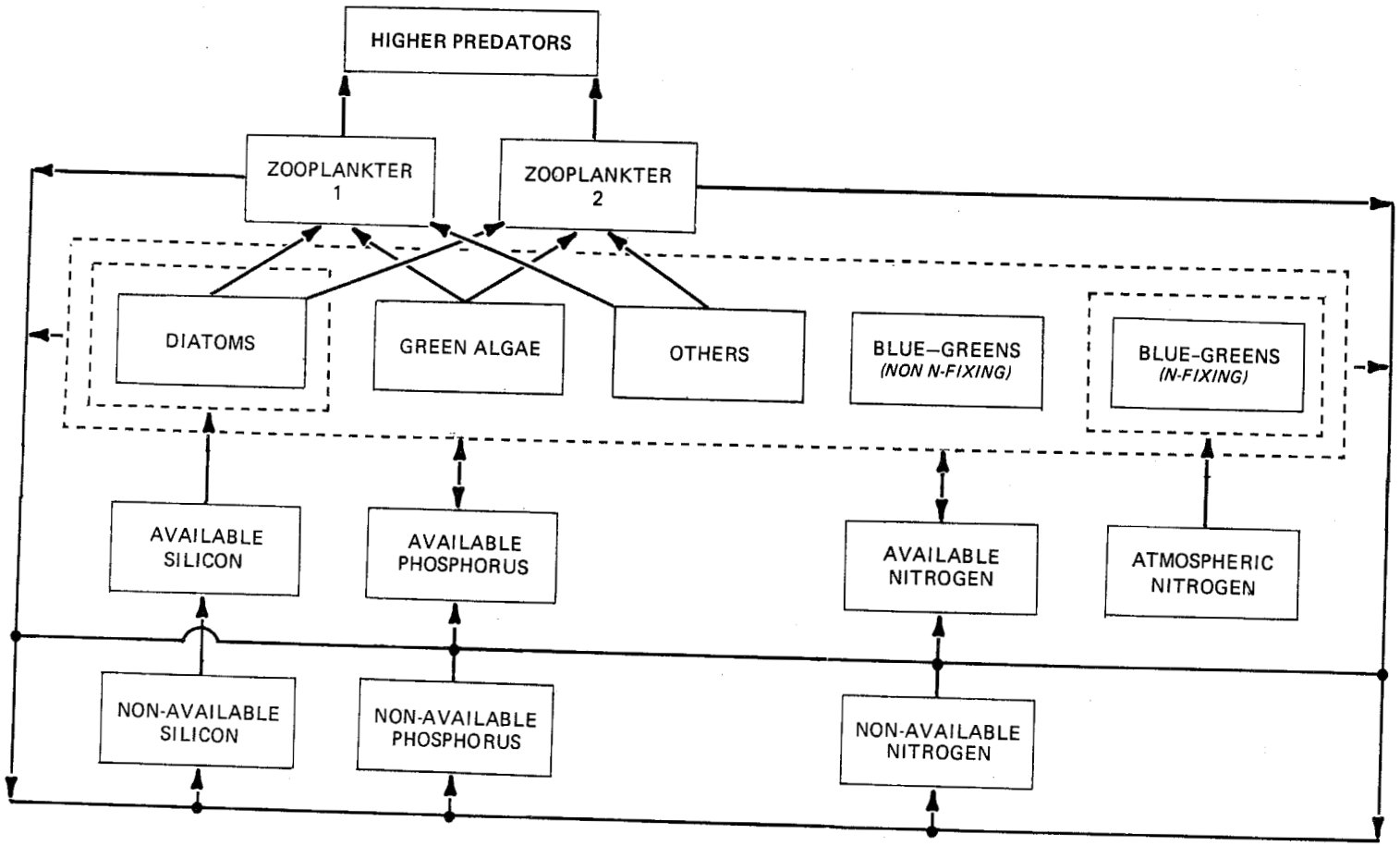


Figure 4. Schematic diagram of the principal model compartments and interaction pathways.

consist of those species which have an absolute requirement for dissolved combined nitrogen. Throughout this report, these two groups of blue-green algae will be referred to as "N_2-fixing" and "non-N_2-fixing" blue-greens, respectively.

The principal reason for this multi-class approach was that there are important physiological differences among the five groups. Diatoms are the only group with a major absolute requirement for silicon. The N_2-fixing blue-greens are the only group which can grow independently of the supply of dissolved available nitrogen, defined as the sum of ammonia, nitrate, and nitrite. The relative maximum growth rates and temperature optima among the groups are such that a typical successional pattern during the growing season begins in spring with diatoms, progresses to greens and "others", and finally leads to the development of blue-greens in late summer and fall. An important characteristic shared by all of the groups is an absolute requirement for phosphorus.

Another important basis for differentiation was that diatoms, greens, and "others" are grazed by zooplankton and blue-greens are not significantly grazed. Freedom from grazing can frequently contribute to blue-green algae forming objectionable floating scums.

The above differences among the five functional groups are directly related to important issues in the Great Lakes. Schelske and Stoermer (1971) hypothesized that increasing silica depletion in Lake Michigan will lead to a species shift from diatoms to green and blue-green algae. Vanderhoef et al. (1974), and Mague and Burris (1973) reported the occurrence of N_2 fixation in Green Bay and the Western Basin of Lake Erie, respectively, when dissolved nitrogen levels became extremely low. As indicated previously, taste and odor problems in Saginaw Bay are strongly correlated with the blue-green component of the total phytoplankton crop. These issues can only be directly addressed using a model which partitions phytoplankton biomass into separate functional groups.

Nutrients

The nutrients included in the model are phosphorus, nitrogen, and silicon. These are generally considered to be the most important nutrients limiting growth rates and maximum sizes of phytoplankton populations in natural waters. Schindler (1977) re-emphasized the importance of phosphorus as a limiting nutrient. He hypothesized the existence in lakes of biological mechanisms which are capable of correcting algal deficiences of carbon and, at least in some cases, of nitrogen. On the basis of bioassay experiments with natural populations, Schelske et al. (1978) reported that phosphorus is the principal growth-limiting nutrient in all of the Great Lakes except Lake Erie. In Lake Erie, an oversupply of phosphorus leads to severe depletion of dissolved nitrogen. In Saginaw Bay, the importance of silicon is indicated by its severe depletion during the spring phytoplankton peak (Smith et al. 1977).

Although carbon constitutes a larger proportion of phytoplankton biomass than either phosphorus or nitrogen, carbon is not included explicitly in the

model. Considerable evidence that carbon is rarely growth-limiting has been obtained in the in situ work by Schindler et al. (1973a, 1973b) in Canadian Shield lakes, and in the laboratory experiments by Goldman et al. (1974).

Phytoplankton have absolute requirements for small quantities of many other nutrients besides phosphorus, nitrogen, silicon, and carbon. Goldman (1972) reviewed the role of micronutrients in limiting the productivity of aquatic systems. He concluded that it is unusual to find significant deficiencies of micronutrients in eutrophic lakes, but that such deficiencies are more common in oligotrophic lakes.

The actual complexity of phytoplankton nutrient requirements notwithstanding, it was the operational assumption in the present study that no other elements besides phosphorus, nitrogen, and silicon are important in limiting either the rate of phytoplankton production or the maximum sizes of phytoplankton crops.

Space and Time Scales

The spatial and temporal scales used have been largely dictated by the resolution of the field data available for comparison with model output. Other important considerations were computational complexity and the stage of development of the model.

The present spatially simplified version of the model described only the inner portion of Saginaw Bay (Figure 1). This version can not describe any of the spatial gradients in water quality that exist in the inner bay. Smith et al. (1977) showed that there are substantial horizontal gradients in this region; however, the inner bay is well-mixed in the vertical. Since Saginaw Bay constituted the first comprehensive application of the model, it was decided to calibrate a spatially simplified version, prior to introducing the additional complexities of spatial segmentation.

The temporal resolution of the model was on the order of one month. There were 13 sampling cruises on Saginaw Bay in 1974 during the period from late-March to mid-December. The time interval between each cruise varied from 18 days to one month. Neither the high frequency phenomena that occur over a 24-hour cycle, nor the sharp transient variations in water movements that occur due to the shallow nature of the inner bay were described by the model.

PHYTOPLANKTON KINETICS

The present version of the model kinetics has evolved from earlier work that dealt initially with microbial substrate uptake kinetics (Verhoff and Sundaresan 1972; Verhoff et al. 1973). This work was later expanded to include phytoplankton growth kinetics modeling (Bierman et al. 1973; Bierman 1974). Preliminary applications have been described at various stages in the overall study of Saginaw Bay (Bierman 1976; Bierman and Richardson 1976; Bierman and Dolan 1976).

Nutrient Uptake and Cell Growth

The phytoplankton nutrient uptake and growth processes in the model are described by Equations A.1.0 through A.5.0. An internal nutrient pool model was used to describe phytoplankton kinetics as a function of phosphorus and nitrogen. This model considered cell growth to be a two-step process involving separate nutrient uptake and cell synthesis mechanisms. A large body of experimental evidence indicates that these two processes are, in fact, quite distinct (Rhee 1973, 1974, 1978; Droop 1973, 1974; Fuhs 1969; Fuhs et al. 1972; Eppley and Thomas 1969; Caperon and Meyer 1972a, 1972b; Azad and Borchardt 1970). A basic assumption of internal nutrient pool models is that stoichiometric compositions of phytoplankton can vary as a function of the balance between nutrient uptake rate and cell growth rate. In such models it is possible for phytoplankton to accumulate surplus internal nutrients during periods when nutrient concentrations are high, and then to use these internal stores for growth during periods when nutrient concentrations are low. Several other workers have also developed internal pool phytoplankton models (Nyholm 1978; Jorgensen 1976; Lehman et al. 1975; Grenney et al. 1974; Koonce and Hasler 1972).

In contrast to the internal nutrient pool approach, the hyperbolic equation by Monod (1949) is the most widely-used mechanism for describing phytoplankton kinetics in simulation models (Canale et al. 1976; Scavia et al. 1976; Thomann et al. 1975; Larsen et al. 1973; Chen and Orlob 1972). The Monod equation is functionally identical to the Michaelis-Menten equation for enzyme kinetics, and the two names are frequently used interchangeably. A basic assumption of the Monod equation is that specific growth rate is directly coupled to the external concentration of limiting nutrient. A corollary to this assumption is that stoichiometric composition of phytoplankton cells remains constant as the concentration of limiting nutrient changes in the external medium. An instantaneous change in external concentration due to phytoplankton uptake corresponds to production of phytoplankton biomass in a fixed ratio, or yield.

The principal advantages of using an internal nutrient pool model are that more realistic descriptions can be obtained of non-steady-state conditions and nutrient recycle. Major disadvantages include increased computational complexity and the need to specify additional model coefficients.

The principal features of the internal nutrient pool model used here were:

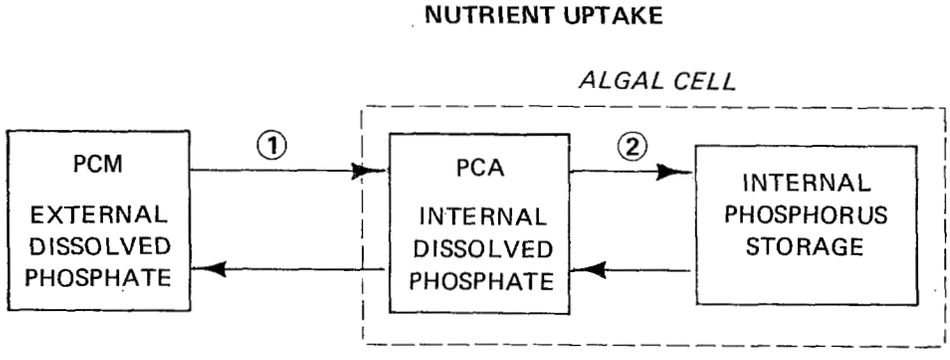
1. Growth rates depended on internal nutrient levels and not on external nutrient levels.

2. Nutrient uptake rate was a function of both external and internal nutrient levels.

3. The active internal nutrient pool which participated in the nutrient transport mechanism was proportional to the total internal nutrient level. This was a feedback me-

chanism which prevented the cell from absorbing arbitrarily large amounts of a nutrient and depleting the external environment.

Figure 5 is an illustration of these features for the special case of phosphorus. Net specific phosphorus uptake rate was a function of the balance between external and internal phosphorus. The internal dissolved phosphorus concentration, PCA, was related to a minimum value, PCAMIN, which was assumed to be a small number. This relationship was a function of P, the total amount of phosphorus in the cell. The quantity PCA was considered to be the active pool which participates in the uptake kinetics reaction with the external dissolved phosphorus. An identical parameterization was used for nitrogen kinetics.



① Net specific uptake rate = Maximum uptake rate • $f(T)\, f(L) \left[\frac{1}{1 + (PK1)(PCA)} - \frac{1}{1 + (PK1)(PCM)} \right]$

② $PCA = (PCAMIN)e^{(P/PO - 1)}$

Figure 5. Nutrient uptake mechanism used in the model for phosphorus and nitrogen

The quantity PK1 has actual physical significance because it was the equilibrium constant for the reaction between phosphorus and an assumed membrane carrier molecule. Such a molecule has been isolated in the bacterium Escherichia coli, and its binding constant with phosphate has been measured (Medveczky and Rosenberg 1970, 1971).

One of the consequences of an internal nutrient pool model is that there does not exist a unique value for net specific uptake rate, given a value for dissolved phosphate concentration in the medium. Instead, there exists a family of values, each corresponding to a different level of internal phos-

phorus (Figure 6). Negative values for net specific uptake rate correspond to the rate of phosphorus leakage back to the medium which can occur under certain conditions (Nalewajko and Lean 1978; Button et al. 1973). If cells are assumed to be starved, that is, if P = PO, then net specific uptake rate becomes half-maximum at 15 µg P/l in the example shown. Since the conventional Michaelis-Menten approach to nutrient uptake kinetics does not include a feedback mechanism, Michaelis-Menten kinetics is actually a special case of the present kinetics theory in which the cell's nutritional state is assumed to be constant. As PCA approaches PCAMIN in step 1 of Figure 5, the first term in brackets approaches unity, and the equation for net specific uptake rate reduces to the familiar hyperbolic form of the Michaelis-Menten equation.

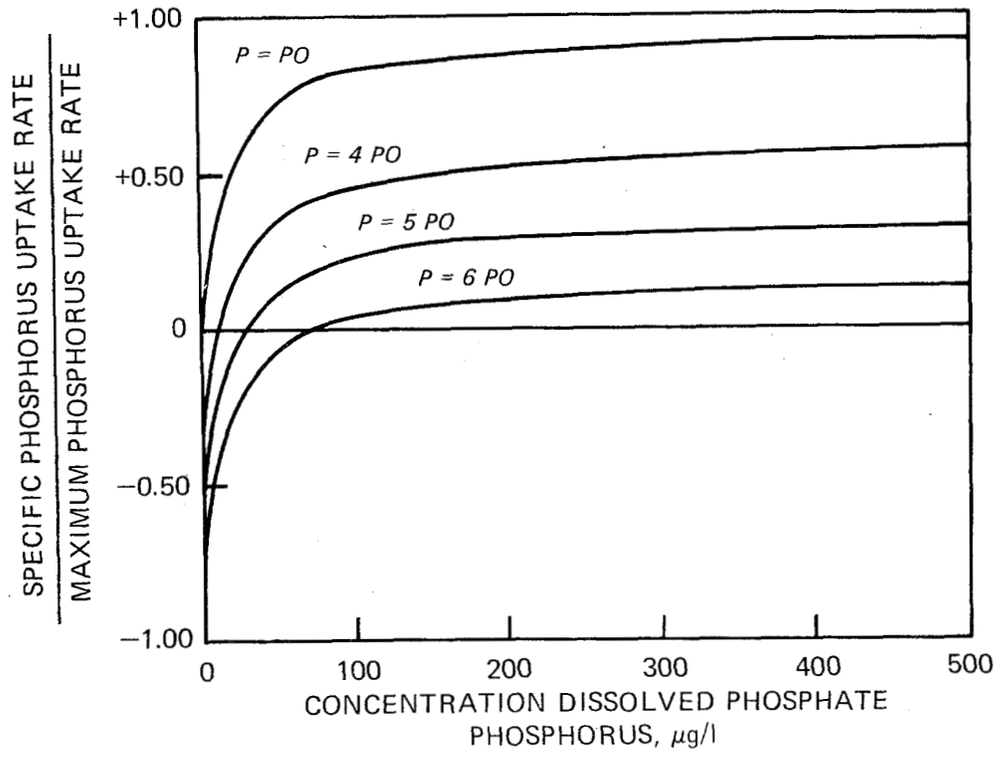


Figure 6. Degree of saturation of the phosphorus uptake system for non-N_2-fixing blue-greens as a function of internal and external phosphorus levels.

In contrast to the phosphorus and nitrogen kinetics in the model, silicon kinetics was described using the conventional Monod hyperbolic equation for specific growth rate as a function of external silicon concentration (Equation A.3.2.3). This approach was consistent with most of the available data for phytoplankton - silicon interactions. Guillard et al. (1973) and Kilham (1975) reported that growth rates of silicon-limited diatoms were related to silicon concentration in the medium by a hyperbolic equation. Paasche (1973)

found a similar hyperbolic relationship, but only after a correction had been made to dissolved reactive silicon concentration to account for the fraction that could apparently not be used by the diatoms tested. Kilham also reported such a "threshold effect", however, she pointed out that this effect was observed with some species and not with others. Guillard et al. did not use a threshold correction for their results.

Recently, there has been some evidence that an internal nutrient pool model might yet be an appropriate description for phytoplankton - silicon kinetics. Conway et al. (1976) reported that silicon uptake by diatoms can be decoupled from cell growth, and that uptake, under certain conditions, appeared to be internally controlled. Davis et al (1978) actually proposed an internal nutrient pool model to describe their experimental results for a silicon-limited diatom under steady-state and transient conditions. In any case, the silicon kinetics used in the present model should be considered provisional, pending the outcome of additional research.

Another important feature of the model is that a threshold hypothesis, as opposed to a multiplicative hypothesis, was used to calculate actual specific growth rate from the individual nutrient reduction terms. These two hypotheses can be stated in the following manner for the case where there is potential growth rate limitation by either phosphorus or nitrogen:

I. Multiplicative

$$\frac{\mu_{sp}}{\mu_{max}} = \frac{(q_p - q_{po})}{K_p + (q_p - q_{po})} \cdot \frac{(q_n - q_{no})}{K_m + (q_n - q_{no})} \qquad 1$$

II. Threshold

$$\frac{\mu_{sp}}{\mu_{max}} = \frac{(q_p - q_{po})}{K_p + (q_p - q_{po})} \qquad \frac{q_p}{q_{po}} < \frac{q_n}{q_{no}} \qquad 2a$$

$$\frac{\mu_{sp}}{\mu_{max}} = \frac{(q_n - q_{no})}{K_n + (q_n - q_{no})} \qquad \frac{q_n}{q_{no}} < \frac{q_p}{q_{po}} \qquad 2b$$

where μ_{sp} = specific growth rate

μ_{max} = maximum growth rate

q_p, q_n = total cellular levels of phosphorus and nitrogen, respectively

q_{po}, q_{no} = minimum stoichiometric requirements, or cell quotas, for phosphorus and nitrogen, respectively

K_p, K_n = half-saturation constants.

The question of which hypothesis to use has been an open one in the modeling literature, although the multiplicative hypothesis has probably been the more popular of the two. Still a third hypothesis, based on electrical resistors in parallel, has been used by Scavia and Park (1976). The basis for the use of the threshold hypothesis here was a series of recent measurements conducted with Scenedesmus sp. under conditions of potential limitation by both phosphorus and nitrogen (Rhee 1978). Results of these measurements were consistent with results of similar measurements by Droop (1974) with Monochrysis lutheri under conditions of potential limitation by both phosphorus and B_{12}. In both studies, laboratory data were subjected to rigorous statistical analyses which confirmed that the threshold hypothesis correctly described the data, and that the multiplicative hypothesis should be rejected.

The kinetic theory developed above for phosphorus, nitrogen, and silicon applies only under conditions of optimal temperature and light intensity. Both nutrient uptake rates and growth rates in the model must be corrected for non-optimal conditions. The light reduction factor used here was based on a standard calculation developed by O'Connor et al. (1973). A vertically-averaged light reduction factor was calculated as a function of incident solar radiation, extinction coefficient, photoperiod, and optimal phytoplankton light intensity (Equation A.15.2). This light reduction factor implicitly included the effect of the depth ratio of photic zone to total water column. The temperature reduction factors in the model (Equations A.16.0-A.16.4) were specified as proportions of maximum growth rates for each phytoplankton group in the model. Discussion of these factors will be deferred to a later section on model calibration.

There remain several unresolved research problems which preclude the development of a truly general set of kinetic equations for describing phytoplankton-nutrient kinetics over the full range of actual environmental conditions. One of these problems is the specification of kinetic rates when temperature and light are simultaneously at non-optimal levels. This is the vertically-averaged condition of epilimnetic waters during most of the year in most lakes. It was assumed here that individual temperature and light reduction factors operated on each other in a multiplicative fashion (Equations A.1.2 and A.3.2.1-A.3.2.3). This approach is standard practice in most phytoplankton models.

Another unresolved problem is interactions among nutrients during the uptake process which have been reported by several workers (Ketchum 1939a; Droop 1974; Conway et al. 1976). No such interactions were included in the present version of the model. It should be noted, however, that the uptake mechanism used here was only one application of a general substrate uptake theory. This theory has already been used to investigate several different types of interactions among substrates, including competition between more than one substrate for a single carrier molecule (Verhoff et al. 1973). Presently, there are insufficient data to fully test these hypotheses for phytoplankton-nutrient interactions.

Respiration

Phytoplankton respiration losses were described using a temperature-dependent, first-order decay term (Equation A.3.5). In the present context, respiration is intended to refer to population losses due to self-maintenance requirements, especially under non-optimal conditions. In laboratory systems under optimum conditions, such losses usually account for a negligible proportion of phytoplankton gross production; however, under natural conditions, such losses can be considerable because vertically-averaged gross production rates are usually much lower.

Decomposition

There has been recent experimental evidence that bacterially-mediated decomposition of phytoplankton under aerobic conditions is an important loss mechanism for viable phytoplankton cells in the water column. DePinto and Verhoff (1977) reported that the presence of heterotrophic bacteria populations greatly accelerated decomposition and subsequent nutrient recycle of Chlorella and Selenastrum cultures as compared to cultures which were kept bacteria-free. Gunnison and Alexander (1975) reported similar results for different species of phytoplankton, and they suggested that decomposition of the cell wall is a major determinant of algal resistance to microbial decomposition.

The model included a temperature-dependent, second-order phytoplankton decay mechanism to simulate the effects of microbial decomposition (Equation A.3.4). A detailed discussion of the rationale for this approach, including comparative simulations, has been presented by DePinto et al. (1976). In essence, the decomposition rate for a given phytoplankton group was assumed to be proportional to the product of the concentration of that group and the concentration of total phytoplankton. This approach was based on the assumption that total phytoplankton concentration was proportional to bacterial concentration. Such an approximation is reasonable because phytoplankton biomass serves as the principal carbon source for bacteria in the water column. This approach to describing phytoplankton decomposition has the important practical advantage of not requiring a separate set of equations for describing bacterial kinetics.

Sinking

Phytoplankton sinking losses were described by assigning a constant sinking velocity, or "escape velocity", to each phytoplankton group in the model (Equation A.3.6). This velocity was intended to correspond to the net, annual average flux of phytoplankton from the water column to the sediment.

The present approach was motivated primarily by lack of viable alternatives. In order to describe sinking losses in rigorous terms, it would have been necessary to consider the hydrodynamics of the system, and the physiology of the phytoplankton. There did not exist a calibrated hydrodynamic model of Saginaw Bay which could describe vertical water movements. In addition, although it is well-known that phytoplankton sinking rates depend

on their physiological state (e.g., Titman and Kilham 1976; Smayda 1974), it is not clear how to quantify this relationship. In previous work (Bierman, unpublished results), variable sinking velocities were used as a function of internal phosphorus and nitrogen levels in the phytoplankton; however, the equations used were somewhat arbitrary, and the results were not significantly different than the present results.

NUTRIENT KINETICS

Total and Available Forms

Each of the nutrients in the model was assumed to exist in two different forms: an available form which could be used directly for phytoplankton growth, and an unavailable form which could not be used by phytoplankton. Available phosphorus in the model was considered to be the same as dissolved ortho-phosphorus in the field data; available nitrogen was considered to be the sum of ammonia and nitrate/nitrite nitrogen; and available silicon was considered to be dissolved silicate silicon. Each of the unavailable nutrients was assumed to consist of both a dissolved and a particulate fraction, although no explicit distinction was made between these fractions in the model. A temperature-dependent, first-order mechanism was used to describe the transformations from unavailable to available nutrient forms in the water column (Equations A.8.6 and A.9.5). The unavailable nutrient forms were each assigned a sinking velocity because they each contained a particulate fraction. The sinking velocity for the unavailable nutrient forms was conceptually identical to the sinking velocity for the phytoplankton; i.e., it corresponded to a net, annual average flux from the water column to the sediments.

Nutrient Recycle

One of the advantages of using an internal nutrient pool kinetics model is that nutrient recycle can be described in a manner consistent with experimental observations. Nutrient recycle in the model consisted of two distinct components: a component associated with the minimum cell quota required by the phytoplankton, and a component associated with the internal nutrient level in excess of the minimum cell quota. Such a two-component recycle phenomenon has been observed for both phosphorus and nitrogen (e.g., Foree et al. 1970; DePinto 1974; Rhee 1973). When phytoplankton losses occurred in the model, the nutrient component associated with the minimum cell quota was recycled to the unavailable compartment in the water column, and the nutrient component associated with the excess internal level was recycled directly to the available nutrient compartment in the water column. This is in agreement with evidence (e.g., Rhee 1973) that the latter component consists of available nutrient forms and loosely-bound compounds which rapidly convert to available nutrient forms. This two-component recycle mechanism was included in the model for phytoplankton population losses due to grazing, decomposition, and respiration.

Silicon recycle in the model was handled differently than phosphorus or nitrogen recycle because an internal nutrient pool mechanism was not used

for silicon. When the above population losses occurred for diatoms, the entire silicon content of the cells was recycled only to the unavailable silicon compartment in the water column. As was the case for phosphorus and nitrogen, unavailable silicon was subsequently transformed to available silicon by a temperature-dependent, first-order mechanism.

ZOOPLANKTON KINETICS

Two zooplankton types were included in the model and they were assumed to graze on the diatom, green, and "other" phytoplankton groups. Blue-greens were not grazed. The zooplankton types were differentiated on the basis of their maximum feeding rates, or ingestion rates. Higher predators, such as carnivorous zooplankton and fish, were not included explicitly as state variables. It was recognized that zooplankton grazing is a complex process which involves phytoplankton size-selectivity and other preference factors (e.g., McNaught 1975); however, no attempt was made to describe these observations in the present version of the model.

Zooplankton specific growth rate was a function of maximum ingestion rate, assimilation efficiency, temperature, and phytoplankton concentration (Equation A.10.0). Mechanisms proposed by Scavia and Eadie (1976) were used to calculate effective phytoplankton half-saturation coefficients (Equation A.10.1) and estimates for minimum concentrations of individual phytoplankton groups necessary to stimulate feeding (Equation A.11.1). The need for such mechanisms arises from the fact that most of data for phytoplankton-zooplankton interactions are not of the type that can be used directly in models which include more than one predator-prey pair.

Zooplankton loss rate was described by a temperature-dependent, two-component decay mechanism (Equations A.14.1 and A.14.2). The first component represented zooplankton respiration; i.e., population losses due to self-maintenance requirements. The second component represented an assumed second-order predatory death mechanism. Such a mechanism was a substitute for explicitly including an additional trophic level above zooplankton. For both phytoplankton and zooplankton, a constant refuge concentration was specified. For the phytoplankton, this was a concentration below which no zooplankton grazing could occur. For the zooplankton, this was a concentration below which no second-order predation could occur.

SECTION 6

DATA BASE

INTRODUCTION

As part of the ULRS, intensive field surveys were conducted on Saginaw Bay during 1974 and 1975. These surveys were coordinated by the Large Lakes Research Station (LLRS) of the United States Environmental Protection Agency (USEPA). They involved close cooperation among several different institutions. One consequence of this cooperation was that experimental designs for phytoplankton and zooplankton analyses were modified during the project for the specific purpose of supporting the model development effort.

This report contains only brief descriptions of contributions of the different institutions involved in the Saginaw Bay surveys. Complete information is contained in the individual project reports. All data collected during the 1974 and 1975 surveys reside in data files at the EPA Washington Computer Center, either as part of the STORET system, or as files in the Great Lakes Data Base. In addition, as part of an international cooperative effort, these data have been placed in the library of the International Institute for Applied Systems Analysis (IIASA) in Laxenburg, Austria. Henceforth, only results of the 1974 survey will be discussed.

CHEMICAL DATA

Cranbrook Institute of Science (CIS) had principal responsibility for organizing the sample collection effort, and for conducting water chemistry and chlorophyll analyses (Smith et al. 1977). Thirteen sampling cruises were conducted on a 59-station grid at multiple depths (Figure 7). Analyses were conducted for 22 different parameters, including phosphorus, nitrogen, silicon, chlorophyll, chloride, temperature, and Secchi depth. Average results for 33 stations in the inner portion of the bay were used for comparison with model output. Results for stations located in the Saginaw River, the principal tributary to Saginaw Bay, were used to calculate external nutrient loadings.

PHYTOPLANKTON DATA

Phytoplankton samples were collected and analyzed by the Great Lakes Research Division (GLRD), University of Michigan (Stoermer et al. 1979). Samples were collected on the same cruises and at the same stations as the

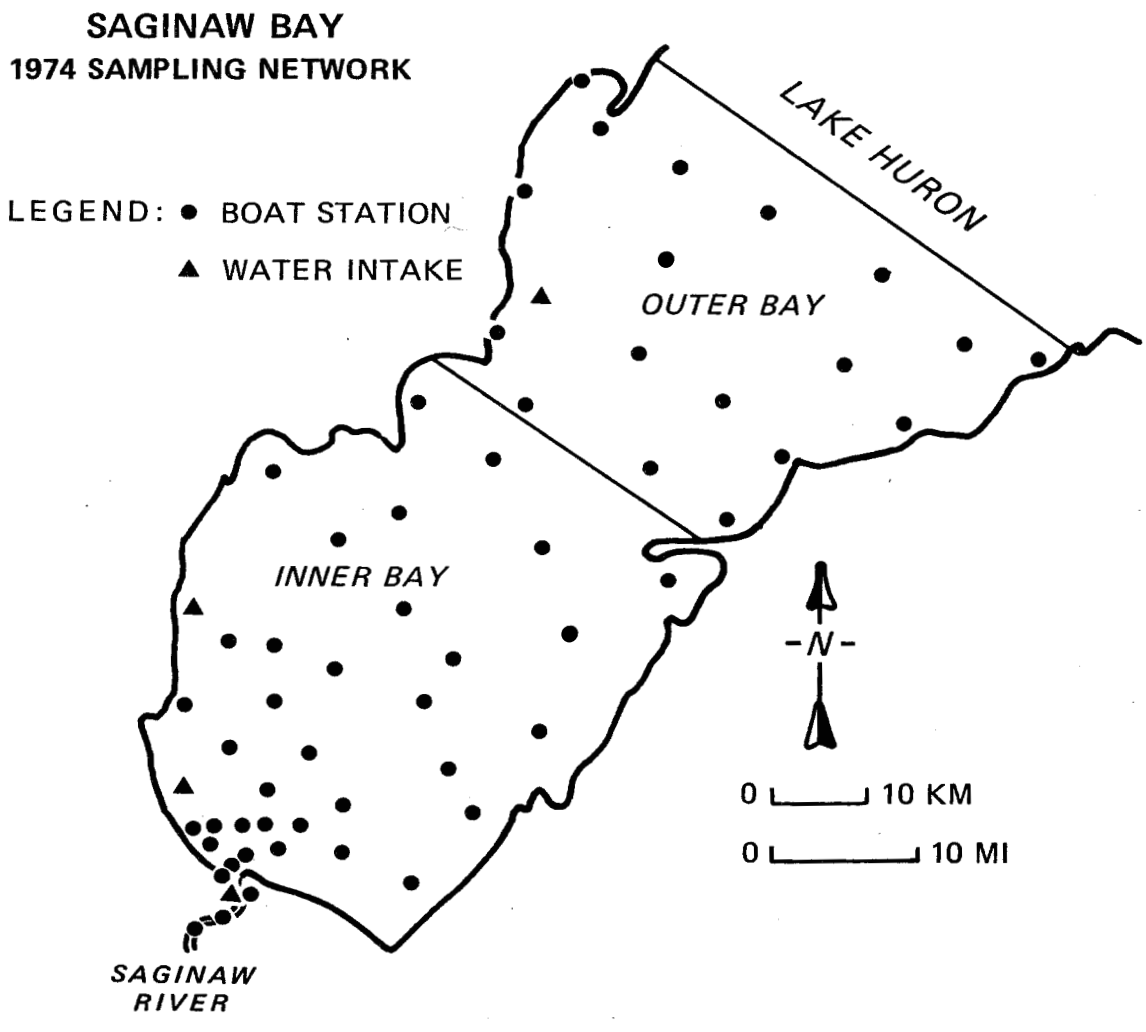


Figure 7. Saginaw Bay sampling station network in 1974.

chemical data. The only difference in the sampling design was that the phytoplankton samples were collected only at a depth of 1 meter. In the initial phase of the project, analyses were to have consisted only of species identifications and number concentrations. Later, an extensive series of cell volume measurements were conducted to transform the species count data to biomass values which were required for comparison with model output.

Approximately 200 phytoplankton species were identified and counted in Saginaw Bay. Cell volumes for these species were measured under a light microscope. The species volumes were first integrated to the genus level. The genera were then assigned to one of five functional groups in the model, and a final volume integration was performed. For comparison with model output and for dimensional consistency with other model state variables, the cell volume concentrations were converted to dry weight concentrations. The assumption was made that dry weight was 25 percent of wet weight, and that specific gravity was unity. These assumptions were based on a review of the literature (Kuenzler and Ketchum 1962; Nalewajko 1966; Oksiyuk and Yurchenko 1971; Healey 1975).

Cell volumes for the principal genera and sub-groups observed in Saginaw Bay are contained in Tables 1-3. As an independent check on the internal consistency of the data, dry weight per cell and carbon content per cell were calculated from measured cell volumes using two independent methods.

TABLE 1. CELL VOLUMES, DRY WEIGHTS, AND CARBON CONTENT OF PRINCIPAL DIATOM TYPES IN SAGINAW BAY, 1974

Type	Cell volume μ^3	Dry weight[1] mg/cell	Carbon[2] mg/cell	% Carbon by dry weight
Large Stephanodiscus	17994	4.50×10^{-6}	0.879×10^{-6}	20
Fragilaria	283	0.071	0.038	53
Rhizosolenia	3576	0.894	0.257	29
Tabellaria	1835	0.459	0.155	34
Synedra	311	0.078	0.040	52
Diatoma	601	0.150	0.066	44
Cyclotella	1469	0.367	0.131	35
Melosira	2191	0.548	0.177	32
Coscinodiscus	7964	2.00	0.473	24
Navicula	1449	0.362	0.130	36
Asterionella	1406	0.352	0.127	36
		Average percent carbon by dry weight		36%

[1]Assumes that dry weight is 25% of wet weight and that specific gravity is 1.00.

[2]Using regression equation between cell volume and cell carbon from Mullin, et al., 1966.

TABLE 2. CELL VOLUMES, DRY WEIGHTS, AND CARBON CONTENT OF PRINCIPAL GREENS, DINOFLAGELLATES, AND CRYPTOMONADS IN SAGINAW BAY, 1974

Type	Cell volume μ^3	Dry weight[1] mg/cell	Carbon[2] mg/cell	% Carbon by dry weight
Scenedesmus	774	0.194×10^{-6}	0.080×10^{-6}	42
Phacotus	2205	0.551	0.178	32
Sphaerocystis	112	0.028	0.019	66
Gleocystis	69	0.017	0.013	74
Oocystis	389	0.097	0.048	49
Staurastrum	48188	12.0	1.86	15
Mougeotia	392	0.098	0.048	49
Dinobryon	555	0.139	0.062	45
Cryptomonas	3268	0.817	0.240	29
Dinoflagellate	674	0.168	0.072	43
Flagellate	107	0.027	0.018	67
Mallomonas	1255	0.314	0.116	37
Peridinium	16708	4.18	0.831	20
Gymnodinium	283000	71.8	7.13	10
		Average percent carbon by dry weight	41%	

TABLE 3. CELL VOLUMES, DRY WEIGHTS, AND CARBON CONTENT OF PRINCIPAL BLUE-GREEN TYPES IN SAGINAW BAY, 1974

Type	Cell volume μ^3	Dry weight[1] mg/cell	Carbon[2] mg/cell	% Carbon by dry weight
Non-Heterocystous (non N_2-fixing)	984	0.246×10^{-6}	0.097×10^{-6}	39
Heterocystous (N_2-fixing)	848	0.212×10	0.082×10	38

[1]Assumes that dry weight is 25% of wet weight and that specific gravity is 1.00.

[2]Using regression equation between cell volume and cell carbon from Mullin, et al., 1966.

The ratio of carbon to dry weight was then calculated and compared with literature values. Dry weights were calculated in the manner indicated above. Carbon contents were calculated using a regression equation developed by Mullin et al. (1966) from measurements on 14 different phytoplankton species. A range of 36 to 41 percent was obtained for the carbon to dry weight ratio using the data in Tables 1-3. This range compares favorably to values reported in the literature (Ketchum 1939b; Boyd and Lawrence 1967; Healey 1975).

As a by-product of the mathematical modeling effort on Saginaw Bay, an opportunity developed to compare phytoplankton cell volume concentration to chlorophyll concentration, a more traditional measure of phytoplankton abundance. This was of interest because, in an earlier phase of model development, only chlorophyll data were available for comparison with model output (Bierman 1976; Bierman and Richardson 1976). When cell volume data were subsequently obtained, it was immediately apparent that the pattern of phytoplankton abundance in Saginaw Bay on the basis of cell volume was drastically different than on the basis of chlorophyll (Figure 8). An order-of-magnitude variation in the chlorophyll to total cell volume ratio was observed. This variation was apparently related to the species composition of the total crop (Figure 9). Chlorophyll concentration is an indicator of total phytoplankton concentration, but contains no information on individual species groups.

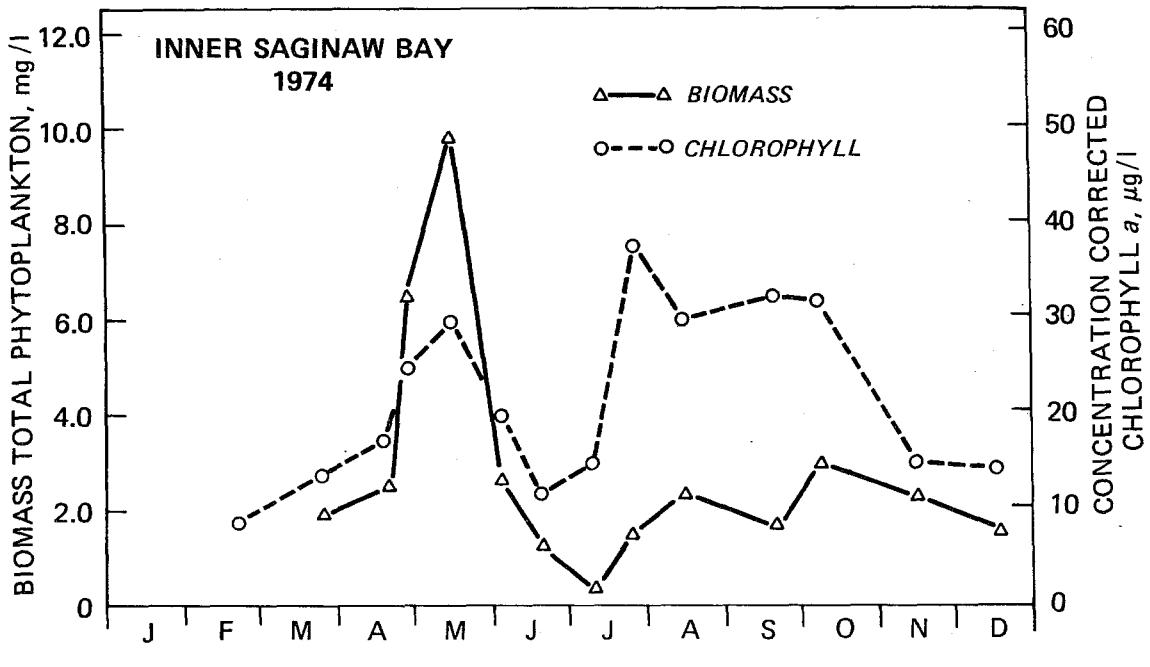


Figure 8. Comparison between dry weight biomass concentration and chlorophyll concentration as indicators of phytoplankton abundance.

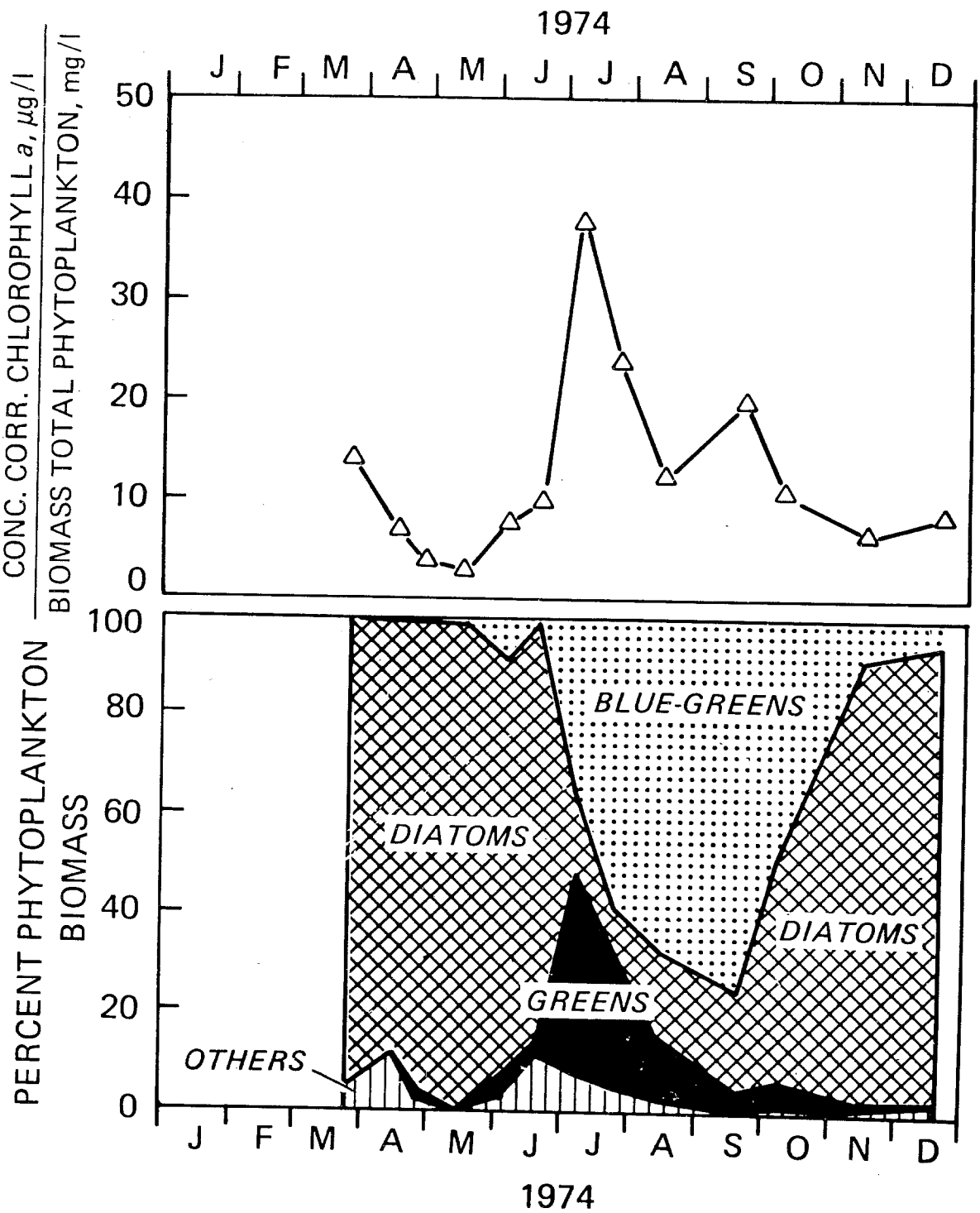


Figure 9. Comparison between chlorophyll: biomass ratio and percent composition of total phytoplankton crop.

Rigorous statistical analyses of the above data by Dolan et al. (1978) confirmed that significant differences existed between cell volume and chlorophyll as measures of phytoplankton abundance. These differences were found to be a function of both space and time in the bay. A large part of the variation in the chlorophyll to cell volume ratio was explained by correlating the ratio with the fraction of diatoms present. These results provided strong additional support for the development of a multi-class phytoplankton model for Saginaw Bay, as opposed to a model based solely on chlorophyll concentration.

ZOOPLANKTON DATA

Zooplankton samples were collected and analyzed by the University of Michigan Biological Station (UMBS), Pellston, Michigan (Gannon and Bricker 1979). The sampling design for zooplankton was identical to that for the chemical data. As with the phytoplankton, the initial phase of the project only involved species identification and number concentration; however, measurements were later conducted for dry weights of the principal zooplankton species to provide data for comparison with model output.

Twenty-seven crustacean zooplankton species were identified in Saginaw Bay. Of this number, the ten most abundant species were judged to comprise greater than 90 percent of the total zooplankton biomass on any given cruise. Mean dry weights were calculated for these ten species using length-weight regression equations. The equations were based on total length (exclusive of caudal setae in copepods and caudal spines in Daphnia) measurements of 50-70 organisms for each species, and dry weight measurements of 5-20 organisms in at least three length classes for each species. Results indicated that there were large seasonal differences in the weights for most species (Table 4). In general, zooplankton sampled in the spring were represented by much larger and heavier organisms than their summer and fall counterparts. Accordingly, three different seasonal sets of conversion factors were used to transform the zooplankton species counts to dry weight concentrations, depending on the times of the individual sampling cruises.

A special acknowledgement is made to D.C. McNaught, State University of New York-Albany, for his advice on partitioning the zooplankton species into the groups indicated as "fast" and "slow" feeding forms, or ingesters. This information was based on an extensive series of zooplankton feeding measurements in Saginaw Bay and Lake Huron (McNaught et al. 1979).

EXTERNAL LOADINGS

Determination of external loadings is one of the most important factors in the application of a mathematical model. In the case of Saginaw Bay, these loadings originated from three different sources: tributary inputs, atmospheric deposition, and inflow of water from Lake Huron across the boundary between the inner and outer portion of the bay. By far, the largest of these sources was tributary inputs, principally from the Saginaw

TABLE 4. DRY WEIGHTS OF PRINCIPAL ZOOPLANKON TYPES IN SAGINAW BAY, 1974

Type	Dry weight, µg/individual		
	Spring	Summer	Fall
Fast Ingesters			
Bosmina longirostris	2.9	0.7	1.0
Eubosmina coregoni	2.8	1.2	2.1
Chydorus sphaericus	2.6	1.0	1.1
Diaptomus spp. copepodites	3.8	2.4	2.1
Daphnia retrocurva	2.5	1.2	1.7
Slow Ingesters			
Eurytemora affinis	2.4	2.4	2.4[1]
Cyclopoid copepodites	3.4	1.6	2.7
Cyclops bicuspidatus	8.4	3.0	5.0
Cyclops vernalis	7.8	3.2	4.2
Mesocyclops edax	3.1	2.4	2.9

[1]No data for spring or fall. Assumed to be the same as summer value.

River. The Saginaw River contributes approximately 95 percent of the total tributary loading to Saginaw Bay.

Nutrient loadings from the Saginaw River were determined on the basis of an intensive field sampling program. For the first half of the year, samples were collected at two-to-three-day intervals at the Dow Chemical Company water intake plant at the mouth of the Saginaw River (Figure 7). From July to December, samples were taken from the Midland Street bridge in Bay City every two weeks. During the latter period, the Dow intake was strongly influenced by intrusion of water from the bay because of low-flow conditions in the river. The Midland Street bridge is approximately 8 km upstream from the river mouth and is not subject to intrusion. Chloride, total and dissolved forms of phosphorus and nitrogen, and dissolved silicon were measured. These data were augmented with similar measurements by the Michigan Department of Natural Resources (MDNR) on samples collected from the Midland Street bridge every two weeks.

Daily average flow rates were obtained from the United States Geological Survey (USGS) for the four major tributaries to the Saginaw River: the Cass, the Flint, the Tittabawassee, and the Shiawassee. A daily average flow for the Saginaw River was obtained by summing these four rates, along with a correction factor for the ungauged area near the mouth of the river.

Saginaw River loading rates were determined by calculating the product of flow and concentration for each constituent, and then identifying all

significant peaks and troughs. Subsequently, annual time-series were formed for each constituent by linear interpolation between these significant values (Figures 10-14). Tabulated values of loading rates used to construct the time-series are contained in Appendix D. Integration of the time-series produced the total annual load for each constituent (Table 5). Results indicated a sharp seasonal dependence in the loading for each constituent. Approximately 70 percent of the loading occurred in the first half of the year. This is a typical pattern in temperate-zone lakes due to snowmelt and heavy spring runoff.

Atmospheric contribution to the total Saginaw Bay load was based on data from collection stations on Lake Huron that were established as part of the ULRS (Mullin 1976). Results indicated that the atmospheric load for total phosphorus was approximately 4 percent of the total phosphorus load from tributary sources. Incomplete data were obtained for nitrogen and silicon.

Boundary exchange for total phosphorus and total nitrogen constituted a nutrient sink for the inner bay because concentrations of these constituents were always lower in the outer bay. During periods of severe nitrogen depletion in late summer, boundary exchange could constitute a temporary source for dissolved available nitrogen. During most of the year, boundary exchange constituted a sink for dissolved available silicon; however, after severe silicon depletion due to the spring diatom peak, boundary exchange

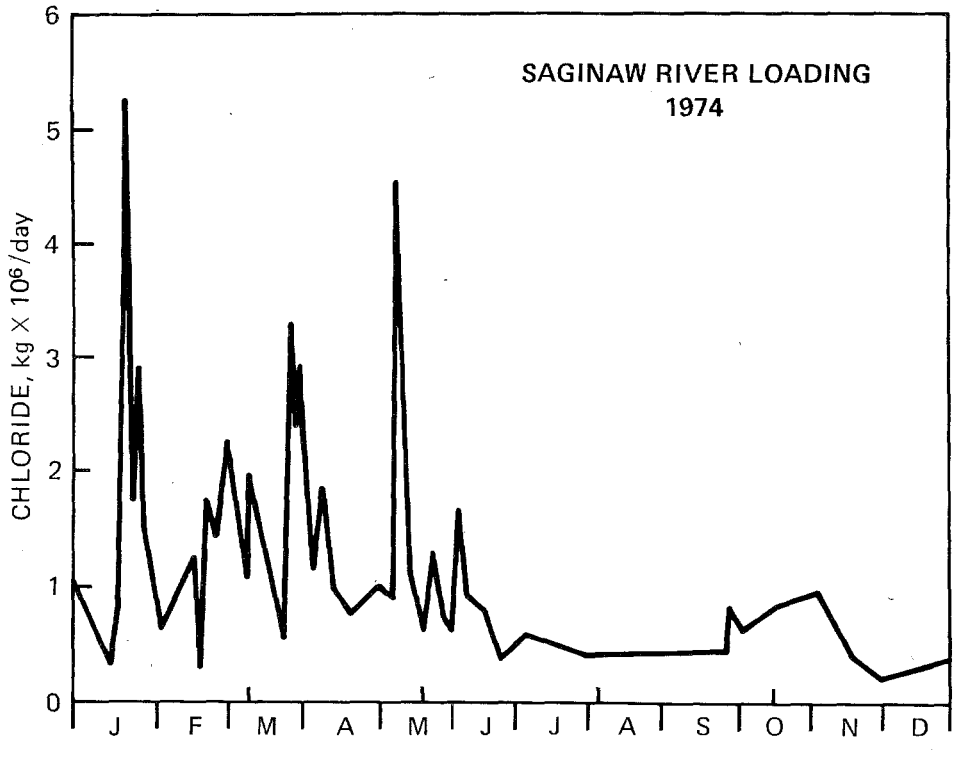


Figure 10. Time series for Saginaw River load for chloride.

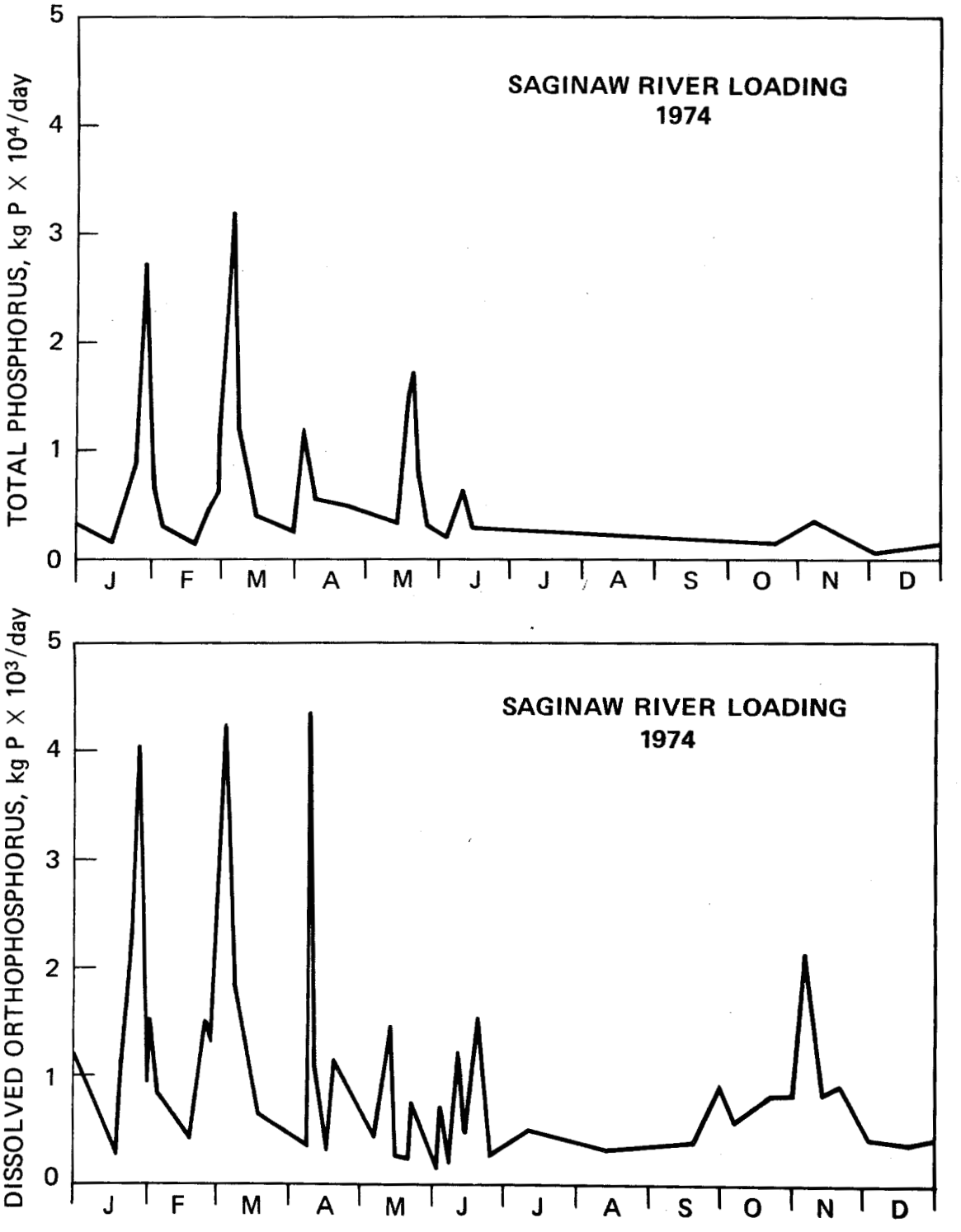


Figure 11. Time series for Saginaw River loads for total phosphorus and dissolved ortho-phosphorus.

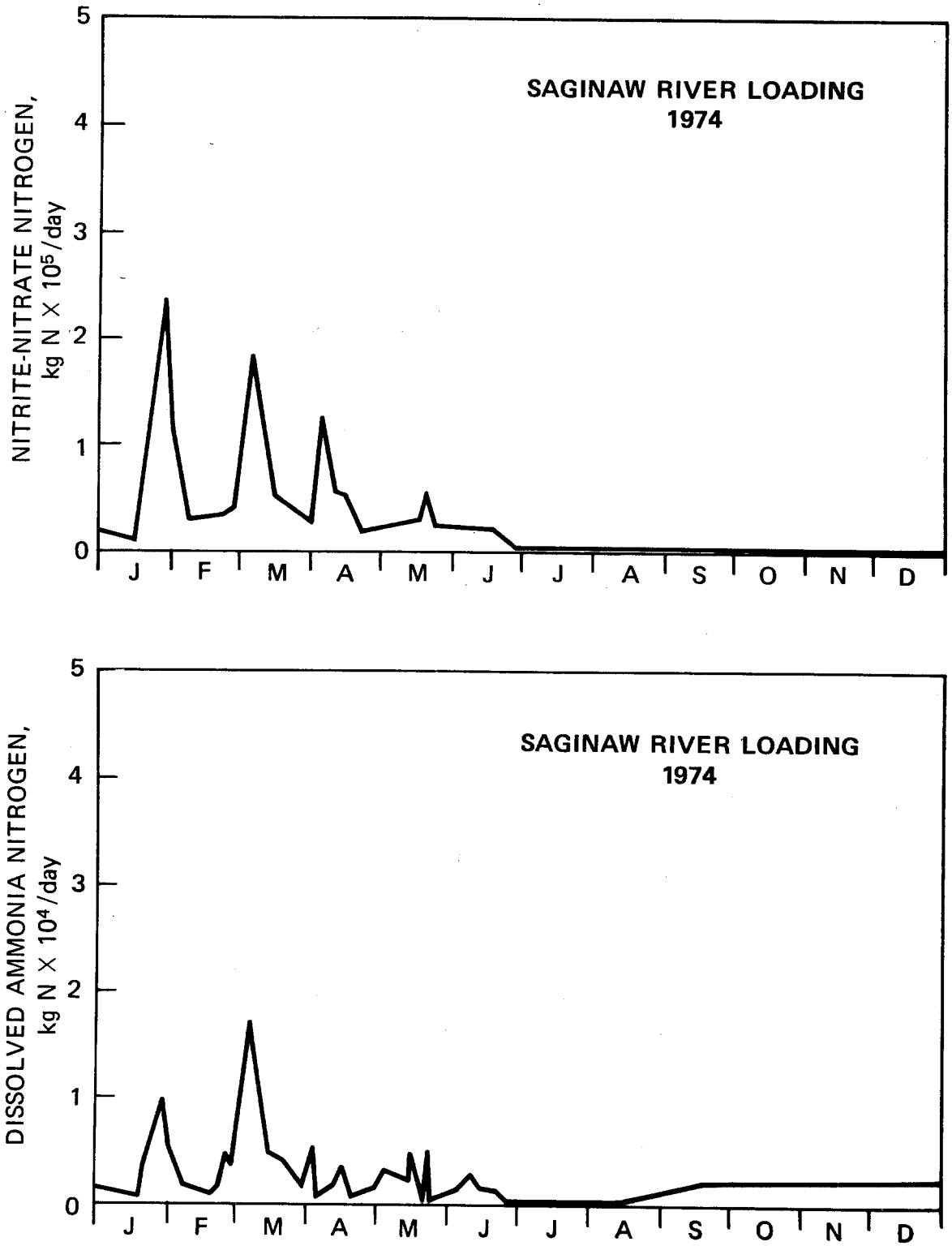


Figure 12. Time series for Saginaw River loads for dissolved nitrite plus nitrate nitrogen and dissolved ammonia nitrogen.

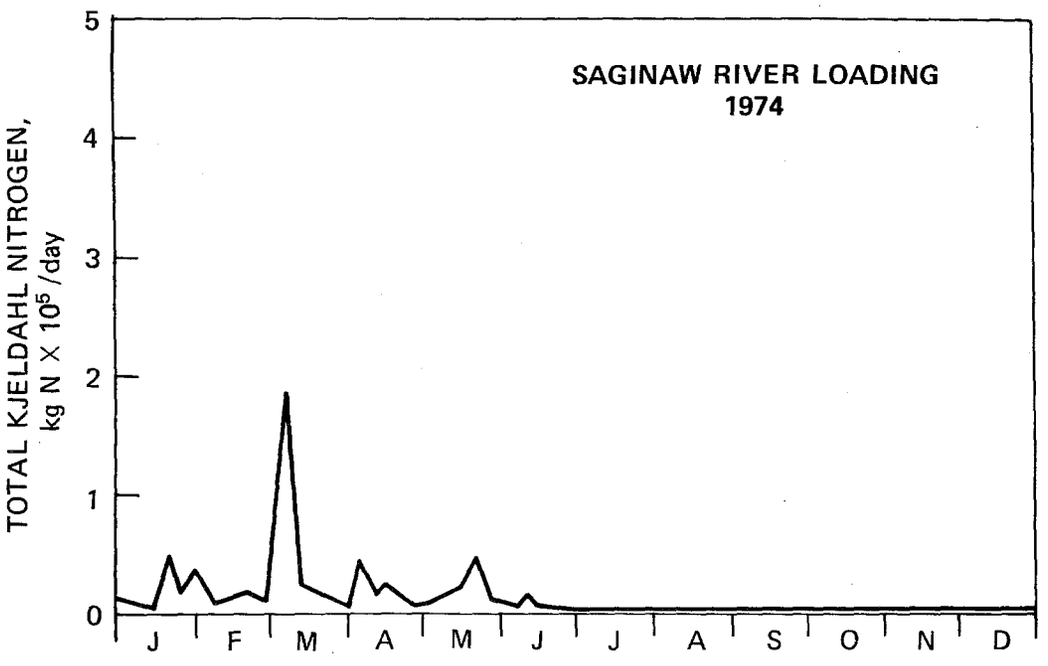


Figure 13. Time series for Saginaw River load for total kjeldahl nitrogen.

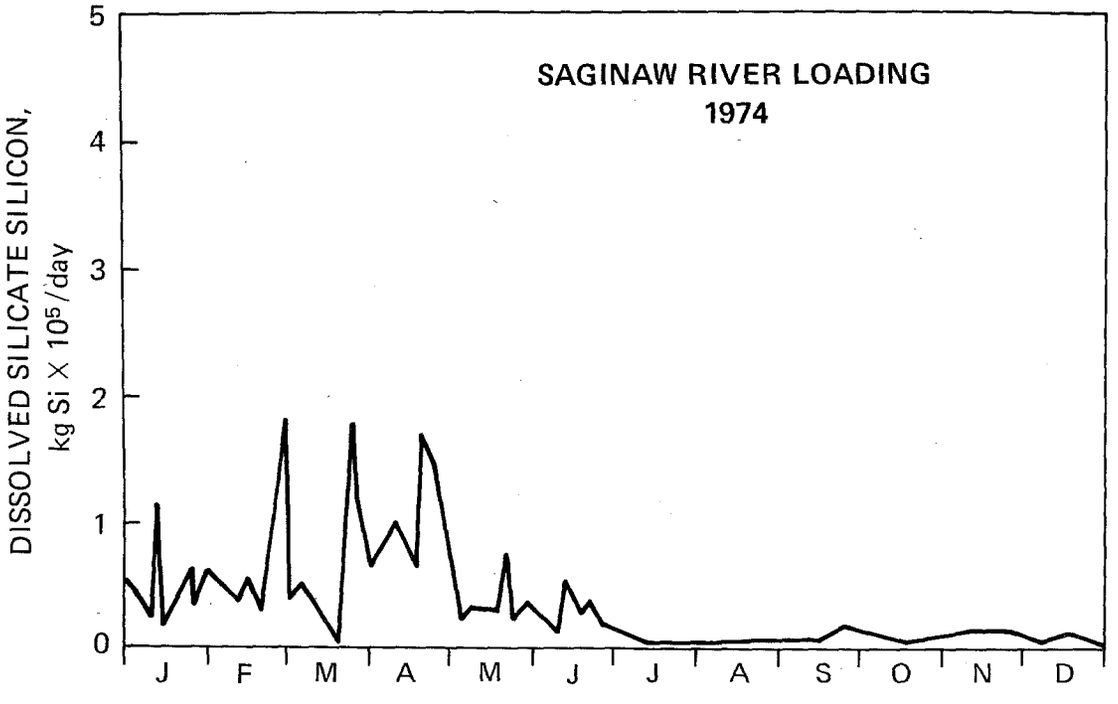


Figure 14. Time series for Saginaw River load for dissolved silicate silicon.

TABLE 5. SUMMARY OF SAGINAW RIVER LOADS FOR 1974

Parameter	Total annual load in metric tonnes[1]
Total P	1265
Dissolved PO_4-P	282
Total N	14110[2]
Total Kjeldahl N	5240
Dissolved (NO_3 + NO_2)-N	8870
Dissolved (NH_3-N)	934
Dissolved SiO_2-Si	11550
Chloride	325600

[1]Saginaw River consititutes approximately 95% of the total tributary load to Saginaw Bay. In addition, atmospheric phosphorus loading contributes 4% of the total phosphorus loading. Atmospheric loads for nitrogen and silicon have not been determined.

[2]Sum of annual values for TKN and (NO_3 + NO_2)-N.

constituted a net source of dissolved available silicon. The boundary concentrations used for each constituent are contained in Appendix D. These concentrations represent cruise averages of results from three field stations in the region of net inflow across the boundary between inner and outer bay.

SECTION 7

MODEL CALIBRATION

INTRODUCTION

In the application of a mathematical model to an actual physical system, it is useful to distinguish three separate operational phases: development of model equations, specification of coefficients used in the equations, and specification of forcing functions, or external quantities which are necessary to run the model. Section 5 of this report contains the development of the model equations. The present section contains the specification of forcing functions and model coefficients, and results of comparisons between model output and field data.

In the present context, forcing functions include water temperature, incident solar radiation, external loadings, boundary conditions, and water exchange rates. These quantities were not calculated internally by the model; instead, they were determined independently and then supplied as input to the model. All forcing functions were specified to the model on a daily basis using linear interpolation between measured values. In some cases, values for forcing functions were estimated on the first and last days of the year for the purpose of continuity.

Specification of model coefficients and comparison of the resulting model calculations with field data constitutes the model calibration process. This process is partly a science and partly an art. If all of the equations in the model were developed strictly from first principles, then it would be possible to uniquely determine all of the coefficients. In practice, the scientific literature is used as a basis for determining ranges and boundaries for model coefficients. The modeler then varies these coefficients within their reported ranges to obtain the best correspondence between model calculations and actual data. This is not strictly a curve-fitting process because coefficients are not allowed to assume arbitrary values to obtain the best fit in a strictly mathematical sense. If the model equations correspond well to the most significant dynamic processes which occur in the system, then the calibrated model will be physically realistic.

In applying a mathematical model, the process of calibration should be distinguished from the process of verification. Verification constitutes an independent check on the physical realism of a calibrated model. Verification involves an attempt to use a calibrated model in a predictive mode for the same physical system under a substantially different set of forcing conditions. Frequently, verification is not possible, either due to lack of

adequate resources or to lack of significant change in the system forcing functions over a period of time. An alternate type of independent check on the physical realism of a model is to apply the model to a different physical system.

FORCING FUNCTIONS

Water Exchange Rates

Saginaw Bay is only a part of the larger Lake Huron system. Water exchange with Lake Huron is an important component of the variation in chemical and biological parameters in Saginaw Bay. Current meter measurements were used to construct the steady-state current pattern in the bay for typical wind conditions. Net circulation in the inner bay is counterclockwise, with Lake Huron water flowing in along the northwestern shore and out along the southeastern shore (Figure 15). During the winter months, movement of Saginaw River water beneath the ice is also an important component of the inner bay circulation.

In the present study, chloride, a conservative tracer, was used to quantify water exchange rates in Saginaw Bay on a time-variable basis. Richardson (1974, 1976) applied both steady-state and time-variable chloride models to the bay. He concluded that the steady-state approximation was not realistic, except during stable periods in summer and fall. This result was significant because only a small part of the external nutrient loading to Saginaw Bay occurs during these stable periods. In addition, since the hydraulic retention time of the bay is only approximately four months, it was important to quantify water circulation on a time-variable basis.

A time-variable chloride model, similar to that used by Richardson (1976), was applied to the inner portion of Saginaw Bay to quantify advective flows and dispersions. The external chloride load was specified to the model on a daily basis using linear interpolation between the measured chloride loads (Table D-1). A good fit was obtained to field data (Figure 16). Advective flows and dispersions from the model were transformed to net exchange flows (Figure 17 and Table D-10). These net exchange flows were, in turn, used as input to the phytoplankton model in a piecewise linear fashion.

Water circulation in Saginaw Bay is characterized by a slow, stagnant period early in the year, followed by a period of very rapid flushing during May-June. Subsequently, a stable summer-fall circulation is established.

Light

A time-series for incident solar radiation was developed using monthly average values from Thomann et al. (1975) for Lake Ontario (Figure 18 and Table D-12). Saginaw Bay and Lake Ontario lie at the same latitude. Lake Ontario values were modified for Saginaw Bay to account for an ice cover which existed on the inner bay for 75 days in 1974. The effect of ice cover on light transmission can vary over wide limits (e.g., Bolsenga 1978). For

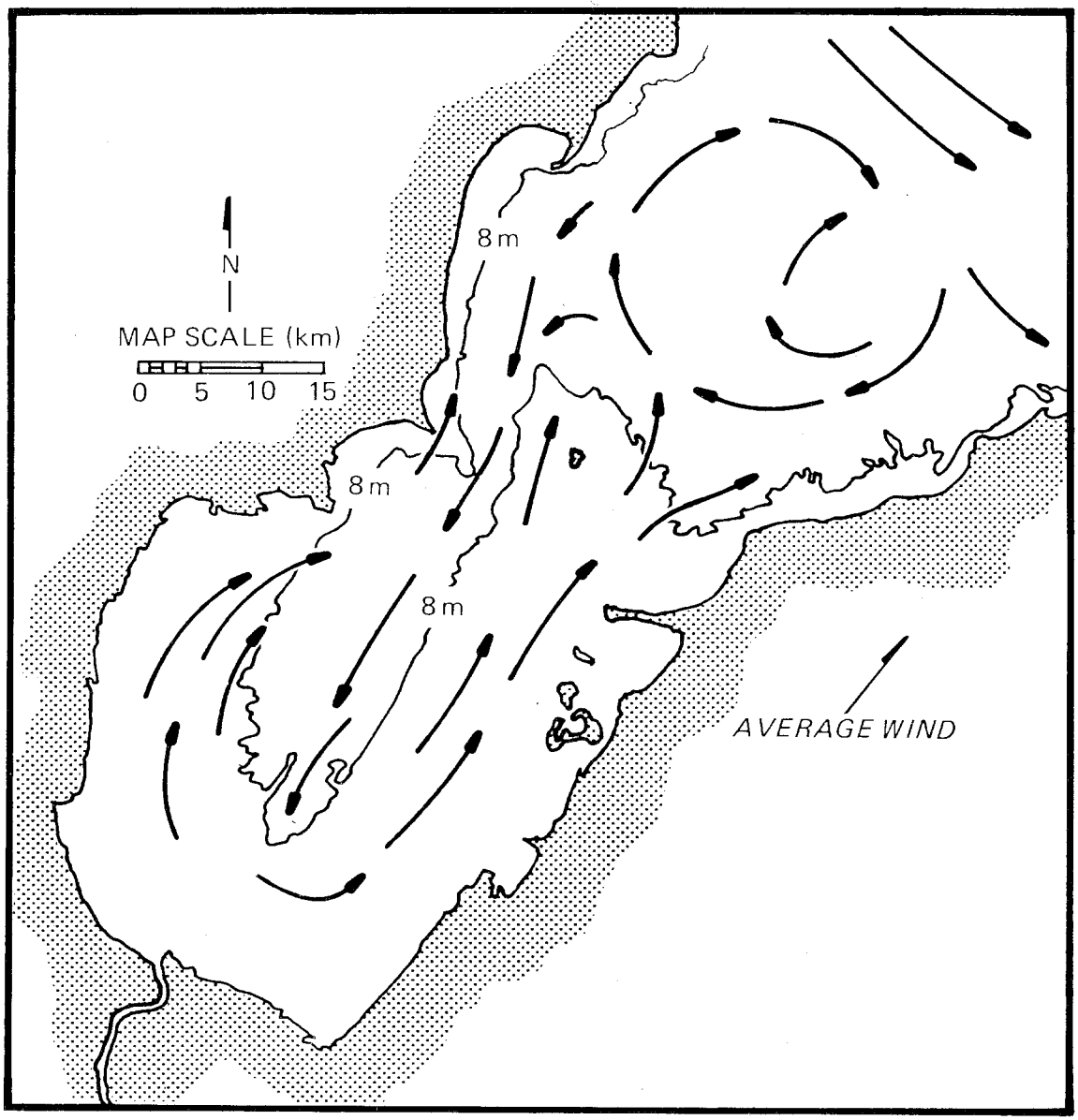


Figure 15. Dominant water circulation pattern in Saginaw Bay (from Danek and Saylor 1977).

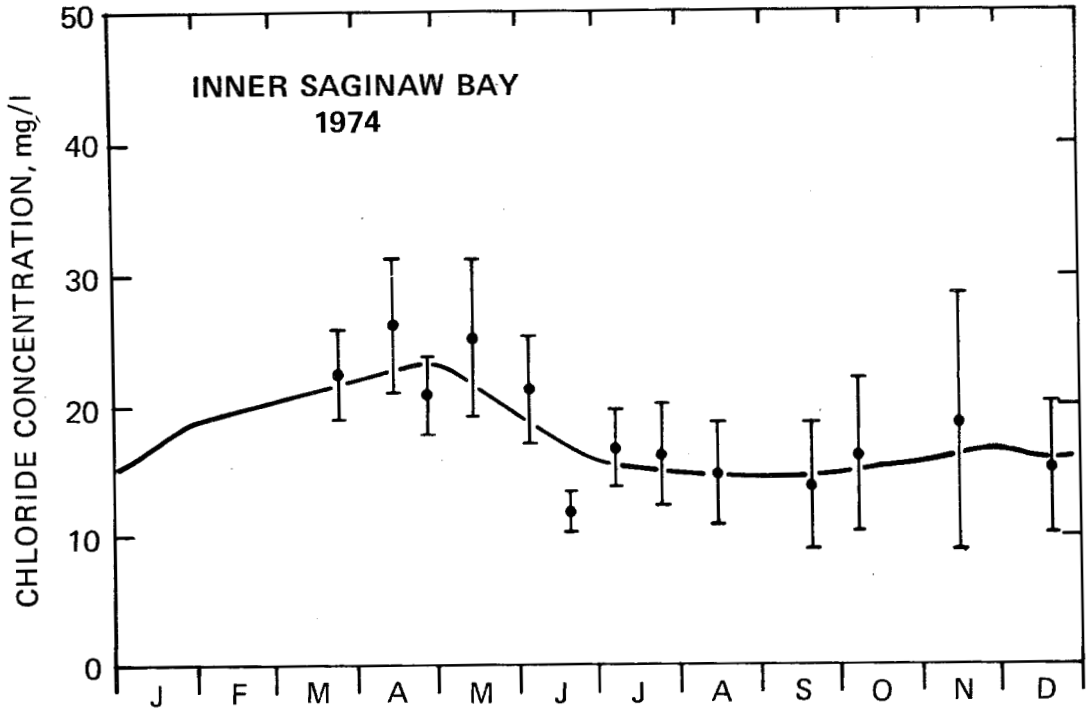


Figure 16. Comparison between model output and field data for chloride-based circulation model.

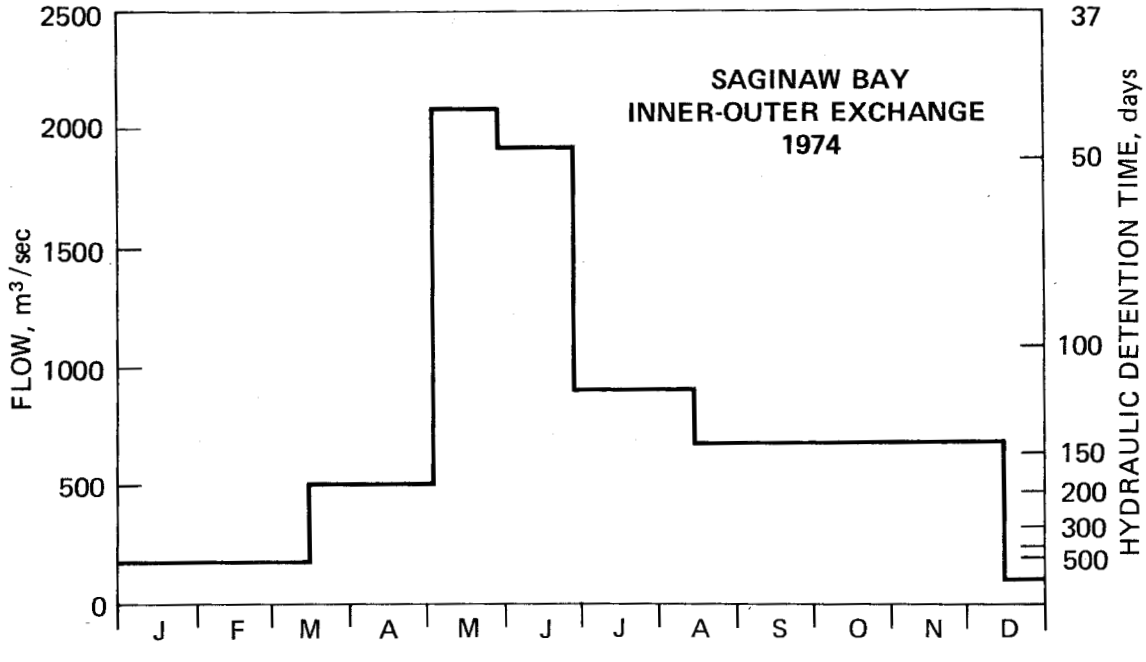


Figure 17. Results for net water exchange between inner and outer Saginaw Bay from chloride-based circulation model.

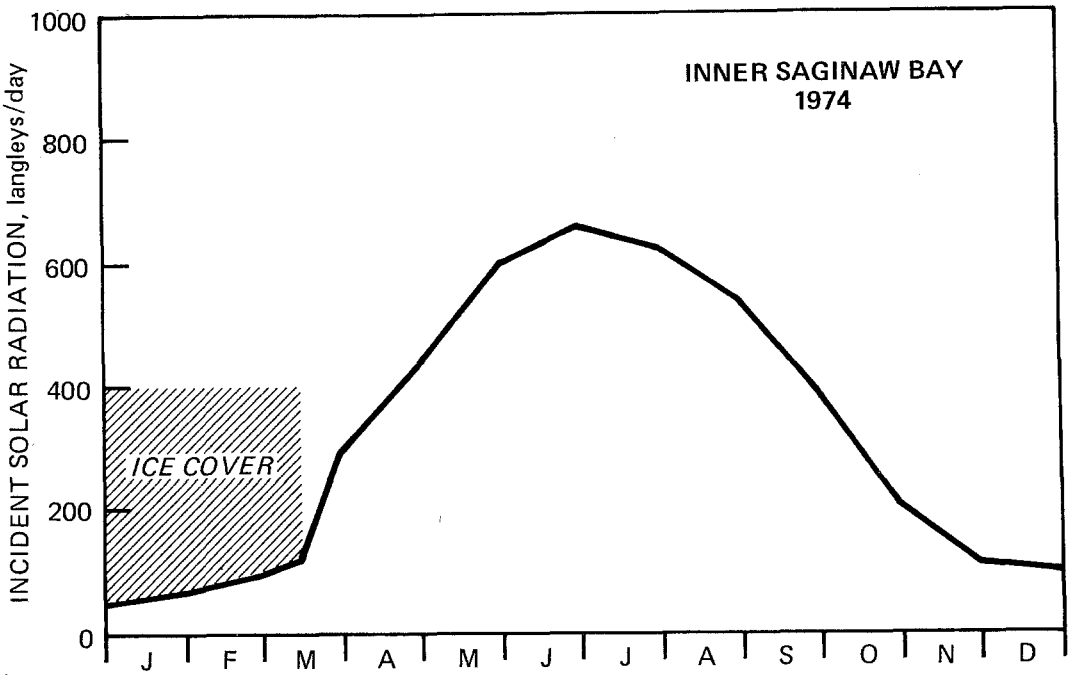


Figure 18. Time series used for incident solar radiation.

reasons of simplicity and lack of a more rigorous alternative, incident solar radiation to Saginaw Bay was reduced by 50% during the period of ice cover.

Inner bay average Secchi depths (Figure 19 and Table D-13) were used to directly specify the light extinction coefficient in the water column. Phytoplankton "self-shading" was not explicitly included in the model because most of the light extinction in Saginaw Bay was of non-planktonic origin. Secchi depth showed little variation with time, in spite of large variations in phytoplankton concentration (compare Figures 8 and 19). Any "self-shading" effects that did occur were included implicitly in the Secchi depth measurements.

Secchi depth measurements were transformed to extinction coefficients by a regression equation (Equation A.15.2.4) developed using simultaneous quantum measurements and Secchi depth measurements taken at 16 stations on each of 12 sampling cruises on Saginaw Bay during 1976. This equation constituted a revision to results of a similar study conducted earlier on Lake Huron by Beeton (1958).

Temperature

A time series for water temperature was developed using inner bay cruise averages (Figure 20 and Table D-11).

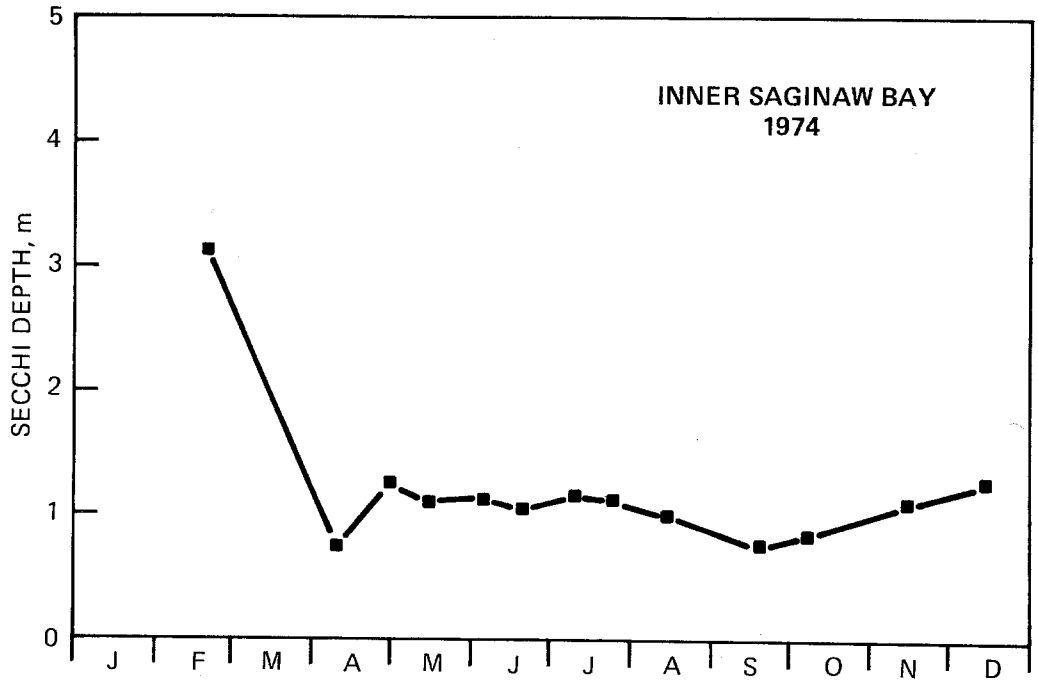


Figure 19. Time series used for Secchi depth.

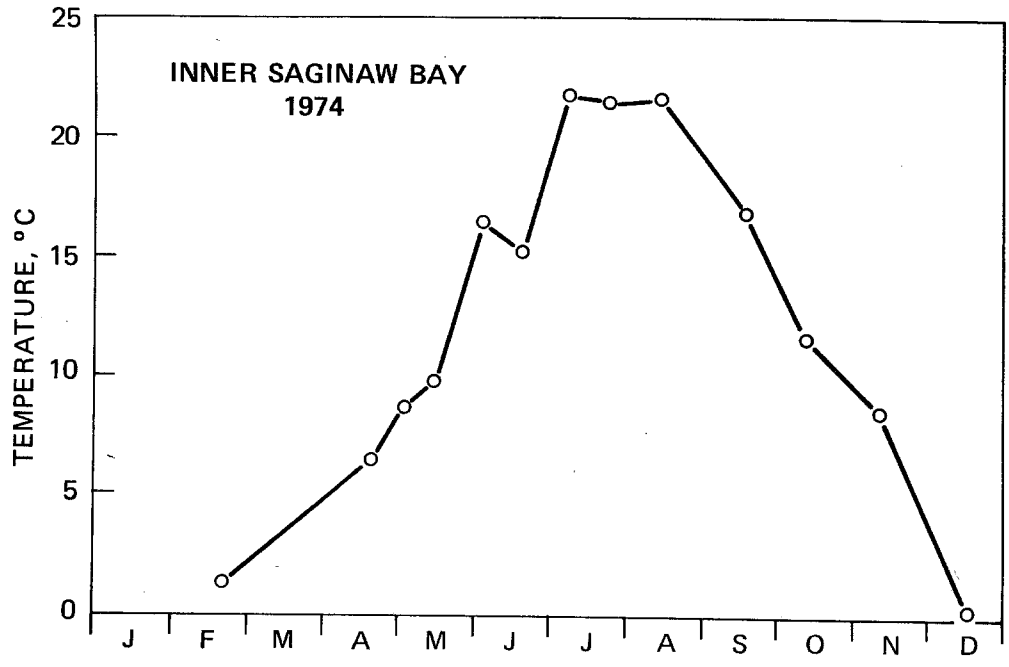


Figure 20. Time series used for water temperature.

External Loads and Boundary Concentrations

The basis for development of external loadings and boundary concentrations was presented in Section 6. Tabulated values for all loads and boundary concentrations are contained in Appendix D.

MODEL COEFFICIENTS

Approach

Determination of model coefficients is an integral part of the calibration process. Some model coefficients were determined independently of this process and were left unchanged during the calibration runs. At the opposite extreme, some coefficients were determined strictly by calibration to field data. Most coefficients, however, were varied within their ranges reported in the literature until the best fit was obtained to the data. All final calibration coefficients are tabulated in Appendix B. A discussion of the rationale and sources for the coefficients is contained below.

Cell Quotas for Phosphorus and Nitrogen

Biological state variables in the model were expressed in terms of dry weight concentrations, and percent phosphorus and nitrogen by dry weight. There was no explicit consideration of cell sizes or number concentrations. The variables PSA and NSA (percent P and N by dry weight) were proportional to the variables P and N (moles P and N per cell) through the conversion factor FACT (mg dry weight per cell). In practice, starting with values for FACT, values were chosen for PO and NO such that the corresponding values for PSAMIN and NSAMIN were consistent with reported values for minimum cell quotas of these nutrients. It should be noted that PSA and NSA are the more fundamental variables because all nutrient kinetics were expressed in terms of these variables and their minimum values.

The values used for FACT were based on results contained in Tables 1 to 3. The grouped category labeled "large Stephanodiscus" was responsible for most of the diatom biomass in the bay, and its value of FACT was used for diatoms in the model. For the same reason, the value of FACT for *Scenedesmus* was used for green algae in the model. The average of individual values of FACT for "other" phytoplankton species was used for this group in the model because no single species dominated the observed assemblage. The values of FACT for the blue-green groups were taken directly from Table 3.

Values for PO were selected so that the corresponding values for PSAMIN for blue-greens and non-blue-greens were 0.07% and 0.05%, respectively. These choices were consistent with a literature review by Healey (1975). An independent method of estimating these values is to consider the value of 0.08% for surplus internal phosphorus proposed by Fitzgerald and Nelson (1966) as a threshold between growth rate limitation by phosphorus and phosphorus sufficiency. If it is assumed that this threshold occurs when the value of PSA is two to five times the value of PSAMIN (e.g., Rhee 1978; Droop 1973), then this corresponds to a range of 0.02 - 0.08% for PSAMIN.

More recently, Shuter (1978) reviewed the literature and reported a range for minimum cell phosphorus quota of 0.025 - 0.584%. The difference in the values used here for PSAMIN between blue-greens and non-blue-greens was in the same proportion as the difference reported by Shuter.

Determination of values for NO and hence, NSAMIN, was more straightforward than for PSAMIN because nitrogen constitutes a much higher proportion of cellular biomass than phosphorus. Accordingly, the reported data show much less variation. A value for NSAMIN of 2.5% N by dry weight was used for all phytoplankton groups in the model. This choice was consistent with the results of Healey (1975), Fitzgerald (1969a), and Shuter (1978).

The parameters KPCELL and KNCELL were internal half-saturation levels for phosphorus and nitrogen, respectively. These were specified equal to the individual values of PSAMIN (PO) and NSAMIN (NO) for each phytoplankton group in the model (Rhee 1978; Droop 1973). This implies that specific growth rates become half the maximum growth rates when either total cellular phosphorus or total cellular nitrogen, whichever is controlling, is twice the minimum cell quota.

Phosphorus and Nitrogen Uptake Kinetics

Several coefficients needed to be specified for the phosphorus and nitrogen uptake kinetics equations. The parameters PCAMIN and NCAMIN corresponded to minimum concentrations of phosphorus and nitrogen, respectively, to which the phytoplankton could deplete the external environment. In practice, given values for PCAMIN and NCAMIN, Equation A.15.0 was used to calculate phosphorus and nitrogen concentration factors, CONCP and CONCN. The assumptions of specific gravity equal to unity, and of dry weight equal to 25% of wet weight in Equation A.15.0 have been discussed earlier. Values used for PCAMIN and NCAMIN (Table 6) were consistent with the results of Nalewajko and Lean (1978) and Rhee (1974, 1978). The corresponding values for CONCP and CONCN were consistent with the results of Provasoli (1969), Button et al. (1973), and Fitzgerald (1969a).

Given values for the above coefficients, specification of PK1 and NK1 determined the half-saturation concentrations for the phosphorus and nitrogen uptake mechanisms, respectively. Literature values for such phosphorus concentrations were not extensive, although somewhat more information was available for nitrogen. Phosphorus uptake half-saturation concentrations from 18 - 87 µg P/l have been reported for several diatoms (Kilham et al. 1977; Fuhs 1969). Rhee (1973) reported a concentration of 20 µg P/l for Scenedesmus sp., and Healey (1973) reported a range of 30 - 60 µg P/l for Anabaena, depending on the cation concentration in the medium. As a general guiding principle, there was considerable evidence in the literature that the phosphorus uptake mechanisms of blue-green algae, especially non-N_2-fixing blue-greens, were more efficient than the phosphorus uptake mechanisms of other algae (Bush and Welch 1972; Huang et al. 1973; Hammer 1964; Shapiro 1973; Pearsall 1932). Fitzgerald (1969b) presented evidence that non-N_2-fixing blue-greens could effectively out-compete N_2-fixing blue-greens for available phosphorus at low concentrations. Nitrogen uptake half-saturation concentrations from 1.4 - 70 µg N/l have been reported in the literature

TABLE 6. SUMMARY OF PRINCIPAL PHOSPHORUS AND NITROGEN COEFFICIENTS FOR THE PHYTOPLANKTON GROUPS IN THE MODEL

	Parameter					
Phytoplankton group	PSAMIN % P by dry wt	NSAMIN % N by dry wt	PCAMIN µg P/l	NCAMIN µg N/l	P-uptake half-saturation concentration µg P/l	N-uptake half-saturation concentration[1] µg N/l
Diatoms	0.05	2.5	0.5	3	60	30
Greens	0.05	2.5	0.5	3	20	30
Others	0.05	2.5	0.5	3	60	30
Blue-greens (non-N_2)	0.07	2.5	0.5	3	15	30
Blue-greens (N_2)	0.07	2.5	0.5	3	60	30

[1]Cells assumed to be nutrient-starved; i.e., PCA → PCAMIN and NCA → NCAMIN.

(Eppley and Thomas 1969; Carpenter and Guillard 1971; Toetz et al. 1973; Eppley et al. 1969). There did not appear to be any evidence for systematic variations among different phytoplankton groups. The values used for phosphorus and nitrogen uptake half-saturation concentrations for the five phytoplankton types in the model are contained in Table 6.

No distinctions were made among phytoplankton types in the model with regard to either R1PM, maximum phosphorus uptake rate, or R1NM, maximum nitrogen uptake rate. Values used for these coefficients were based on the literature survey by Healey (1975).

A comparison of relative phosphorus uptake efficiencies for the five phytoplankton groups in the model is presented in Figure 21. This comparison assumed that the cells were phosphorus-starved (PCA → PCAMIN as P → PO), and that temperature and light were at optimal levels (f(T) = f(L) = 1). For the coefficients used, non-N_2-fixing blue-greens had the most efficient phosphorus uptake kinetics, followed by green algae. Efficiencies of diatoms, "others", and N_2-fixing blue-greens were all equal to each other, and at a lower level than non-N_2-fixing blue-greens and green algae. For the coefficients used, there were no distinctions among the phytoplankton groups in the model with regard to nitrogen uptake kinetics. Under the same assumptions as in Figure 21 for phosphorus, specific nitrogen uptake rates for all five phytoplankton groups became half-maximum at a dissolved available nitrogen concentration of 30 µg N/l.

Phytoplankton Growth Rates

Maximum growth rate, RAMAX, and a temperature reduction factor, f(T), must be specified for each phytoplankton group in the model. The typical pattern of seasonal succession in most temperate-zone lakes is from diatoms to greens to blue-greens. Results of an extensive literature review by Canale and Vogel (1974) support the hypothesis that this pattern is correlated with progressively higher temperature optima and progressively lower maximum growth rates. Values for RAMAX and the functions for f(T) used in the model were generally consistent with these results. One difference is that the specific growth rate for diatoms in the model reached a plateau at 10°C, and declined after 14°C. Lin and Schelske (1978) reported the existence of such plateaus in specific growth rates for various Great Lakes diatoms. Stoermer and Ladewski (1976) reported that natural populations of Stephanodiscus binderanus and Stephanodiscus tenuis prefer temperatures in the range from 6 - 9°C, and then rapidly decline after approximately 14°C. These two species account for most of the diatom biomass in the inner portion of Saginaw Bay. Another difference is that "others" in the model had higher maximum growth rates at lower temperatures. This phytoplankton group was especially difficult to characterize because it contained a wide variety of species. The temperature-dependent specific growth rates used in the model are presented in Figure 22. Values for each phytoplankton group represent the product of RAMAX (Table B.1) and f(T) (Equations A.16.0 - A.16.4) for that group.

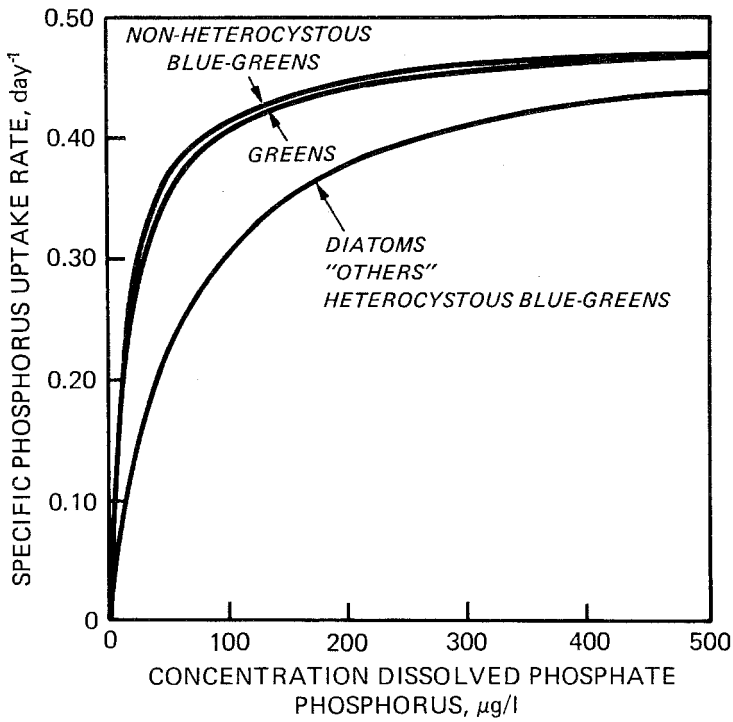


Figure 21. Specific phosphorus uptake rates as a function of external phosphorus concentration for the phytoplankton groups in the model (assuming (P = PO).

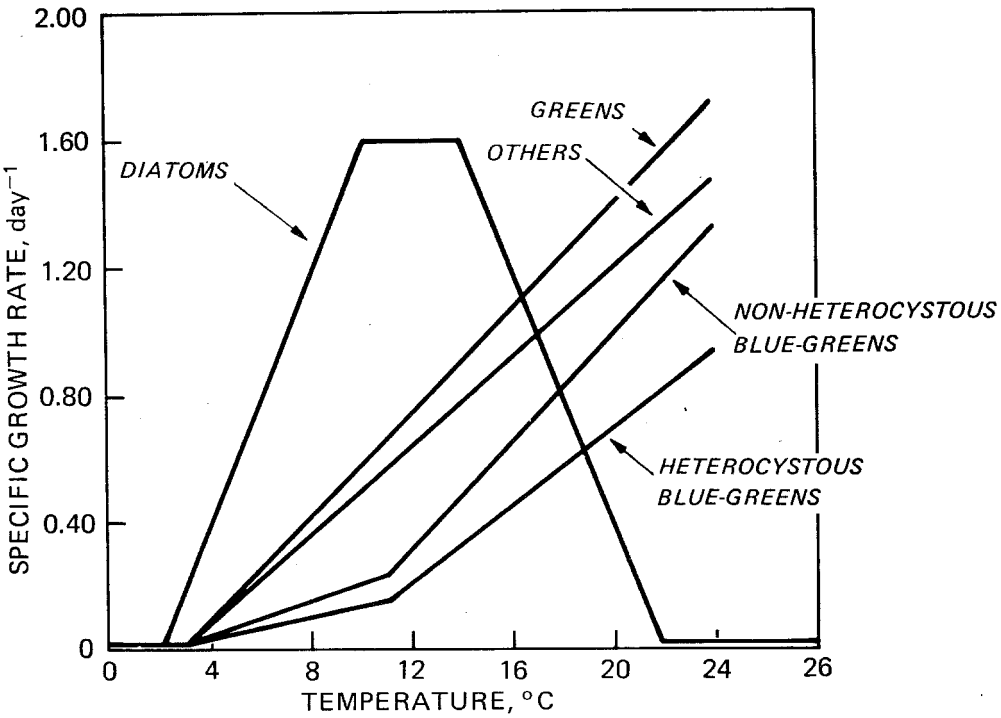


Figure 22. Temperature dependence of specific growth rates for the phytoplankton groups in the model.

Silicon Coefficients

Silicon-related coefficients need to be specified only for diatoms in the model. The value used for SSA, the fixed silicon stoichiometry, corresponded to 20% silica (SiO_2) by dry weight. Reported values for this coefficient span a wide range from 4 - 75% (Lewin 1962; Parker et al. 1977; Lund 1965). The value used for KSCM, the half-saturation concentration for silicon-controlled growth, was 100 µg Si/l. A range of 8 - 94 µg Si/l has been reported for this coefficient (Guillard et al. 1973; Paasche 1973; Kilham 1975).

Atmospheric Nitrogen Fixation

Fixation of atmospheric nitrogen could occur in the model if the calculated concentration of dissolved available nitrogen fell below 150 µg N/l (Ogawa and Carr 1969). Operationally, the internal nitrogen level for the N_2-fixing blue-greens was specified to be an inverse function of the external dissolved available nitrogen concentration. In the limit as this external concentration approaches zero, total cellular nitrogen level approaches four times the minimum cell quota. This limit was based on observed ranges for internal nitrogen accumulation (Fitzgerald 1969a).

Miscellaneous Coefficients

Values used for RADSAT, the saturation light intensity for diatoms, greens, and "others", was consistent with the results of Strickland (1958), Lin and Schelske (1978), Davis (1976), and Rhee (1978). The value for RADSAT for blue-greens was consistent with results by the U.S. Environmental Protection Agency (1971).

The value used for RRESP, phytoplankton respiration rate, was consistent with results summarized by O'Connor et al. (1973), and with recent measurements by DePinto (personal communication) using light and dark stage chemostats.

Values used for RLYS, phytoplankton decomposition rate, were estimated from the results of DePinto (1974) and Gunnison and Alexander (1975). A second-order kinetics mechanism was applied to decomposition data for Chlorella from DePinto (1974). The result was used to specify RLYS for diatoms, greens, and "others" in the model. The value of RLYS for blue-greens was estimated to be approximately three times higher on the basis of comparative results by Gunnison and Alexander (1975).

Net sinking rates must be specified for each phytoplankton group (ASINK) and for each of the unavailable nutrient forms (TOPSNK, TONSNK, TOSSNK). These rates are very dependent on the morphometry of a particular system, especially in shallow systems such as Saginaw Bay. A value of 0.05 m/day for unavailable nutrient forms was found to give the best calibration results for total nutrient concentrations. As an estimate, this same value was used for ASINK for all five phytoplankton groups. This was contrary to the conventional practice of using lower sinking rates for blue-greens as compared to non-blue-greens. In the present study, consistently better calibration re-

sults were obtained when no distinctions were made among phytoplankton groups with regard to sinking rates. This would tend to imply that vertical dispersion within the water column, and boundary conditions at the sediment-water interface were more important in determining phytoplankton vertical dynamics than were any inherent differences in sinking rates among the various phytoplankton groups. Another reason might be that the tendency of blue-greens to form large colonies and filaments may more than offset their superior buoyancy under certain circumstances (Rhee, personal communication).

A value of 0.005 day^{-1} was used for RTOP, RTON, and RTOS, the conversion rates from unavailable nutrient forms to available nutrient forms in the water column. This choice was based primarily on literature conversion rates for phosphorus and nitrogen. The value used was an estimate for the silicon conversion rate. Jewell and McCarty (1971) reported a range for phosphorus and nitrogen conversion rates from 0.01 - 0.03 day^{-1}, based on measurements with decomposing algae. Hefner (1978) reported a range for phosphorus conversion rate from 0.002 - 0.004 day^{-1}, based on bioassays with various samples of tributary inputs to Lake Erie. Another approach can be taken for estimating the phosphorus conversion rate using the results of Cowen and Lee (1976) for runoff, precipitation, and river samples from Madison, Wisconsin, and the Lake Ontario basin. These workers concluded that on the average, approximately 20 percent of the difference between total phosphorus and dissolved ortho-phosphorus became available over the course of an 18-day bioassay. This conclusion, combined with the fact that 76 percent of the total phosphorus load from the Saginaw River is in a form other than dissolved ortho- phosphorus (Table 5), leads to a conversion rate of 0.01 day^{-1}.

It is interesting to note that the conversion rate used in the model corresponds to a half-time of 4.6 months. This implies that ignoring hydraulic washout, approximately 50 percent of the unavailable nutrients in the peak spring tributary load will be available for the growth of blue-green algae during the late summer-fall period.

Zooplankton Coefficients

In general, the data were not as extensive for zooplankton coefficients as they were for phytoplankton coefficients. Values used for RZMAX, maximum ingestion rate, and ZASSIM, assimilation efficiency, were consistent with the results of McNaught et al. (1979). The value used for AZMIN, phytoplankton refuge concentration, was consistent with the literature results summarized by Scavia and Eadie (1976). All values of ZEFF, a preference factor, were set equal to unity because no distinctions were made among the various phytoplankton-zooplankton pairs in the present version of the model. All of the remaining zooplankton coefficients were based on estimates and/or calibration to field data.

The fixed phosphorus and nitrogen stoichiometries of the zooplankton were set equal to the values for PSAMIN and NSAMIN, respectively, used for diatoms, greens, and "others". This was done to avoid development of a complicated system to account for mass transfer among model compartments with different stoichiometric compositions. The assumption that zooplankton have the

same basic requirements for phosphorus and nitrogen as the phytoplankton was probably a good approximation.

MODEL IMPLEMENTATION

The 23 simultaneous, ordinary, non-linear differential equations in the model were coded in FORTRAN and implemented on a Digital Equipment Corporation PDP-11/45 computer. The equations were solved numerically using an Adams-Moulton predictor-corrector algorithm. The time steps used were 30 minutes for internal and external dissolved nutrient concentrations, and 3 hours for all other equations. The initial conditions for each state variable are contained in Appendix C. A typical 365-day run required approximately 15 minutes of CPU time.

Model output was compared to cruise averages for the inner bay sampling stations. Geometric statistics were used to reduce the phytoplankton and zooplankton data. Dolan et al. (1978) reported that the phytoplankton data are log-normally distributed. Since the zooplankton data were based on species counts in a manner similar to the phytoplankton data, it was decided to use geometric statistics for these data as well. Arithmetic statistics were used for all other parameters because they were based on direct concentration measurements.

All phytoplankton and zooplankton data are presented as the geometric mean plus or minus one standard deviation of the data points about the mean. All other data are presented as the arithmetic mean plus or minus one half standard deviation of the data points about the mean. The arithmetic deviations are presented differently because the data show large variations about the mean, due primarily to the spatial aggregation of dissimilar water masses into a single segment.

The operational criterion for a successful calibration was to obtain model output as close as possible to the mean value for each cruise, for each parameter. In cases where it was not possible to obtain model output within a standard deviation or half a standard deviation of the mean, an attempt was made to fit the peak concentrations as closely as possible, thus compromising the fit during off-peak periods. This resulted in the smallest relative error during periods when a given variable was most important. This approach was a realistic compromise from a management perspective, since most management strategies are based on consideration of peak concentrations.

RESULTS

Phytoplankton

Results for total phytoplankton crop are shown in Figure 23. Both model output and field data at each point in time are composites of the five phytoplankton groups. The total crop ranges over greater than an order of magnitude. After a very large spring peak there is a rapid decline and a subse-

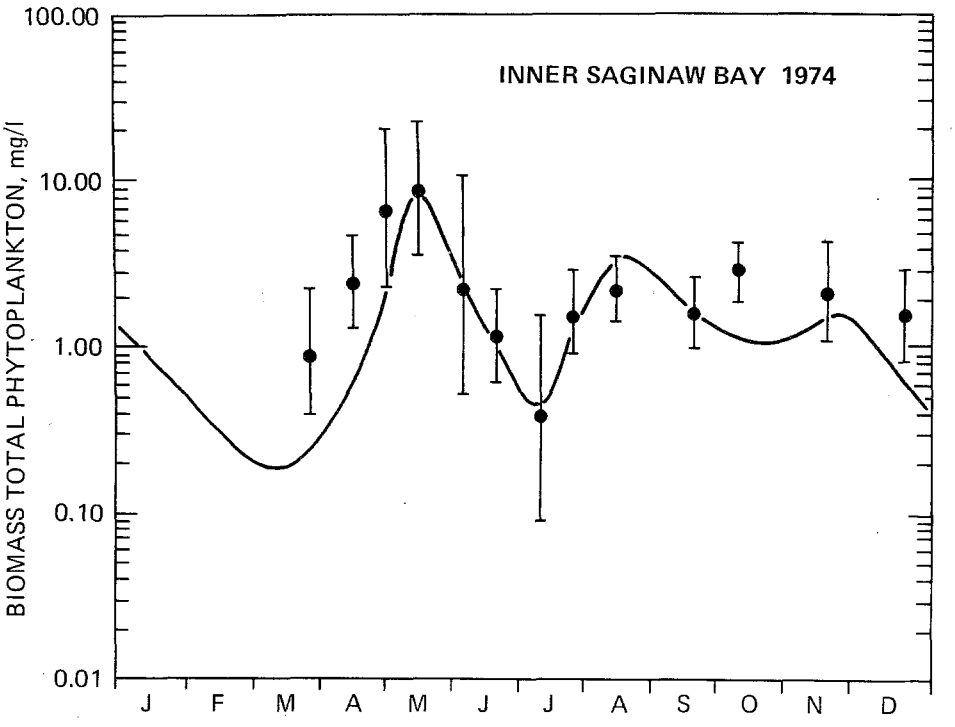


Figure 23. Comparison between model output and field data for total phytoplankton biomass.

quent rise to a relatively steady, but much lower, total crop over the remainder of the year. The model output was within a standard deviation of the field data for most sampling cruises.

Diatoms accounted for approximately 99 percent of the total biomass in the spring peak (Figure 24). After the spring peak, diatoms declined rapidly by over two orders of magnitude. A second well-defined diatom peak occurs in late-fall. The model output corresponded well with both of the diatom peaks; however, the model output was within a standard deviation of the field data for only half of the sampling cruises. Particular problems were encountered in early spring and late summer. The former was a possible consequence of the poorly known kinetic mechanisms under extreme non-optimal conditions. The latter could have been due to transport effects which occurred on a shorter time scale than the model forcing functions, or by failing to explicitly include a resuspension mechanism.

Green algae peaked in mid-summer at a level approximately an order of magnitude lower than the diatoms (Figure 24). The model output was within a standard deviation of the field data for all sampling cruises.

At their peak relative abundance, "others" accounted for only 12 percent of total phytoplankton biomass. The concentrations of "others" remained re-

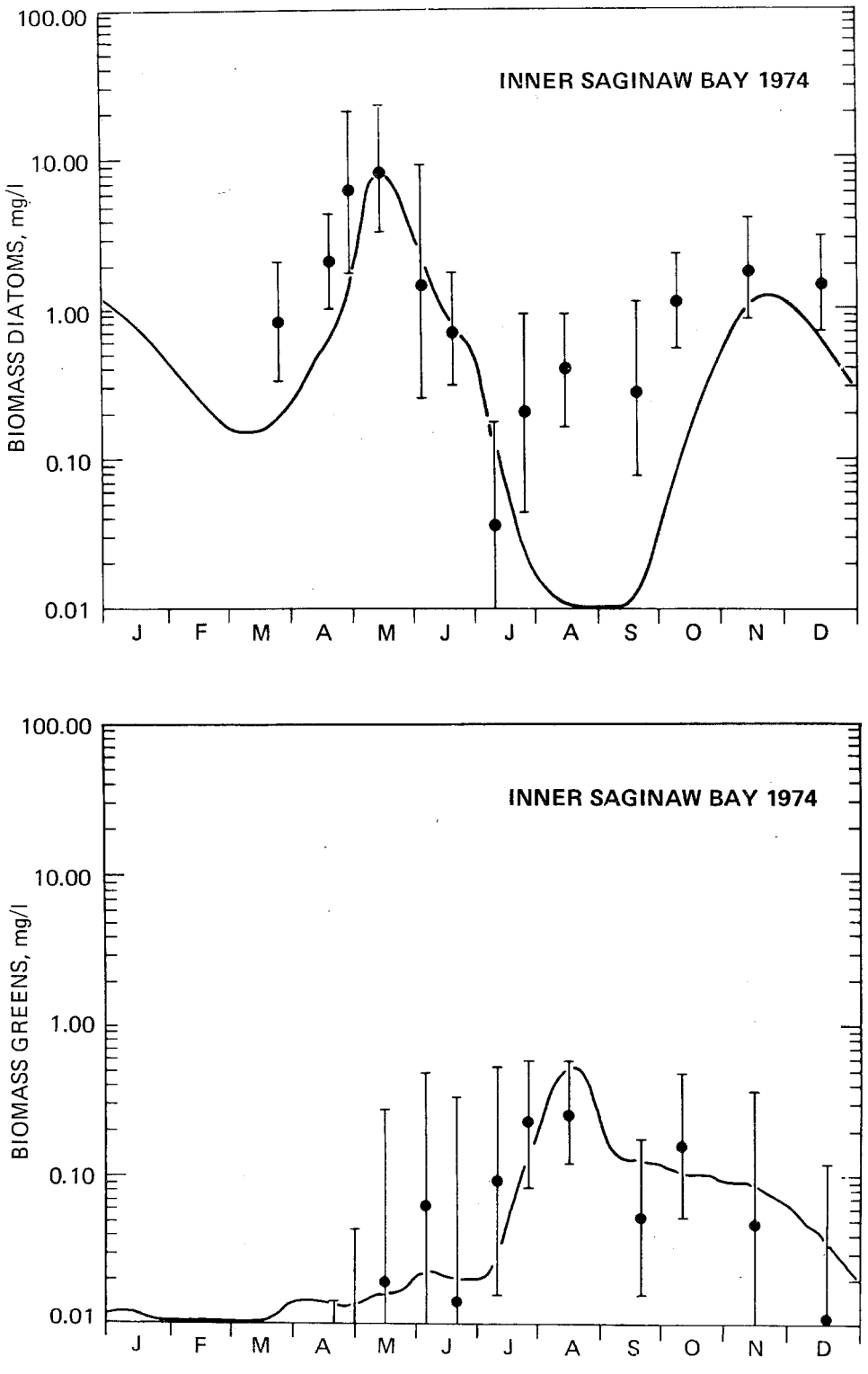


Figure 24. Comparisons between model output and field data for biomass of diatoms and green algae.

latively steady at low values for most of the year (Figure 25). Model output was within a standard deviation of field data for most sampling cruises.

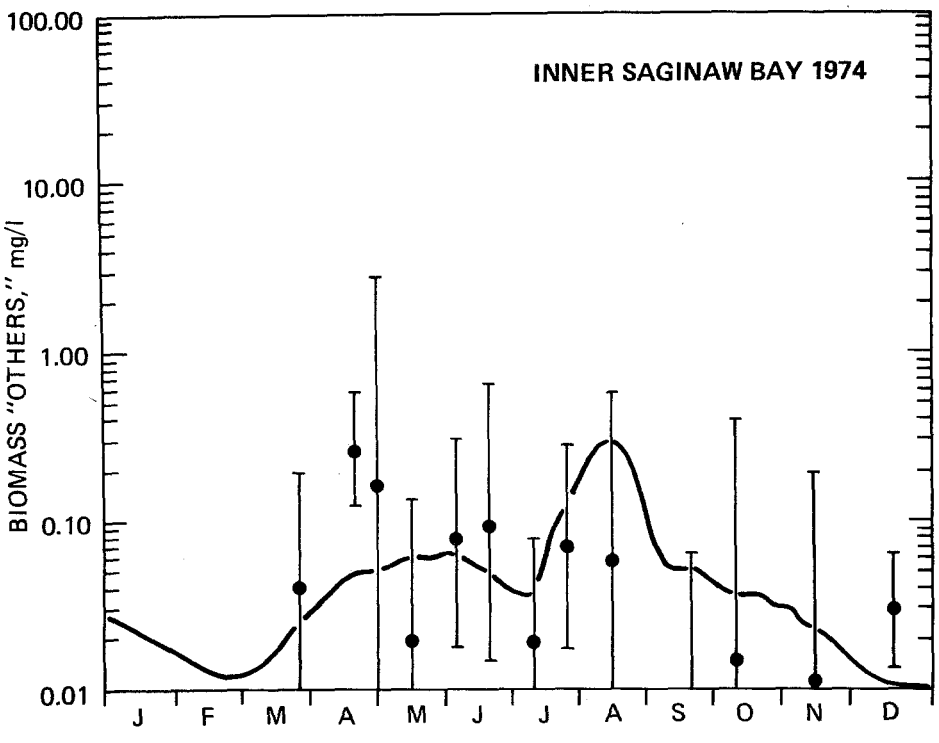


Figure 25. Comparison between model output and field data for biomass of "other" phytoplankton.

The two blue-green phytoplankton groups peaked in late-summer and early-fall (Figure 26). The non-N_2-fixing blue-greens peaked at a substantially higher level than the N_2-fixing blue-greens. Model output was within a standard deviation of field data for each of the blue-green types for most sampling cruises. Simulations were consistent with the hypothesis that no significant degree of atmospheric nitrogen fixation occurred in Saginaw Bay. The rate of supply of dissolved available nitrogen appeared to be sufficient for the non-N_2-fixing blue-greens to exploit their more favorable phosphorus uptake kinetics and faster maximum growth rate. A more detailed discussion is contained in Section 8.

Summaries of peak phytoplankton concentrations and annual integrated gross production values for each phytoplankton group in the calibrated model are contained in Tables 7 and 8, respectively. Note that although the peak total blue-green concentration was only 30 percent of the peak diatom concentration, the annual integrated gross blue-green production was 65 percent of the annual integrated gross diatom production. These differences were reflected in the fact that the blue-green peak was much broader than the diatom peak. The persistence of the blue-greens was a consequence of their freedom

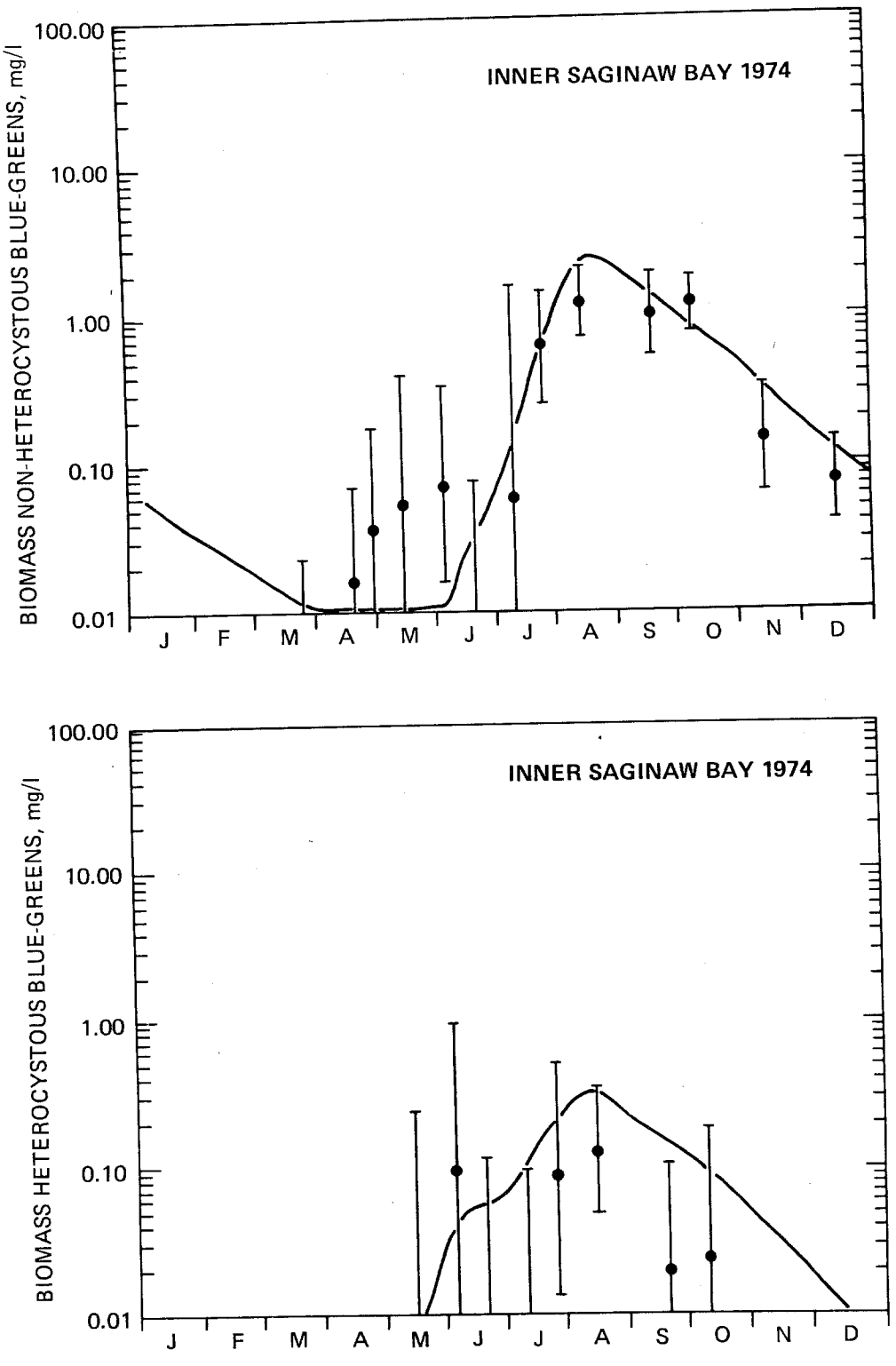


Figure 26. Comparisons between model output and field data for the blue-green phytoplankton groups.

TABLE 7. RESULTS FOR PEAK PHYTOPLANKTON CONCENTRATIONS IN FINAL CALIBRATION

Phytoplankton group	Concentration mg dry wt/liter
Diatoms	
spring peak	9.37
fall peak	1.24
Greens	0.574
Others	0.331
Blue-greens (non-N_2)	2.56
Blue-greens (N_2)	0.311

TABLE 8. RESULTS FOR ANNUAL INTEGRATED GROSS PRODUCTION IN FINAL CALIBRATION

Phytoplankton group	Annual integrated gross production mg dry wt/liter
Diatoms	24.8
Greens	3.5
Others	2.33
Blue-greens (non-N_2)	14.0
Blue-greens (N_2)	2.0

from grazing and a prolonged period of near optimal temperature and light conditions.

Zooplankton

There were two peaks in the total zooplankton data which coincided with the rise of the two diatom peaks in the spring and the fall (Figure 27). Model output showed these, plus an additional peak in August which apparently coincided with the peak in green algae. It is not clear whether such an additional peak occurred in the data. In any case, the model output was within a standard deviation of field data for most sampling cruises.

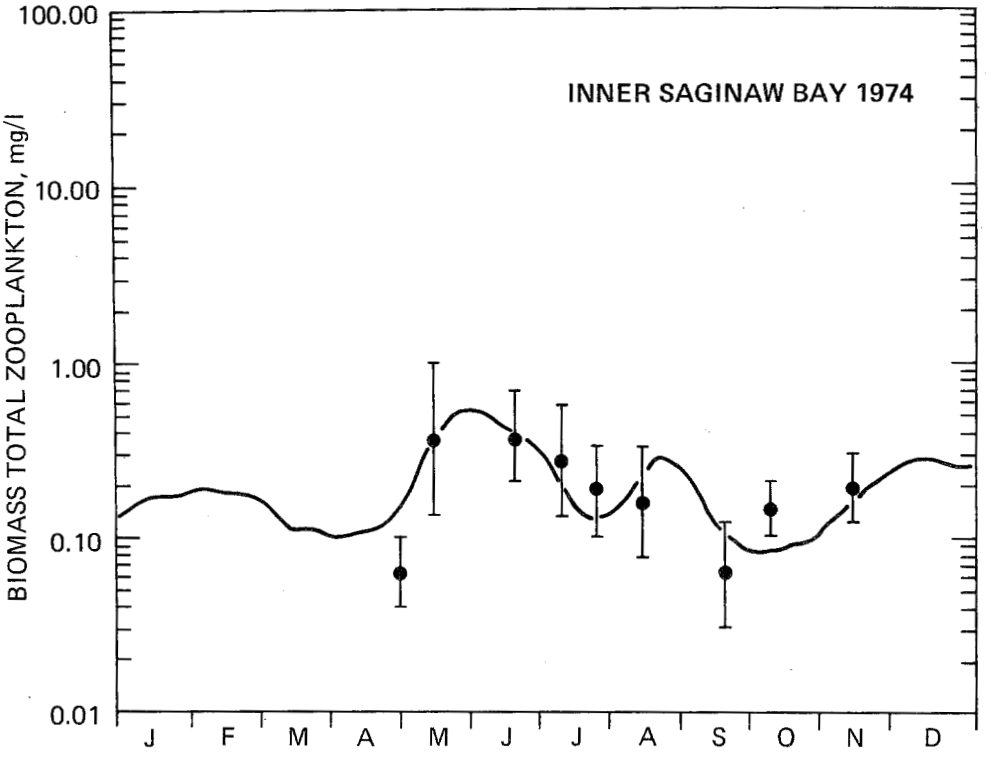


Figure 27. Comparison between model output and field data for total zooplankton biomass.

Nutrients

There was a large build-up of total phosphorus and total nitrogen early in the year due to peak spring loads and reduced water exchange rates between the inner bay and Lake Huron (Figure 28). This build-up was followed by a sharp decline due to the rapid water exchange in May-June, and the decrease in Saginaw River loadings. Although model output closely followed trends in the data for total phosphorus and total nitrogen, agreement was not usually obtained within one half a standard deviation. For both variables, model output tended to be consistently higher than the respective means of the data

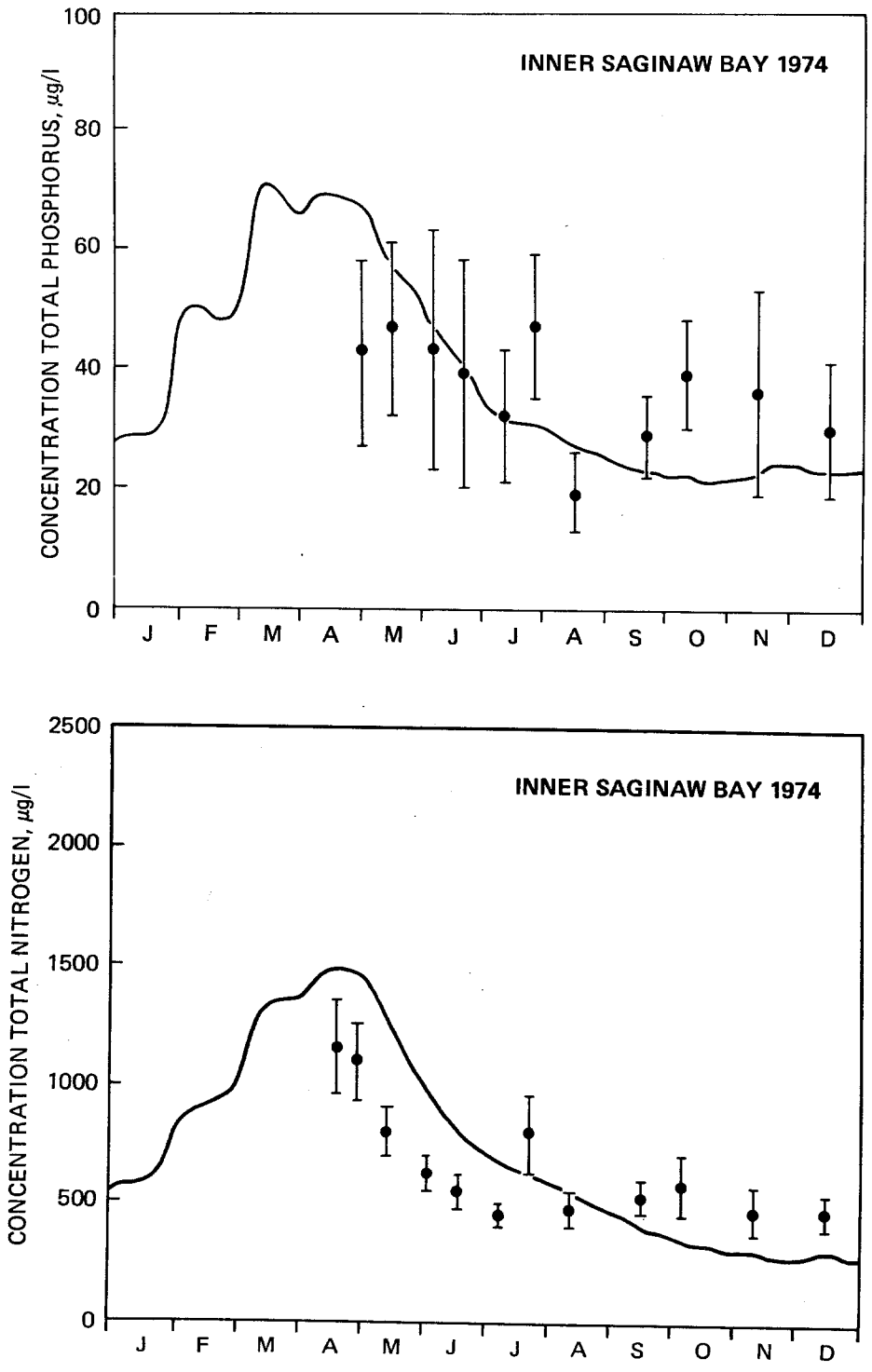


Figure 28. Comparisons between model output and field data for total phosphorus and total nitrogen.

during the first half of the year, and consistently lower than the respective means of the data during the second half of the year. In addition, there were several sharp transient variations which were not accounted for by the model. Much of the difficulty was probably caused by the use of a constant net settling velocity for the entire annual cycle. A three-dimensional hydrodynamic model which includes a mechanism for resuspension is needed to more accurately describe the temporal variation in total nutrient concentrations. Such an approach was beyond the scope of the present study.

The trends observed for dissolved available phosphorus and dissolved available nitrogen were similar to trends for total forms of these nutrients (Figure 29). Declines in dissolved available phosphorus and nitrogen after their spring peaks were associated with nutrient utilization by diatoms. Both nutrients remained at their lowest levels during late-summer and fall because of the prolonged blue-green bloom. For dissolved available phosphorus, model output was within half a standard deviation for most sampling cruises. For dissolved available nitrogen, model output closely followed the trend of the means of the field data; however, agreement was not usually obtained within one half a standard deviation.

Results for dissolved available silicon (Figure 30) tended to be inversely proportional to results for diatoms because only the diatoms had a silicon requirement. Two minima occurred in the silicon data which corresponded to the spring and fall diatom peaks. The sharp increase in silicon concentration after the spring minimum was probably caused by water exchange with Lake Huron because the silicon loading from the Saginaw River was greatly diminished after June (Figure 14). Model output followed the trend of the means of the field data; however, agreement was not usually obtained within one half a standard deviation. Overcalculation of dissolved available silicon in early spring was related to undercalculation of diatom biomass during the same period (Figure 24). Lack of agreement after the spring minimum was probably due to lack of sufficient temporal resolution in the water exchange rates.

Primary Production

Primary production data are extremely useful in the model calibration process. Primary production is a rate measurement and not a concentration measurement. This parameter corresponds to the positive term in the differential equation for phytoplankton biomass. Since the solution to this equation, biomass concentration, depends only on the algebraic sum of the various rate processes in the equation, primary production constitutes an independent check on the internal consistency of phytoplankton dynamics.

Primary production data were not available on Saginaw Bay for 1974. Glooschenko and Moore (1973) measured primary production and chlorophyll concentration at two stations on 8 sampling cruises in Saginaw Bay during 1971. These data were of value in that the approximate seasonal magnitudes could be compared to the 1974 model output. Although forcing functions for water circulation, temperature, and light were not determined for 1971, nutrient loading for 1971 was probably somewhat higher than nutrient loading for 1974.

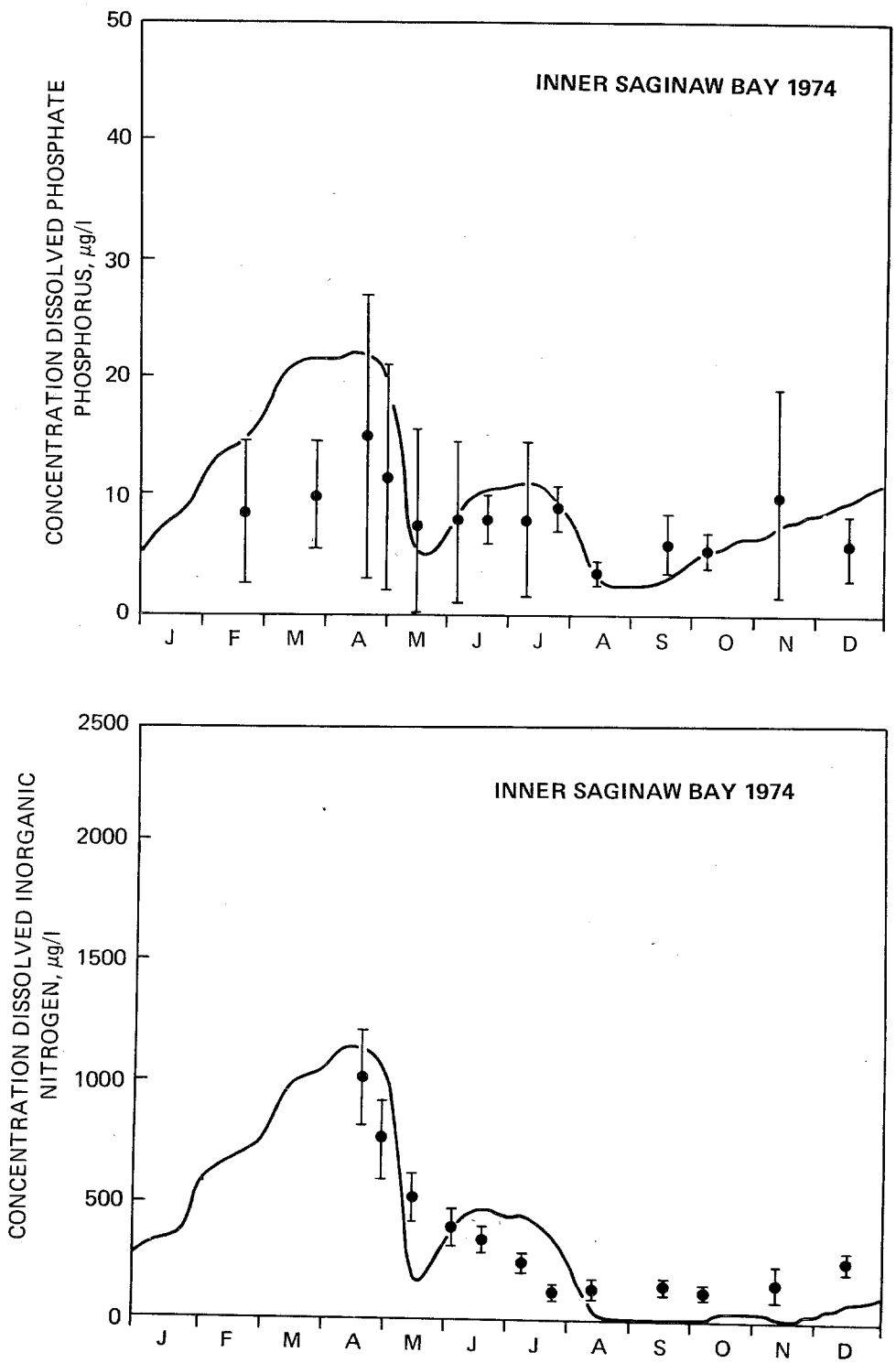


Figure 29. Comparisons between model output and field data for dissolved available phosphorus and dissolved available nitrogen.

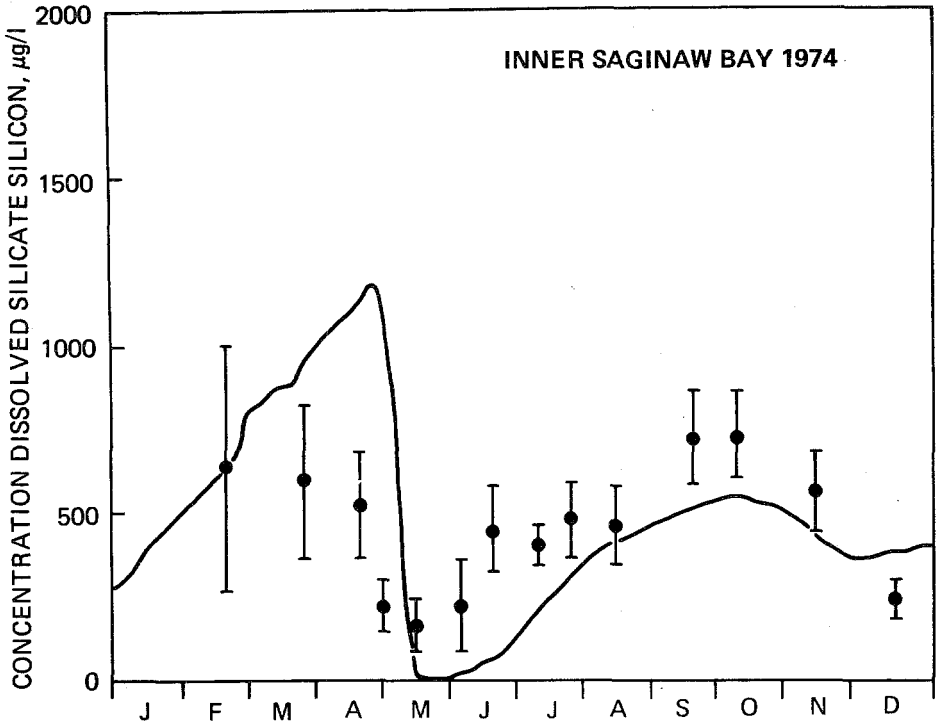


Figure 30. Comparison between model output and field data dissolved available silicon.

The upgrading of wastewater treatment plants in the Saginaw River basin began in 1971.

Model output for estimated gross primary productivity was compared with the cruise averages for the above data (Figure 31). The data were estimates of near-surface primary production. Model output was transformed to surface light intensity and a 12 hour daylight average. Dry weight to carbon conversion factors used were 35 percent for diatoms and 50 percent for non-diatoms. There was good agreement with regard to seasonal trends and magnitudes.

It is of interest to note the absence of a sharp spring peak in the 1971 primary production data. Glooschenko and Moore (1973) reported an apparent inconsistency between the unimodal structure of their primary production data, and the bimodal structure of their corresponding chlorophyll data. The model results provided a possible explanation for this observation. The model indicated that a very large phytoplankton crop resulted from a very short, yet intense, period of primary production. Specifically, the half-width for the calculated spring biomass peak was 22 days. The half-width of the biomass curve was its width in time at half of its maximum value. In contrast, the half-width of the calculated spring primary production peak was only 8 days. It follows that depending on the timing of the measurements, it is not inconsistent to observe relatively low values for primary production, simultaneously with relatively high values for phytoplankton biomass.

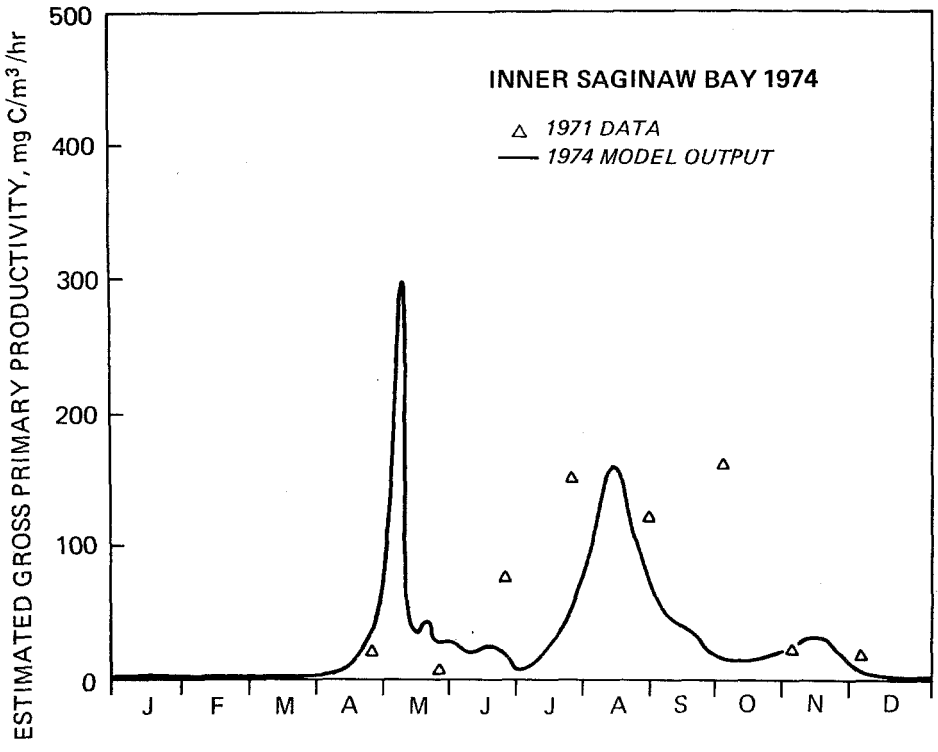


Figure 31. Comparison between estimated 1974 model output and 1971 field data for near-surface gross primary production.

Phytoplankton Internal Phosphorus

Data for phytoplankton internal phosphorus concentrations were not acquired for Saginaw Bay in 1974. Such data were obtained in 1975 for nine stations in the inner portion of the bay on four sampling cruises from July to October. An acknowledgement is made to C. Kwei Lin, GLRD, University of Michigan, for providing us with his unpublished internal phosphorus data.

Model output for phytoplankton internal phosphorus concentration corresponds to the sum of internal phosphorus above the minimum cell quota for all five phytoplankton groups, divided by the total phytoplankton biomass. Data for phytoplankton internal phosphorus corresponded to internal phosphorus above the minimum cell quota, as measured by the one hour boiling water extraction method of Fitzgerald and Nelson (1966). This value for phytoplankton internal phosphorus was then divided by the measured value for total phytoplankton biomass.

Comparison between 1974 model output and 1975 data was confounded by differences in forcing functions and external nutrient loads between the two years. In addition, excess internal phosphorus and phytoplankton biomass concentration were not measured using aliquots from the same water sample.

Sampling for these two parameters was, however, conducted at the same times, stations, and depths.

The magnitudes of model output and field data compared well during August and October, and poorly during July and September (Figure 32). This was consistent with known differences in external loading of dissolved available phosphorus between 1974 and 1975. Phytoplankton internal phosphorus is a sensitive function of the supply rate of dissolved available phosphorus. The annual load of dissolved available phosphorus from the Saginaw River was 50 percent higher in 1975 than in 1974 (Dolan, unpublished results). Most of the load increase occurred during the month of September. Differences between model output and field data in this case can be partially normalized by taking time averages. The average phytoplankton internal phosphorus concentration for the four sampling cruises in 1975 was 2.59 $\pm$ 1.25 µg P/mg algae. The average for the 1974 model output corresponding to the same time period was 1.5 $\pm$ 0.29 µg P/mg algae. Given the fact that the dissolved available phosphorus load was 50 percent higher in 1975, there was generally good agreement between model output and field data.

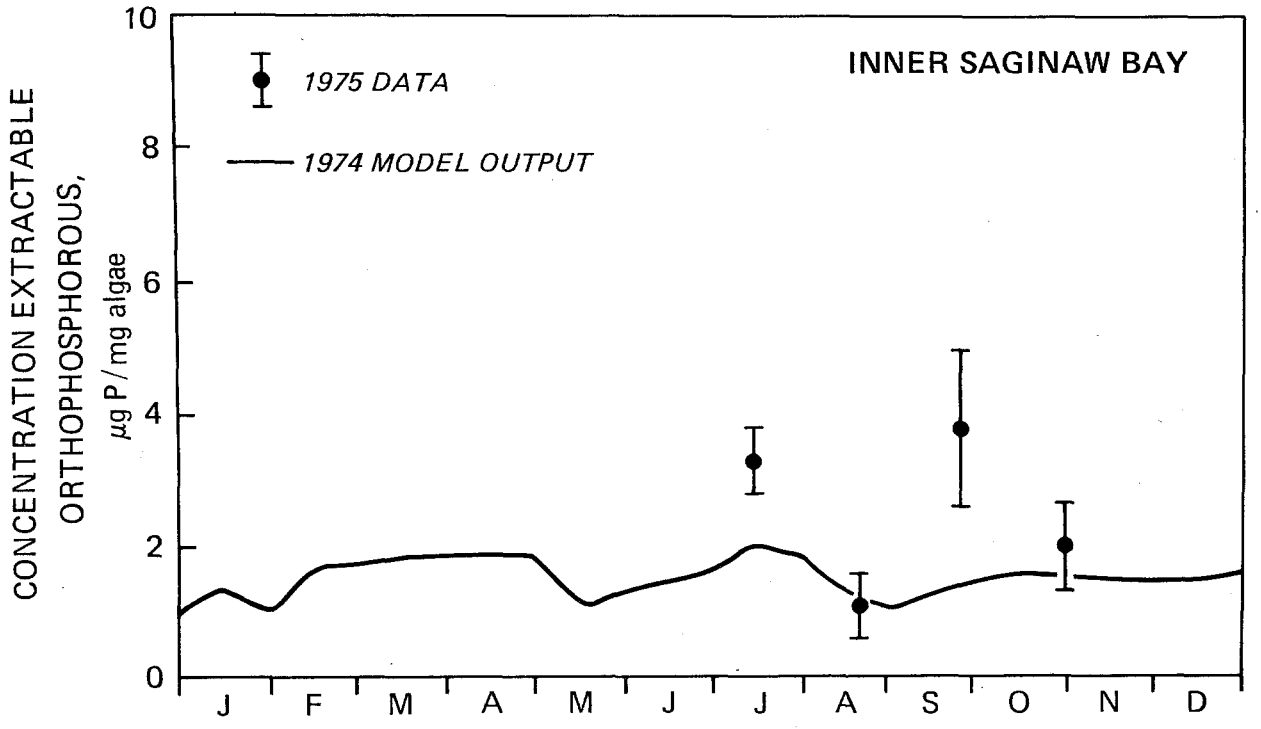


Figure 32. Comparison between 1974 model output and 1975 field data for excess internal (extractable) phytoplankton phosphorus concentration.

Sensitivity Analyses

To provide additional insight into the behavior of the model, 72 sensitivity analysis runs were conducted after final calibration was obtained. These sensitivity analyses included effects of systematic variations in three

principal types of model input: first, variations of plus or minus 20 percent and 50 percent in water exchange rates, temperatures, incident light intensities, and light extinction coefficients; second, variations of plus or minus 50 percent in phytoplankton growth rates; and third, variations of plus or minus 50 percent in all other model coefficients. Results were expressed in terms of percent changes in peak concentrations and annual integrated gross productions, relative to the final calibration. Discussions of selected results is included in the text. A complete tabulation of results from all 72 runs in contained in Appendix E.

SECTION 8

DISCUSSION

INTRODUCTION

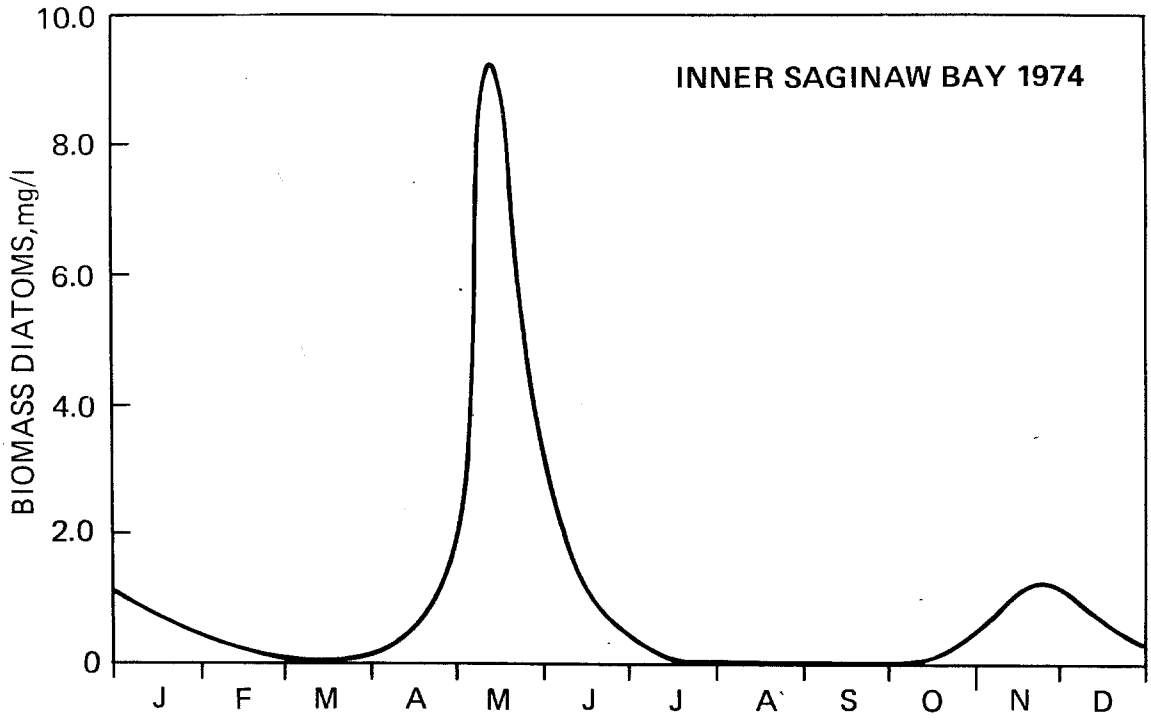
In the preceding section of this report, the solutions of model equations were compared to values for the corresponding field measurements. In contrast, the present section contains a discussion of the principal process components in the calibrated model for phytoplankton and nutrients. To the degree that the calibrated model constitutes a realistic description of the actual processes which occur in the physical system, insights can be gained by a detailed analysis of these components. The relative importance of temperature, light, and nutrients in determining actual specific growth rates is discussed for three of the dominant phytoplankton groups in Saginaw Bay. Subsequently, the relative importance of each loss mechanism is discussed for each of these groups. A discussion is included regarding the relative importance of phosphorus, nitrogen, and silicon as limiting nutrients. Finally, some important aspects of phytoplankton-nutrient dynamics are discussed, with special attention to the role of internal nutrient pool kinetics.

PHYTOPLANKTON GROWTH RATES

The differences between maximum phytoplankton growth rates and actual specific growth rates that occur in the natural environment is a function of ambient temperature, light, and nutrient conditions. In general, these actual growth rates are much less than maximum rates. Although phytoplankton have absolute requirements for various nutrients, temperature and light effects are more important than is generally realized.

Figures 33-35 illustrate the results of component analyses of growth rate terms in the model equations for diatoms, greens, and non-N_2-fixing blue-greens. The curves in each figure represent progressive reductions from the maximum growth rate for each phytoplankton group. These reductions were calculated using the values of individual terms in Equations A.3.2.1-A.3.2.3 for each group. The indicated resultant growth rates correspond to gross production rates.

Water temperature places an upper limit on the actual growth rate that can occur at any given time, independent of light and nutrient conditions. For all three phytoplankton groups, maximum growth rates can only occur during limited periods of the year. A bimodal pattern occurred for diatoms, partly because their growth rate was assumed to be optimal at lower tempera-



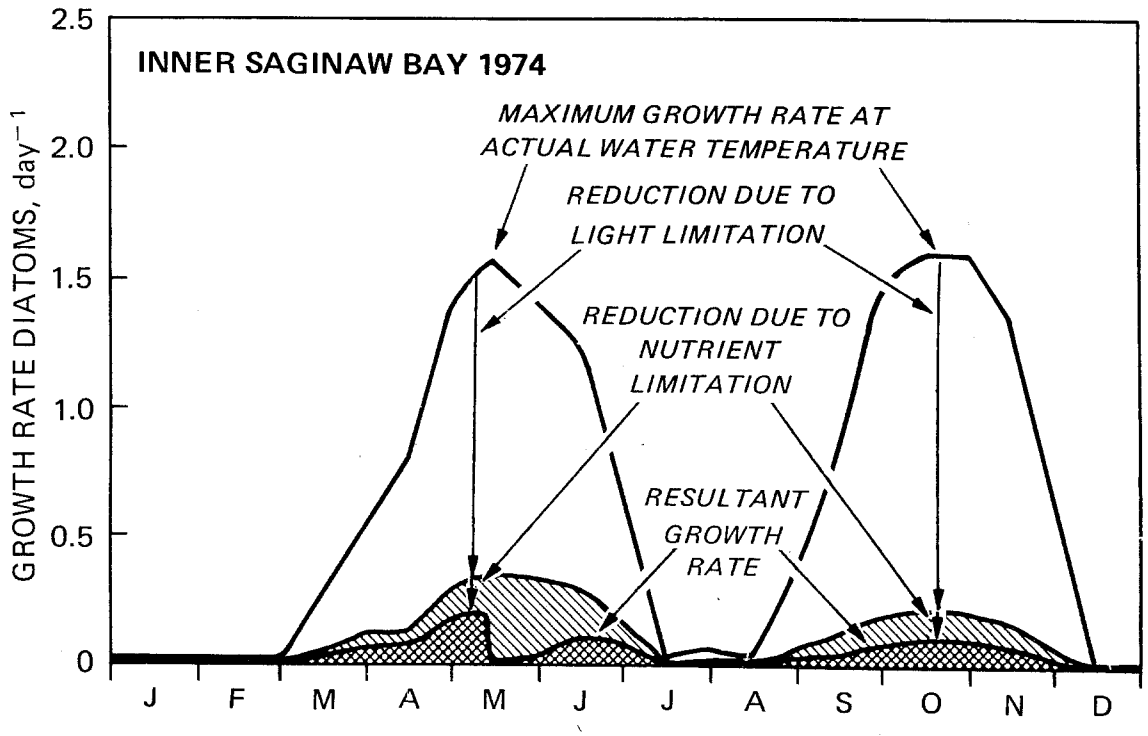


Figure 33. Component analysis of diatom growth rates.

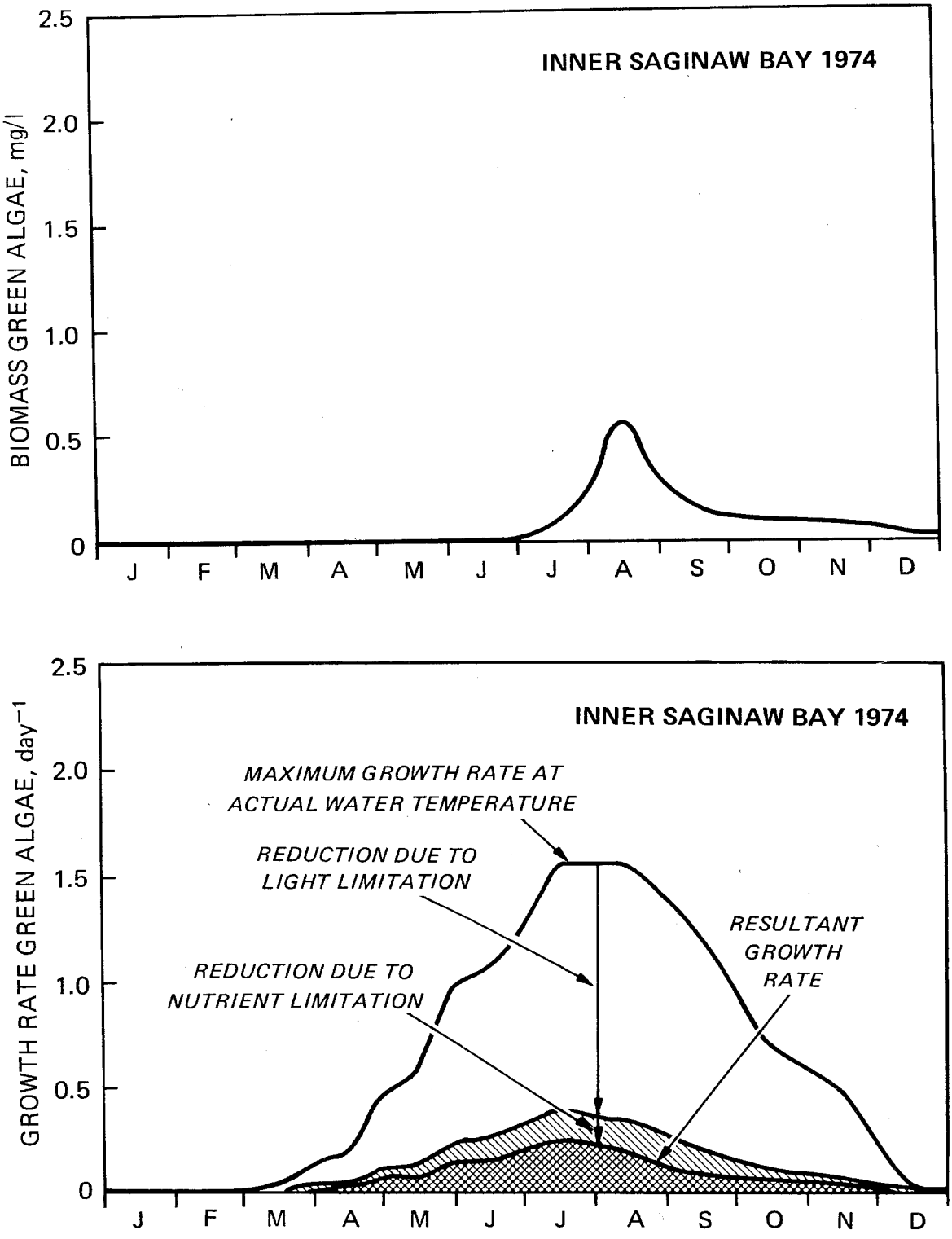


Figure 34. Component analysis of growth rates for green algae.

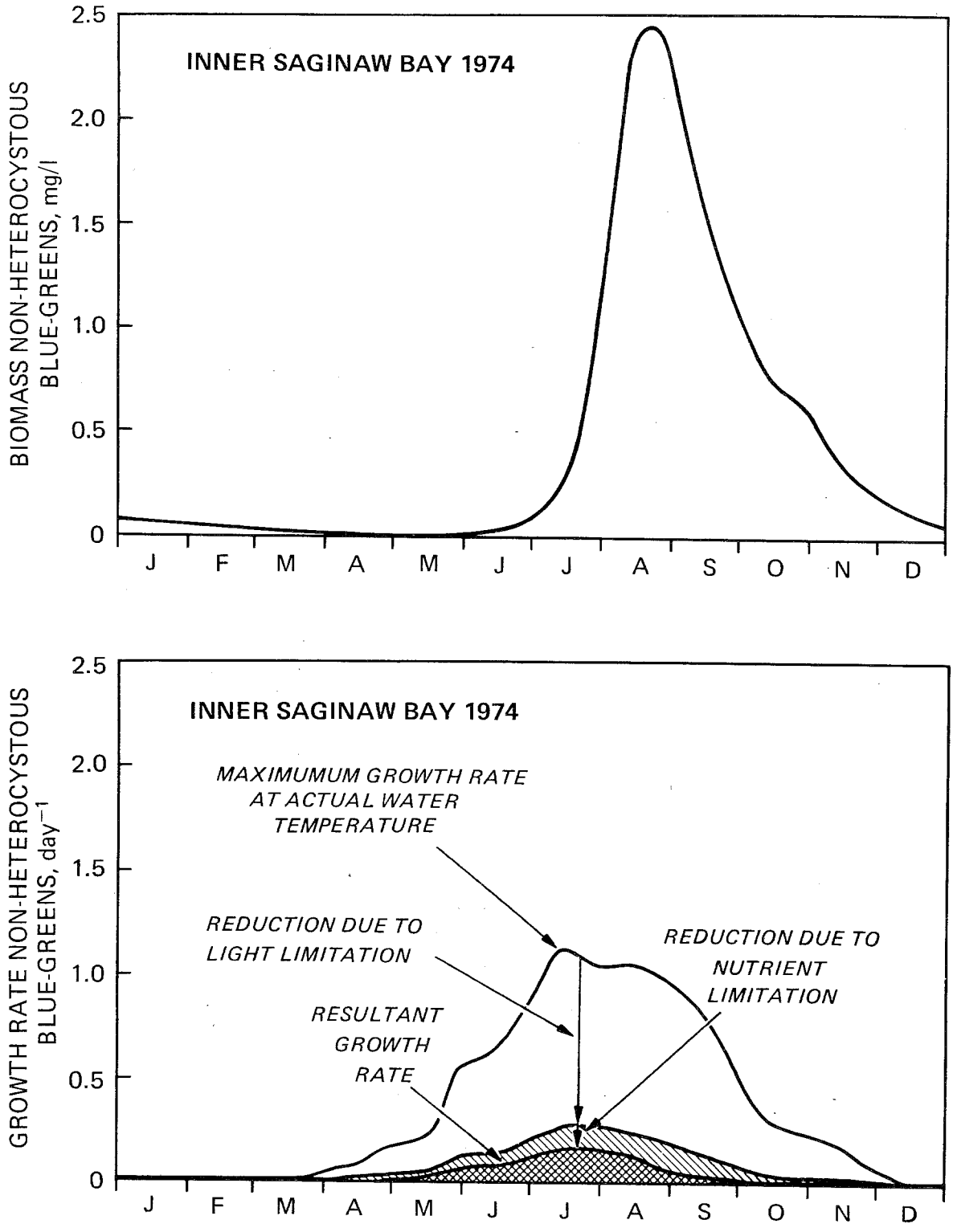


Figure 35. Component analysis of growth rates for non-N_2-fixing blue-greens.

tures and to decline at higher temperatures. The pattern for greens and non-N_2-fixing blue-greens was unimodal and coincides with higher temperatures.

Substantial reductions in growth rates occurred due to light limitation. This was because gross production rates in the model were vertically averaged, and thus included the effect of exponential light extinction in the water column. Mortimer (1969) pointed out that actual growth rates are a function of the ratio of illuminated depth to stirred depth. Using Equation A.15.2.4, average values for Secchi depth (Table D-13), and incident solar radiation (Table D-12) for the June-September period, it can be shown that incident solar radiation was reduced to 75 langleys/day at a depth of 1.4 meters. This light intensity was the average of saturation light intensities for all phytoplankton groups in the model. In this case, 1.4 meters was the illuminated depth and the water column depth of 5.83 meters was the stirred depth. Thus, only 24 percent of the water column received a non-limiting light intensity.

Another consequence of exponential light extinction in the water column is that phytoplankton growth is usually more sensitive to changes in extinction coefficient than to changes in incident solar radiation (Tables E-1 and E-2). If, in the previous example, incident solar radiation was varied by plus or minus 50 percent, then this would correspond to 29 percent and 15 percent, respectively, of the water column which would receive a non-limiting light intensity. In contrast, if the extinction coefficient was varied by plus or minus 50 percent, this would correspond to 16 percent and 48 percent, respectively, of the water column which would receive a non-limiting light intensity. These results are consistent with experimental measurements conducted by Fee (1974) in an effort to determine the effect of diurnal variations on phytoplankton production. Fee concluded that the effects of changes in incident solar radiation occurred only in a relatively shallow layer.

After nutrient reduction effects were taken into account, resultant growth rates in the model were found to average approximately 0.05-0.10 day^{-1} over the annual cycle, with peak values of approximately 0.2-0.3 day^{-1}. These average values were consistent with experimental measurements conducted by Schelske et al. (1978) in various regions of the Great Lakes. Peak values corresponded to doubling times of two to four days, and were consistent with experimental measurements by Moll (personal communication) in the Saginaw Bay- Lake Huron system.

PHYTOPLANKTON LOSS PROCESSES

Phytoplankton net growth rate was equal to gross production rate minus the sum of rates for individual loss processes. These loss processes included respiration, sinking, grazing, and decomposition. Boundary flow could represent either a gain or a loss, depending on the direction of the concentration gradient. Recall that the term "respiration" in the present context was intended to refer to population losses due to self-maintenance requirements, especially under non-optimal conditions.

Figures 36-38 illustrate the relative contribution of each loss process for diatoms, greens, and non-N_2-fixing blue-greens. The proportional contribution of a given loss process was calculated at each point in time by taking the ratio of that process rate to the sum of absolute values of all individual process rates. The sum of absolute values of the proportional contributions was equal to unity. All of the processes except boundary flow constituted net losses relative to gross production and were assigned negative values. Boundary flow could constitute either a gain or a loss and was assigned either a positive or a negative value, respectively.

During periods of increasing phytoplankton concentration, boundary flow constituted a net loss for all three phytoplankton groups. Phytoplankton concentrations during these periods were higher in the inner bay than in the inflow across the boundary between the inner and outer portions of the bay. This implied that peak phytoplankton crops observed in the inner bay were actually produced there, and were not due to water movements. During periods of low and/or decreasing phytoplankton concentrations, boundary flow constituted a positive contribution. This reflected the fact that there were spatial gradients in light extinction, temperature, and nutrients between the inner and outer portions of the bay which led to differences in timing of the phytoplankton crops between these two regions. Note that during periods when boundary flow contributions were positive, the sums of other loss terms usually exceeded those of boundary flows and hence, boundary flow was never sufficiently large to cause a net increase in inner bay phytoplankton concentration.

Non-predatory death rates, here expressed as respiration and decomposition, were quite significant, especially for blue-green algae. The importance of including such non-predatory death mechanisms as cellular breakdown and decomposition, and cell death through parasitism in mathematical models has been emphasized by Jassby and Goldman (1974). It is interesting to note that more than thirty years ago, Riley (1946) recognized the importance of phytoplankton respiration. He suggested that as temperature increases, respiration can become a dominant population loss mechanism. Respiration in the model accounted for 15 to 50 percent of population losses for diatoms and greens, and for 20 to 65 percent of population losses for blue-greens. Decomposition accounted for approximately 25 percent of population losses for diatoms and greens, and for 40 percent of population losses for blue-greens during periods of peak total biomass. Recall that the decomposition process was assumed to be second-order with respect to total phytoplankton biomass concentration. Note that even though blue-greens were assigned a non-zero sinking velocity, non-predatory death processes still accounted for most of the difference between their gross and net production rates.

During most of the year, sinking was the least important of the loss processes for all three phytoplankton groups. Part of the reason was that the net sinking rates used were relatively small because of the substantial vertical dispersion in the inner bay due to wind mixing and shallow depth. Note that sinking rate accounted for a larger proportion of total population losses during colder periods. This was because all other loss processes except boundary flow were temperature-dependent, whereas sinking rate was assumed to remain constant.

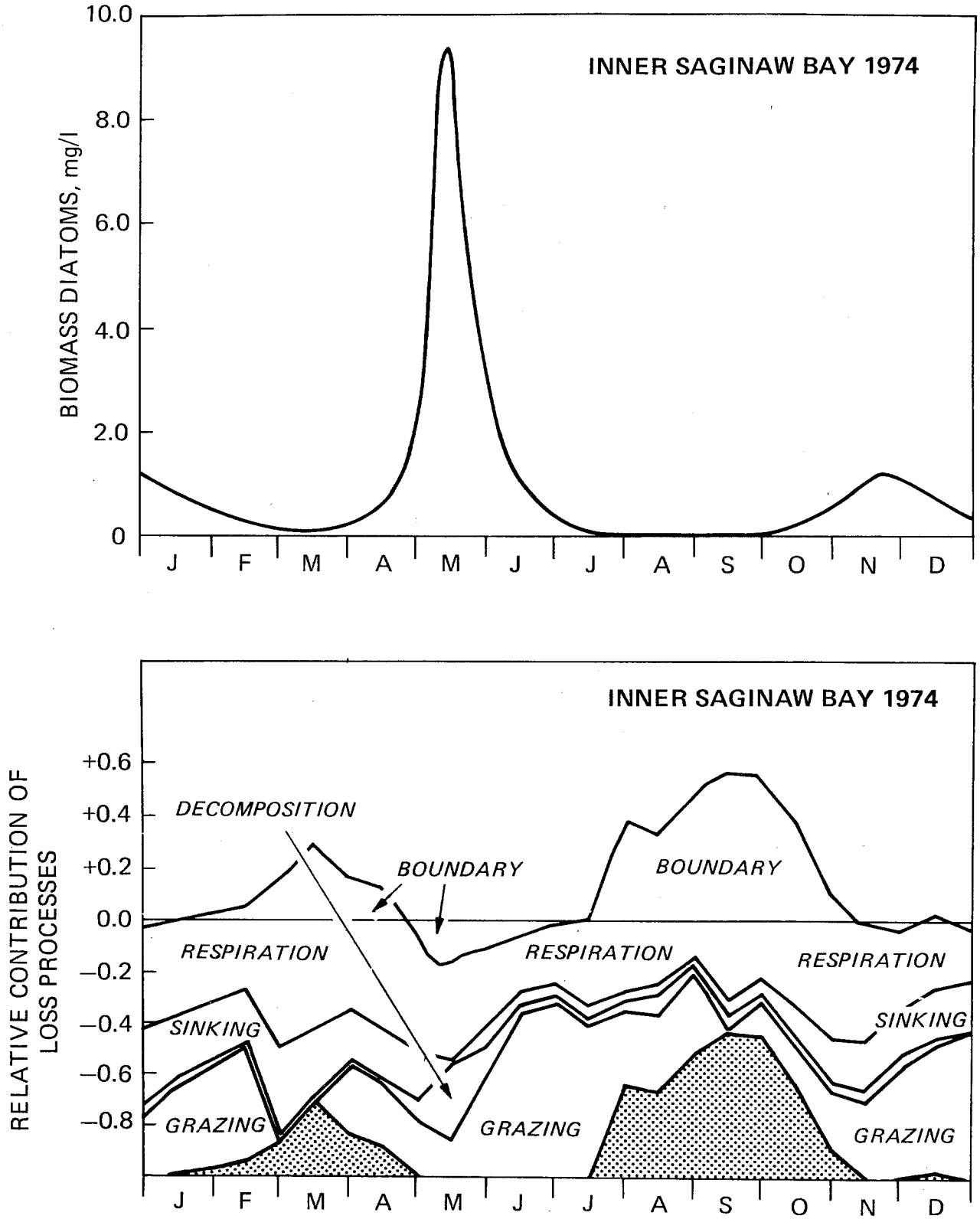


Figure 36. Component analysis of total loss rates for diatoms.

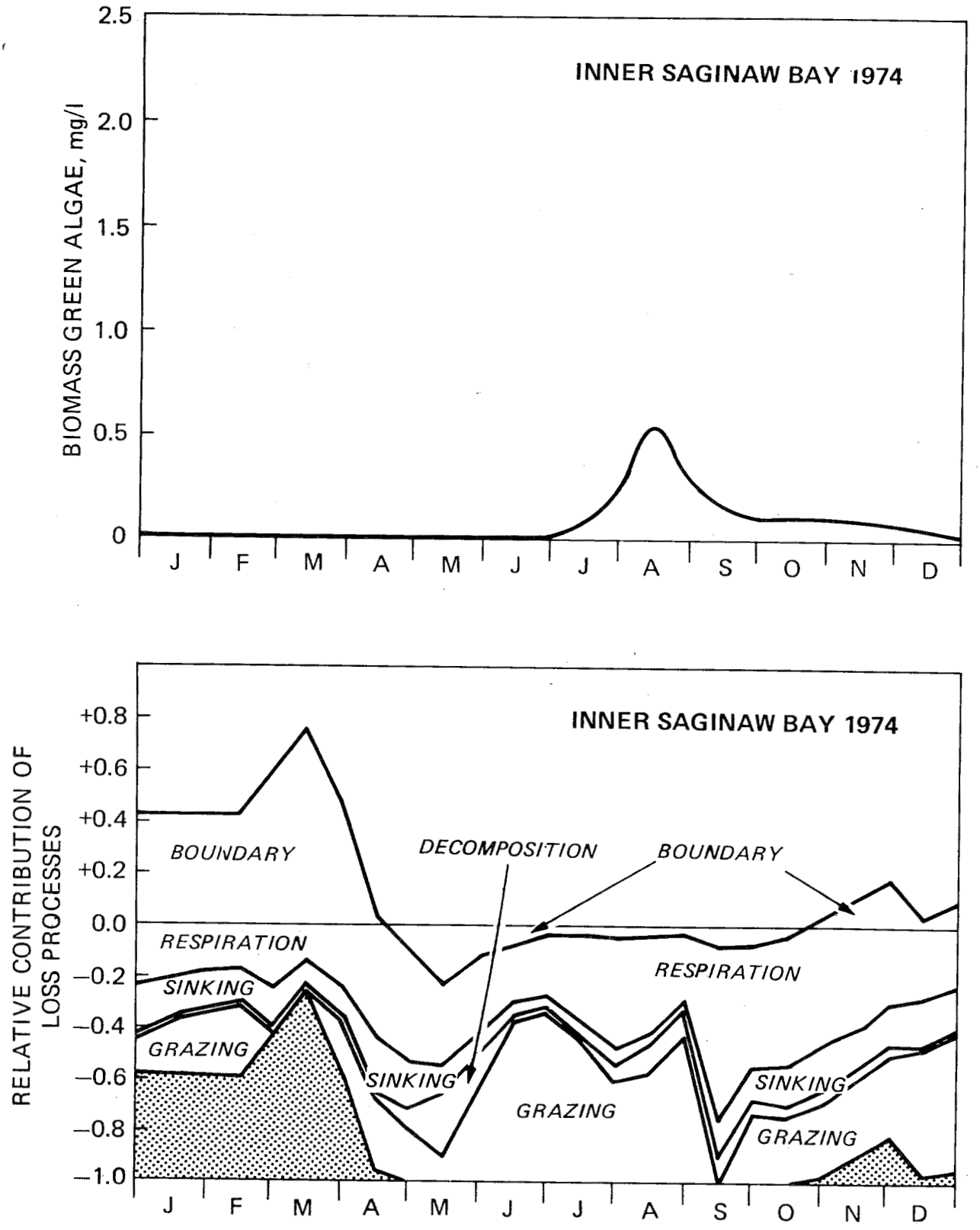


Figure 37. Component analysis of total loss rates for green algae.

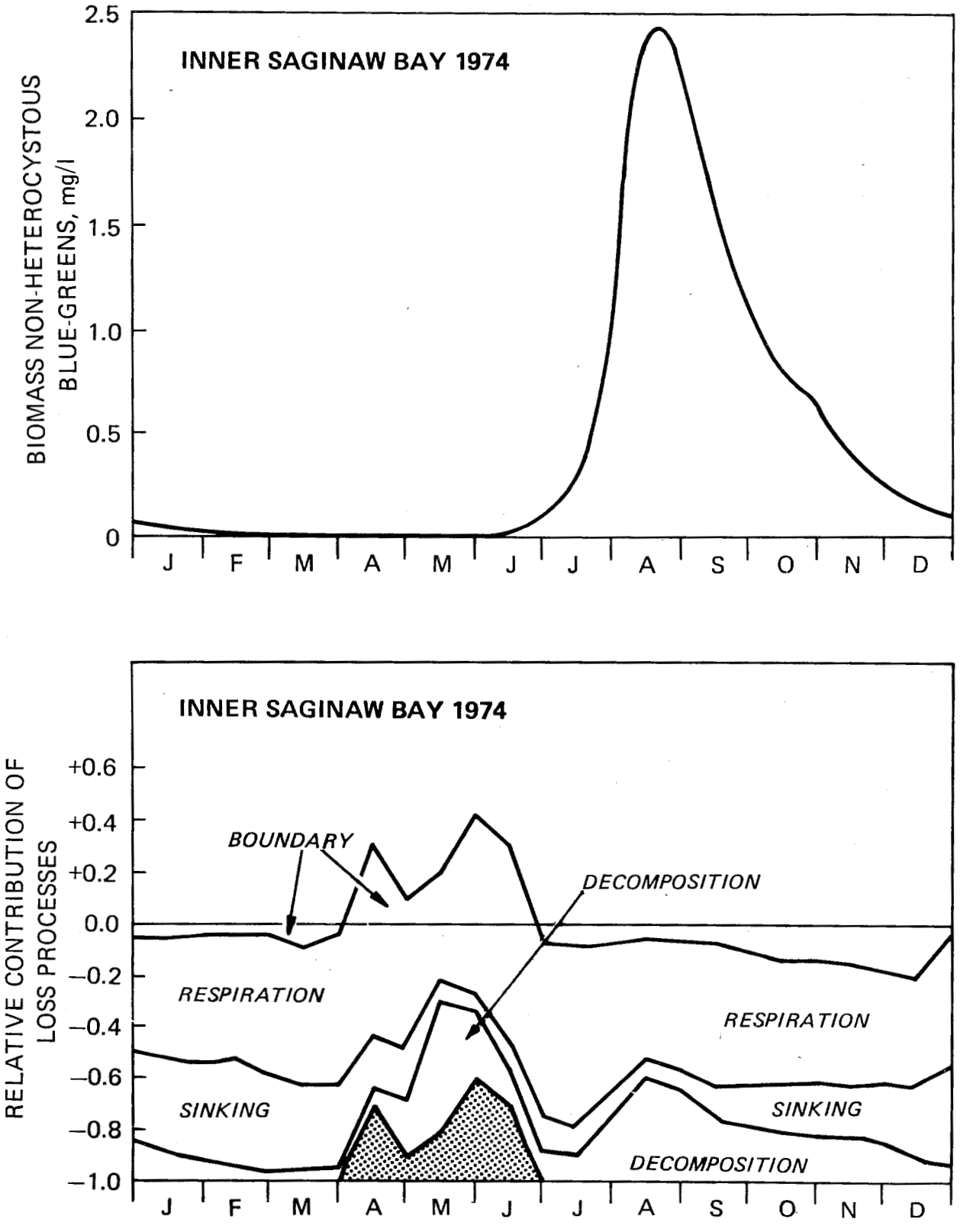


Figure 38. Component analysis of total loss rates for non-N_2-fixing blue-greens.

Grazing was the most significant loss process for diatoms and green algae during the July-August period. Grazing accounted for 25 to 70 percent of population losses for diatoms, and for 40 to 70 percent of population losses for green algae during this period. A detailed examination of model results indicated that from 3 to 90 percent of daily gross diatom production was grazed during April and May, and from 99 to 1850 percent of daily gross diatom production was grazed during the July-August period. Corresponding results for green algae were 9-70 percent, and 24 to 130 percent of gross daily production grazed. These ranges were consistent with experimental measurements of grazing by zooplankton on natural phytoplankton populations in Southern Lake Huron by McNaught et al. (1979). These results implied that phytoplankton in Saginaw Bay did not come under control by grazing until midsummer. Blue-green algae were not subject to grazing in the model.

LIMITING NUTRIENTS

The relative importance of phosphorus and nitrogen as limiting nutrients in the model can be determined by comparing values for the internal levels of these nutrients in the phytoplankton, relative to minimum stoichiometric requirements or cell quotas. The quantities appearing in the top graph of Figure 39 correspond to averages of the ratios PSA/PSAMIN and NSA/NSAMIN for all five phytoplankton groups. Results indicated that nitrogen was consistently more rate-limiting than phosphorus over the entire annual cycle. Only during May and August do internal phosphorus levels approach internal nitrogen levels. At all other times there is phosphorus sufficiency because internal phosphorus levels range from three to five times the minimum cell quotas.

The lower graph in Figure 39 illustrates the results of an independent check on the condition of phosphorus sufficiency in Saginaw Bay. The average of ratios for excess internal phosphorus per mg of algae for the five phytoplankton groups in the model was consistently greater than the 0.08% critical level proposed by Fitzgerald and Nelson (1966). Recall that this level was the threshold between growth rate limitation by phosphorus and phosphorus sufficiency. The model output only approached the critical level during May and August, corresponding to the two minima in average internal phosphorus level.

Although nitrogen was relatively more rate limiting than phosphorus in an average sense, important differences occurred among the individual phytoplankton groups. Figures 40 and 41 contain results for degree of saturation of the individual nutrient reduction terms in the model for diatoms, greens, and blue-greens. Results for diatoms indicated that nitrogen was rate limiting for most of the year; however, all three nutrients were equally limiting in mid-May, and extreme silicon limitation occurred from mid-May to the end of June. These results implied that while nitrogen limited the rate of growth of diatoms for most of the year, a shift to silicon limitation was more important in determining the size of the spring diatom peak. Results for greens indicated that nitrogen was relatively more rate limiting than phosphorus for the entire year.

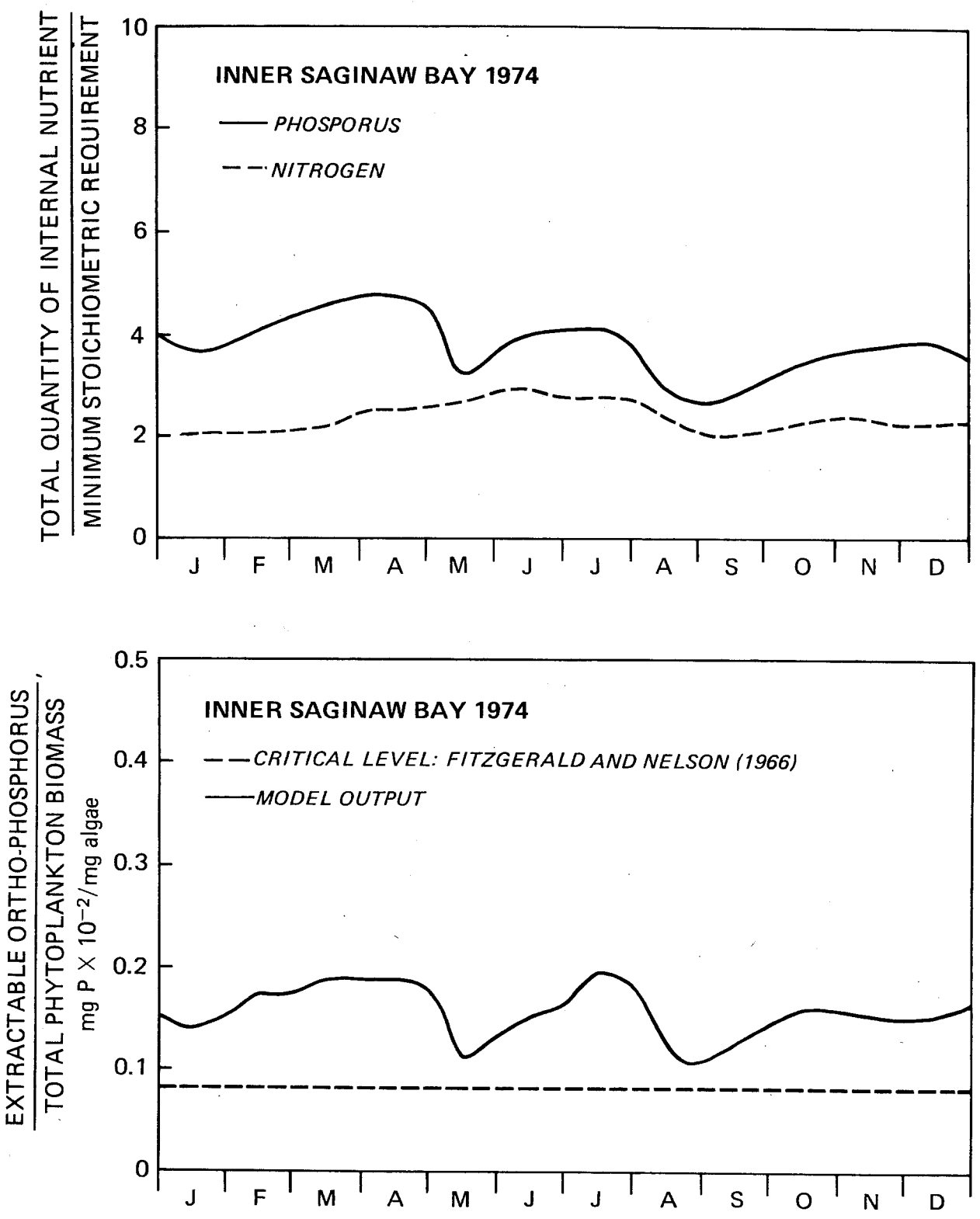
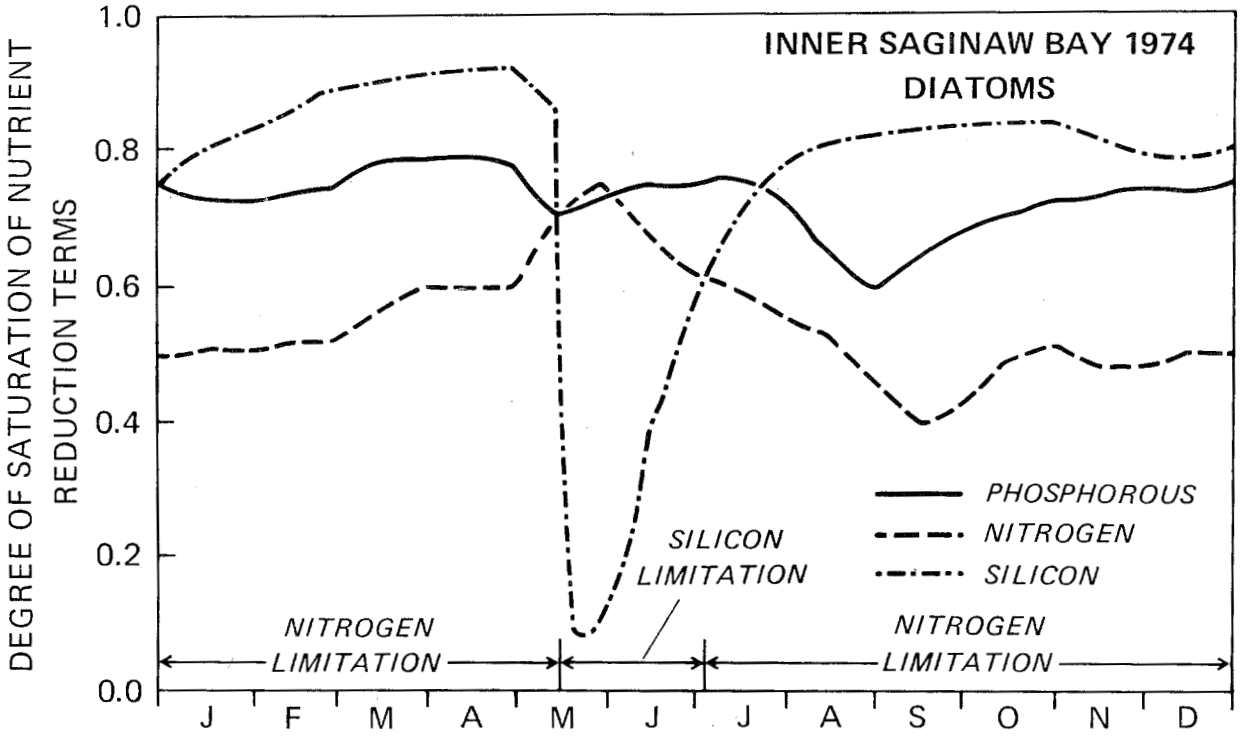


Figure 39. Average of individual phytoplankton groups for total cellular phosphorus and nitrogen levels and excess internal (extractable) phosphorus concentrations.



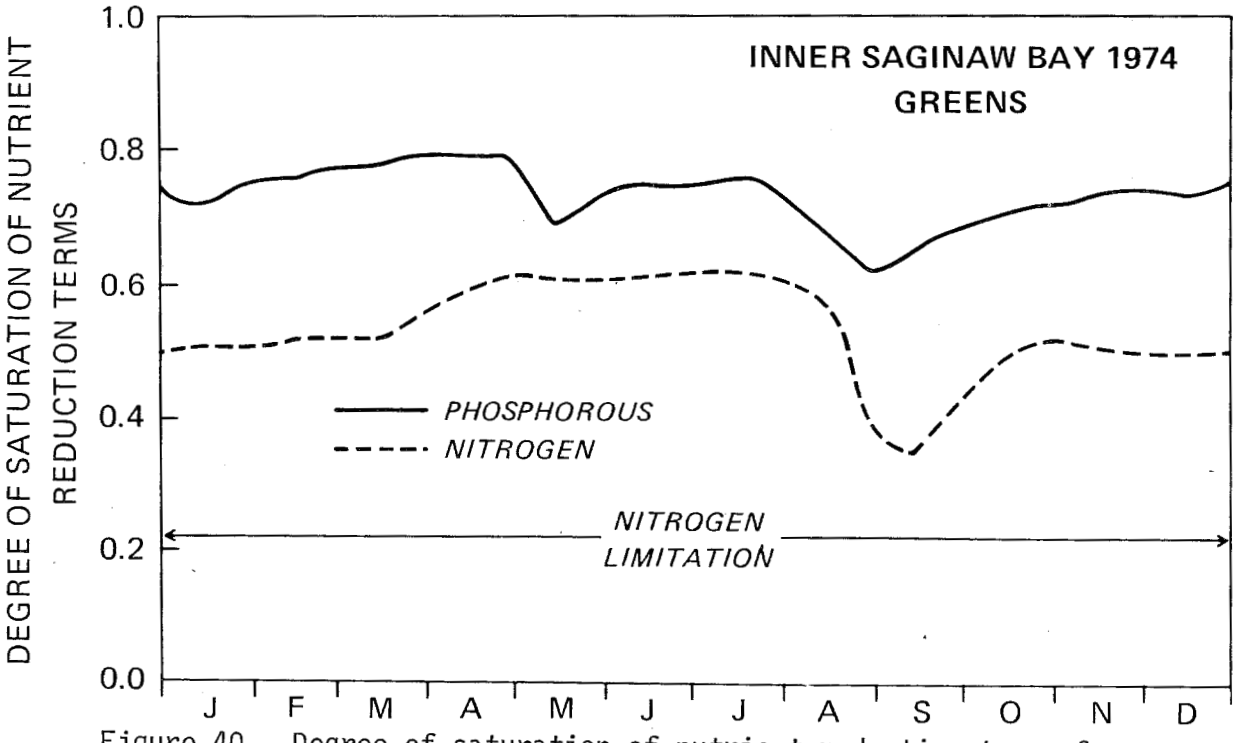
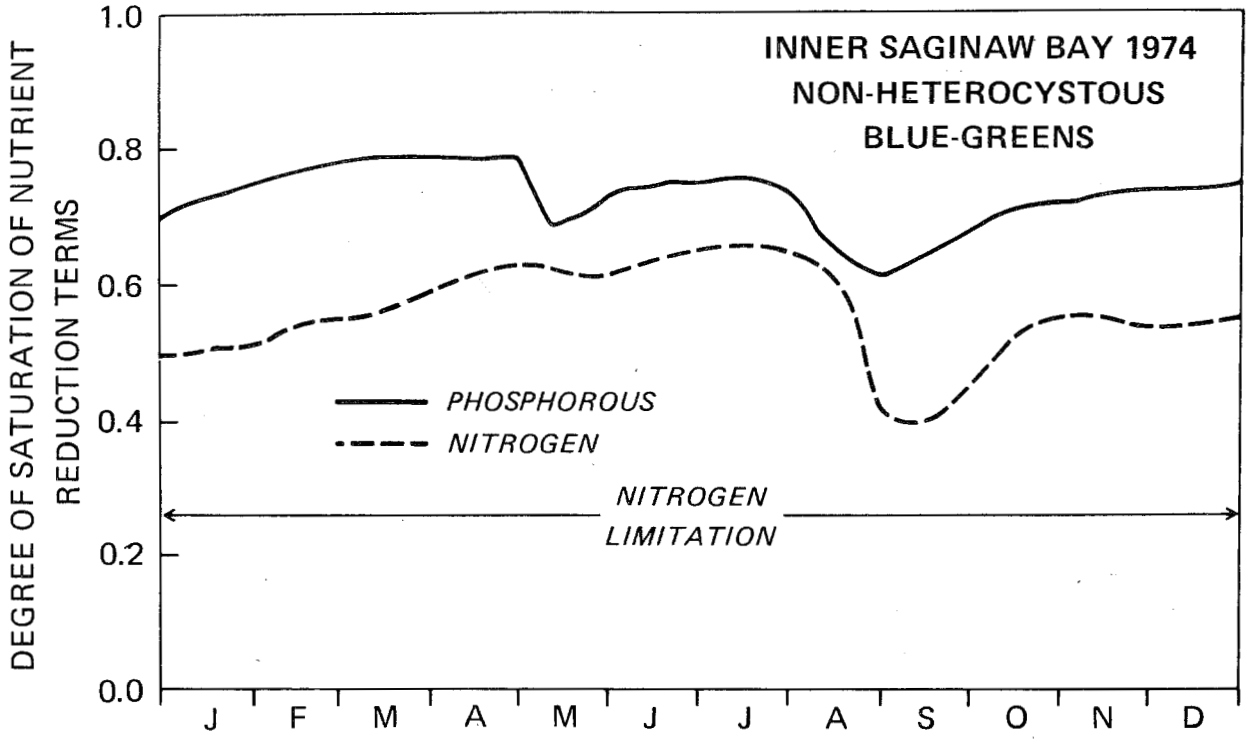


Figure 40. Degree of saturation of nutrient reduction terms for diatoms and green algae.



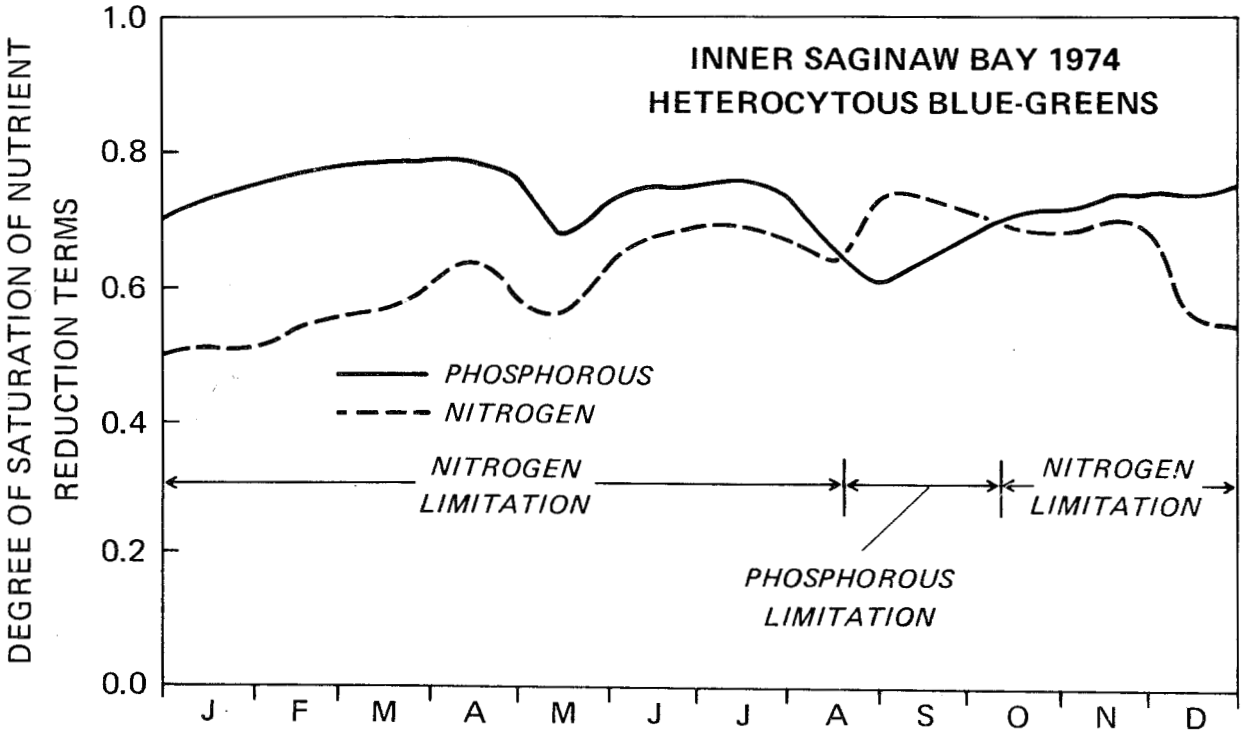


Figure 41. Degree of saturation of nutrient reduction terms for blue-greens.

Results for the blue-greens (Figure 41) were especially interesting because of dynamic changes that occurred during the period of minimum dissolved available phosphorus and nitrogen concentrations in the water column. Nitrogen limited the rate of growth of non-N_2-fixing blue-greens for the entire year; however, the degree of phosphorus limitation nearly converged with the degree of nitrogen limitation in mid-August. For the N_2-fixing blue-greens, nitrogen limited the rate of growth for most of the year, with the exception of a two month period of phosphorus limitation from mid-August to mid-October. This period coincided with the period of lowest dissolved available nitrogen concentration in the water column (see Figure 29). This result was a consequence of the atmospheric nitrogen fixation mechanism in the model. The N_2-fixing blue-greens accumulated excess internal nitrogen stores, thus causing a shift from nitrogen to phosphorus growth rate limitation. In contrast, note that the non-N_2-fixing blue-greens showed a substantial increase in the degree of nitrogen limitation during this same period. Recall (see Figure 26) that mid-August was the time when peak biomass concentrations occurred for both of the blue-green phytoplankton groups. The model output was consistent with the hypothesis that at this time, non-N_2-fixing blue-greens were limited by nitrogen, and N_2-fixing blue-greens were limited by phosphorus. This set of circumstances was identical to that reported by Fitzgerald (1969b) for Lake Mendota on the basis of experimental measurements of internal phosphorus and nitrogen concentrations in mixed blue- green blooms during the period of minimum dissolved available concentrations.

The above results imply that the concept of a single limiting nutrient for a natural system can be overly simplistic. At various times, and for various phytoplankton groups, more than one nutrient can be important in limiting the rate of growth and/or in determining peak biomass concentrations. Another implication is that if bioassays are to be used for determining nutrient limitation in a natural system, then the results may depend on the timing and the proportions of the various individual functional groups of phytoplankton.

NUTRIENT RECYCLE

The importance of internal nutrient pool kinetic mechanisms in phytoplankton models is a matter of some debate. A common agrument against the use of internal nutrient pools is that they describe processes which occur over very short time scales, compared to the monthly or seasonal time scales usually of interest. A corollary to this agrument is that variations of internal nutrient levels over seasonal time scales are usually small, and that the effects of such variations can either be incorporated into other state variables, or compensation made by adjusting the model coefficients. Indeed, the seasonal variations in internal nutrient levels in the present study were not large; however, it will be shown that arguments based on relative time scales are not the sole criterion for using internal nutrient pool kinetics. Consideration of nutrient recycle kinetics is an often-overlooked, yet extremely important, criterion for choosing between fixed and variable stoichiometry models. The choice of a phytoplankton growth kinetic mechanism always includes an implicit choice of a mechanism for nutrient recycle.

Recall that as a consequence of internal nutrient pool kinetics used in the model, nutrients recycled from grazing, decomposition, and respiration consisted of two separate components. The component associated with the minimum cell quota was recycled to the unavailable nutrient compartment in the water column, and the component associated with the excess internal level was recycled directly to the available nutrient compartment in the water column.

To emphasize the importance of two-component nutrient recycle, sensitivity analyses were conducted in which the recycle components corresponding to excess internal nutrients for grazing, decomposition, and respiration were routed directly to the unavailable nutrient compartments in the water column instead of to the available nutrient compartments. This was not as drastic as simply "turning off" these direct recycle components because conservation of mass was still preserved. The difference was that all recycled phosphorus and nitrogen was then required to be shunted through the conversion process from unavailable forms to available forms before they could be reused for phytoplankton growth. This is the conventional approach to nutrient recycle used in most Monod/Michaelis-Menten, fixed stoichiometry models.

Results of the recycle sensitivity analyses are shown in Figure 42 for nutrients and Table 9 for phytoplankton. For both phosphorus and nitrogen, dissolved available concentrations were substantially reduced after the spring diatom peak, relative to the calibration results. This was because most of the external loading occurred in the first half of the year, and hence, recycle processes were relatively more important later in the year.

Results of the recycle sensitivity analyses for phytoplankton are presented in terms of annual integrated gross production. This quantity was a good indicator of the relative amounts of phytoplankton produced in each functional group. In general, non-diatoms were affected to a much greater degree than diatoms. For the case where internal phosphorus was not recycled, both blue-green groups were reduced. The N_2-fixing blue-greens were reduced by a greater degree than non-N_2-fixing blue-greens because they were already phosphorus limited in the calibration. The non-N_2-fixing blue-greens were relatively more nitrogen limited than phosphorus limited, and first needed to be forced into phosphorus limitation before a production decrease could occur. Consistent with this interpretation, the non-N_2-fixing blue-greens were reduced by a greater amount when internal nitrogen was not recycled. The N_2-fixing blue-greens, however, were substantially increased when internal nitrogen was not recycled because nitrogen limitation caused reductions in all of the other phytoplankton groups and, as a result, phosphorus that was previously used by these groups was now left over for the N_2-fixing blue-greens. These results imply that for a system which is relatively more limited by nitrogen than by phosphorus, control of nitrogen in the absence of phosphorus control could actually increase the production of N_2-fixing blue-green phytoplankton.

It might be argued that a fixed stoichiometry model with a single recycle component to the unavailable nutrient compartments in the water column could account for the recycle processes by compensating with a faster con-

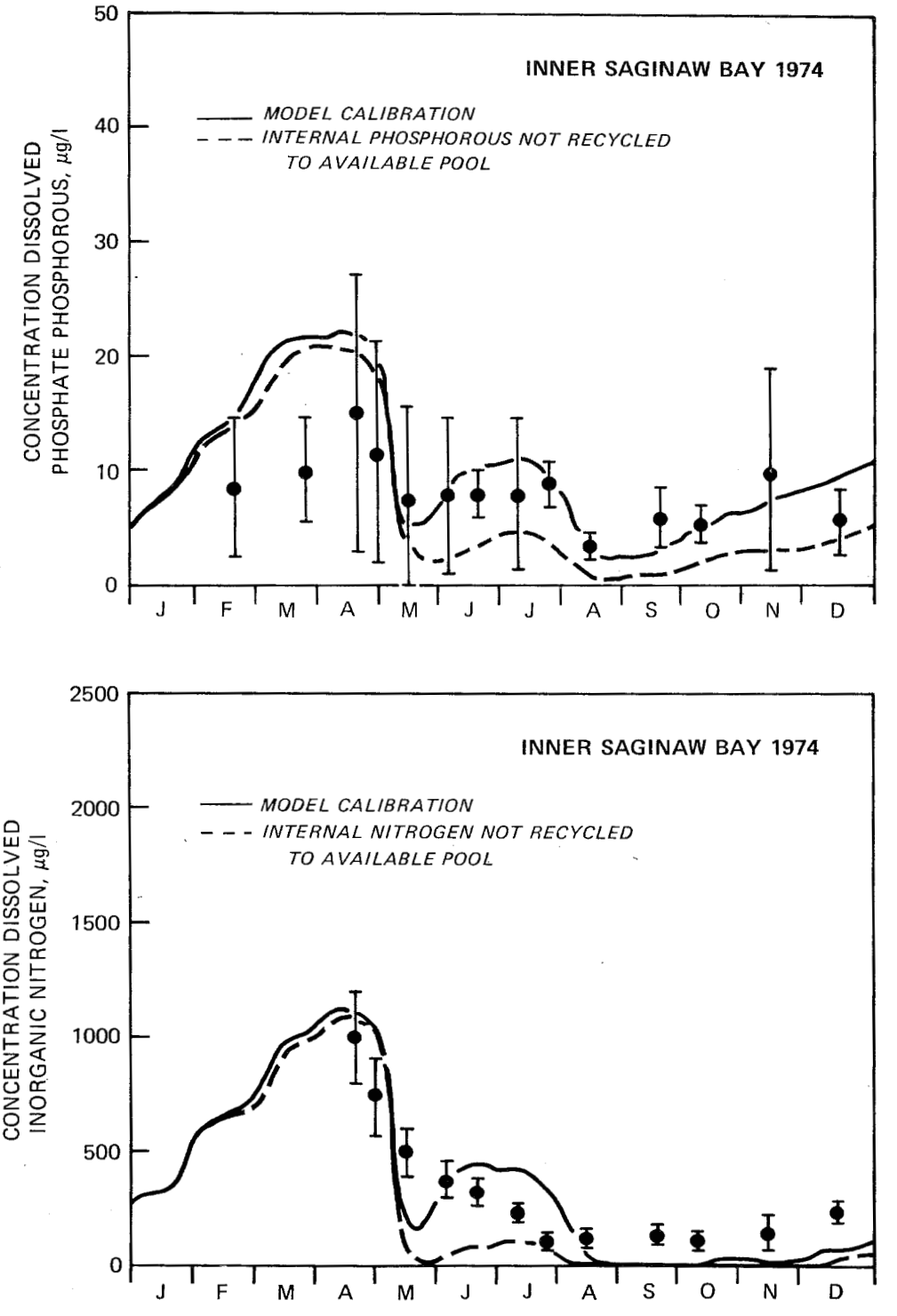


Figure 42. Results of sensitivity analyses for dissolved available phosphorus and nitrogen when excess internal nutrients are not recycled to available pools.

TABLE 9. RESULTS OF SENSITIVITY ANALYSES FOR INTERNAL PHOSPHORUS AND NITROGEN RECYCLE

Condition	Percent change in annual integrated gross production relative to final calibration				
	Diatoms	Greens	Others	Blue-greens (non-N_2)	Blue-greens (N_2)
Internal P not recycled to available pool	+6	-19	-27	-29	-39
Internal N not recycled to available pool	-2	-60	-44	-65	+60

version rate from unavailable to available nutrient forms. Notwithstanding the fact that this would be inconsistent with the known physiological processes, such an approach could lead to serious difficulties. Phytoplankton-related detritus is only one of many components which comprise the unavailable nutrient compartments. These compartments also contain a wide variety of dissolved and particulate materials, both organic and inorganic, which result from other chemical-biological processes in the water column and from external loadings. If a higher value was used for the conversion rate from unavailable to available nutrient forms to satisfy peak requirements for phytoplankton uptake during periods of minimum nutrient concentrations, then there is a risk of overconversion during periods of off-peak demand. In the limiting case of a long-term simulation, this could lead to incorrect results for the distribution of individual nutrient components (Bierman 1977).

RELATIVE CONTRIBUTION OF PHOSPHORUS SOURCES

The above results implied that while nitrogen and silicon were important in the phytoplankton-nutrient dynamics in Saginaw Bay, the supply of phosphorus will ultimately determine the size of the nuisance blue-green component of the total crop because N_2-fixing blue-greens do not have absolute requirements for dissolved nitrogen and silicon. Because of this, it is pertinent to investigate the relative importance of the various possible sources of available phosphorus in the water column.

Figure 43 contains the results of a component analysis of the sources of available phosphorus to the phytoplankton. Phytoplankton net phosphorus uptake rate over the annual cycle has been juxtaposed against the relative contributions of various processes responsible for supplying dissolved available phosphorus to the water column. At any given time, it can be determined which processes are contributing more significantly to the phosphorus requirements of the phytoplankton. Phytoplankton net phosphorus uptake rate corresponded to the net uptake term in Equation A.5.0 for dis-

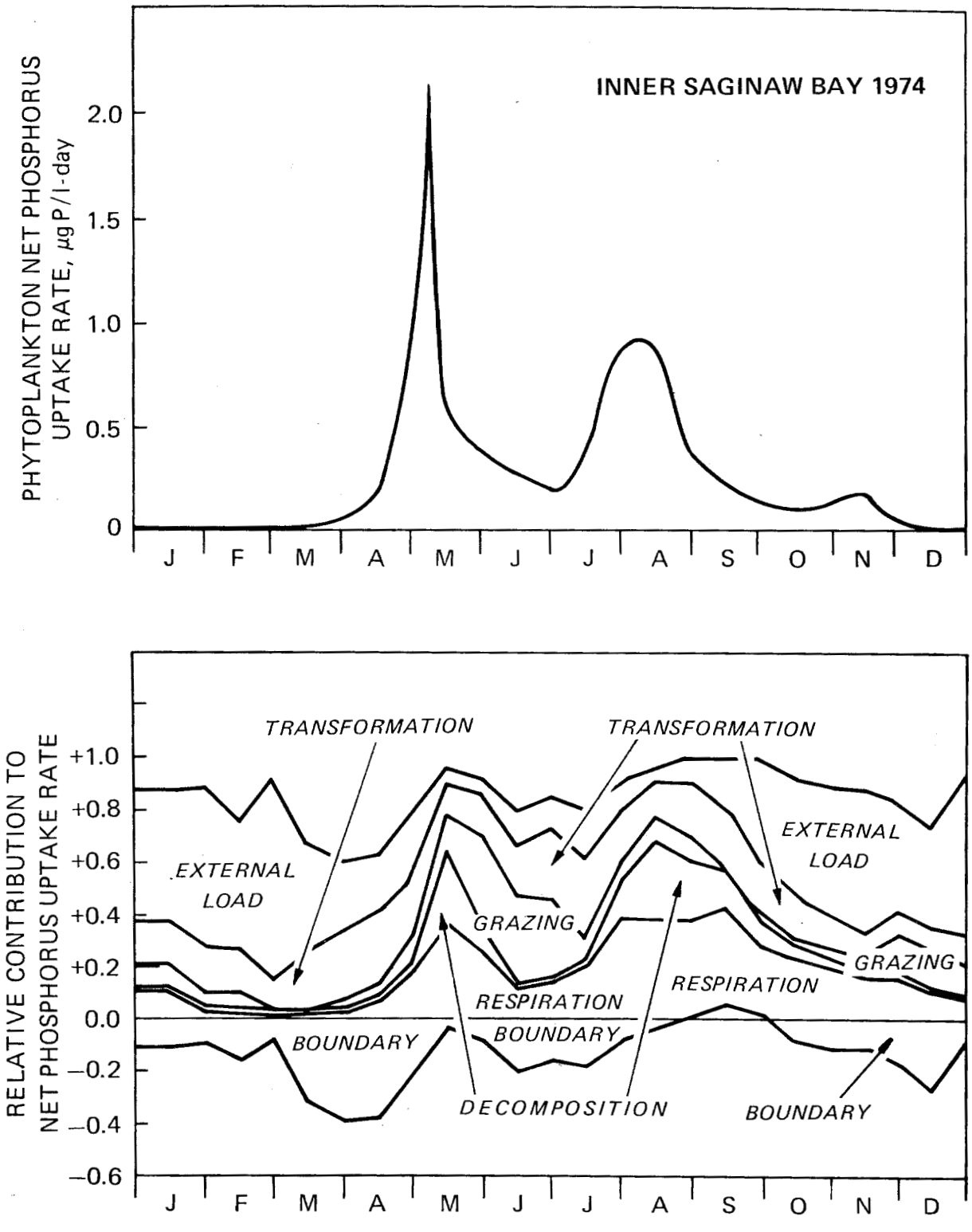


Figure 43. Component analysis of phytoplankton-phosphorus dynamics.

solved available phosphorus. This value was the sum of individual uptake rates for all five phytoplankton groups in the model. The relative contribution of a given process was calculated at each point in time by taking the ratio of that process rate from Equation A.5.0 to the sum of absolute values of all individual process rates. The sum of absolute values of the relative contributions is equal to unity. All processes except boundary flow constituted gains relative to phytoplankton uptake and are assigned positive values. Boundary flow could constitute either a gain or a loss relative to phytoplankton uptake and was assigned either a positive or a negative value, respectively.

One of the most noteworthy aspects of the phytoplankton-phosphorus dynamics was that phosphorus requirements of spring and fall diatom crops were satisfied primarily by external loading, and phosphorus requirements of summer blue-green crops were satisfied primarily by recycle processes within the water column. This was consistent with the above results of the nutrient recycle sensitivity analyses. During the July-September period, external phosphorus load was at a minimum, and there was an almost continual loss of dissolved available phosphorus from the inner bay due to boundary flow. Recycle from zooplankton grazing, and subsequent excretion, contributed up to 35 percent of the available phosphorus required for phytoplankton uptake after the spring diatom peak. Recycle from decomposition and respiration together contributed approximately 70 percent of the available phosphorus during peak requirements for blue-greens in August.

Transformation in Figure 42 refers to the conversion process from unavailable phosphorus to available phosphorus. The relative contribution of transformation to net phytoplankton uptake ranged from 10 to 25 percent over the annual cycle.

SECTION 9

PHOSPHORUS LOAD REDUCTION SIMULATIONS

INTRODUCTION

Results of nutrient load reduction simulations were presented by Bierman et al. (1975) using an earlier version of this spatially simplified model. These results were used by the IJC as part of the ULRS (Bratzel et al. 1977), and later by Task Group III (Vallentyne and Thomas 1978) in developing the phosphorus loading objective for Saginaw Bay as part of the 1978 Water Quality Agreement. It was pointed out earlier that ongoing work involves the calibration of a spatially segmented version of the model to two independent sets of data on the bay for 1974 and 1975. This more advanced version will be used to generate a revised set of predictions corresponding to expected reductions in phosphorus loads. Subsequently, these revised results will be compared to the outcome of a follow-up field survey to be conducted in 1980. Mindful of the fact that present results will be superceded by final results from the spatially segmented model, a brief summary of phosphorus load reduction results using the spatially simplified model will be presented as an example.

RESULTS

Figure 44 contains results of phosphorus load reduction simulations for diatom and blue-green phytoplankton groups in terms of percent changes in annual integrated gross production. Controllable phosphorus in this example corresponded to phosphorus loads from point sources. Best and worst case results corresponded to different limiting assumptions for boundary concentrations on the inflow water between the inner and outer portions of the bay. Only the average results between these extreme cases will be discussed here.

The most important conclusions drawn from the phosphorus load reduction results were:

1. Phytoplankton production in inner Saginaw Bay was sensitive to changes in external phosphorus loads.

2. Blue-green production responded to a much greater degree than diatom production for a given change in phosphorus load.

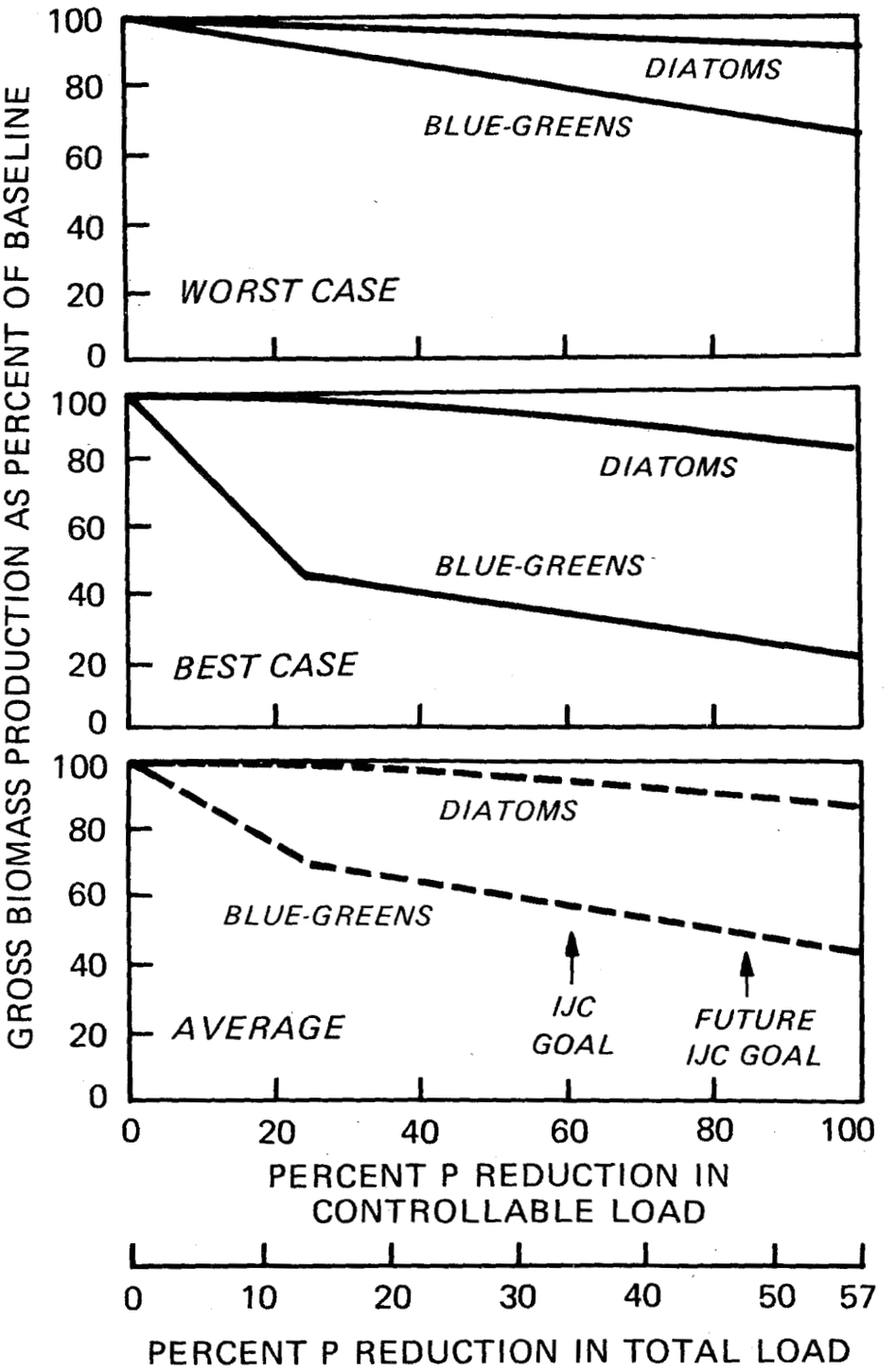


Figure 44. Changes in diatom and blue-green gross production, relative to 1974 calibration, as a function of phosphorus load reductions in Saginaw Bay.

For a total phosphorus load reduction of 57 percent, relative to 1974 conditions, there was a 57 percent reduction in blue-green biomass production, and a 14 percent reduction in diatom biomass production. This implied that the percent change in blue-green biomass production was approximately proportional to the percent change in external phosphorus load. These conclusions were consistent with results of the limiting nutrient analyses and the nutrient recycle analyses presented earlier.

The above results were significant from a water quality standpoint because concentrations of blue-green phytoplankton in Saginaw Bay were closely correlated with taste and odor problems in the municipal water supply. The following correlation equation was found to be statistically significant at the 99 percent confidence level (Dolan 1977):

$$TO = 2.03 + 1.87\ (BG)$$

where: TO = Threshold Odor Number at the Whitestone Point intake plant.

BG = Blue-green biomass concentration in the inner bay in mg dry wt/liter.

Using this correlation, model output for blue-green biomass concentrations from the phosphorus load reduction simulations was used to estimate the corresponding taste and odor at the intake plant. Taste and odor at the Whitestone Point intake plant, and annual average total phosphorus concentration in the inner bay were used as the water quality criteria for the development of the 1978 Water Quality Agreement total phosphorus loading objective for Saginaw Bay.

The most important qualifications that must be stated for the above results are that the model was applied to data for only a single year, and that boundary conditions for the load reduction simulations were arbitrarily specified. The boundary concentrations in the region of the inflow to the inner bay are not independent of the nutrient loads from the Saginaw River because of the high degree of horizontal dispersion in the bay. Under conditions other than calibration conditions, these concentrations can be expected to vary. With the spatially simplified model there was no systematic way to specify these variations. The principal motivation for ongoing work with the spatially segmented model is to address these particular deficiencies. The application of the spatially segmented model to two independent data sets should increase the scientific credibility of the final results. The spatial segmentation scheme used will preclude the need to specify inner bay boundary conditions because it will include both inner and outer portions of the bay. The open boundary in this segmentation scheme will lie along Lake Huron proper. Concentrations in the region of inflow to Saginaw Bay from Lake Huron are relatively constant in time because they represent conditions in a much larger, oligotrophic water mass.

BIBLIOGRAPHY

Azad, H.S. and J.A. Borchardt. 1970. Variations in phosphorus uptake by algae. Environmental Science and Technology. 4(9): 737-743.

Beeton, A.M. 1958. Relationship between Secchi disc readings and light penetration in Lake Huron. American Fisheries Society Transactions. 87: 73-79.

Bierman, V.J., Jr., F.H. Verhoff, T.L. Poulson and M.W. Tenney. 1973. Multi-nutrient dynamic models of algal growth and species competition in freshwater lakes. In: Modeling the Eutrophication Process. Proceedings of a Symposium held at the Utah Water Research Laboratory, Utah State University, Logan, Utah, September 5-7, 1973. pp. 89-109.

Bierman, V.J., Jr. 1974. Dynamic mathematical model of algal growth in eutrophic freshwater lakes. Ph.D. Dissertation. University of Notre Dame, Notre Dame, Indiana. 155 p.

Bierman, V.J., Jr. 1976. Mathematical model of the selective enhancement of blue-green algae by nutrient enrichment. In: Modeling Biochemical Processes in Aquatic Ecosystems. R.P. Canale (ed.). Ann Arbor Science Publishers, Ann Arbor, Michigan. pp. 1-31.

Bierman, V.J., Jr. and D.M. Dolan. 1976. Mathematical modeling of phytoplankton dynamics in Saginaw Bay, Lake Huron. In: Environmental Modeling and Simulation. Proceedings of a Conference sponsored by the U.S. Environmental Protection Agency, Cincinnati, Ohio, April 19-22, 1976. pp. 773-779.

Bierman, V.J., Jr. and W.L. Richardson. 1976. Mathematical model of phytoplankton growth in Saginaw Bay, Lake Huron. In: Water Quality Criteria Research of the U.S. Environmental Protection Agency. Proceedings of an EPA-Sponsored Symposium held at Corvallis, Oregon, August, 1975. EPA-600/3-76-079. pp. 159-173.

Bierman, V.J., Jr. 1977. Evaluation of Hydroscience Lake Ontario Report to the Surveillance Subcommittee, International Joint Commission. Prepared for the Expert Committee on Ecosystems Aspects, International Joint Commission, Windsor, Ontario. 21 p.

Bolsenga, S.J. 1978. Photosynthetically active radiation transmission through ice. NOAA Technical Memorandum ERL GLERL-18. Great Lakes Environmental Research Laboratory. Ann Arbor, Michigan. 48 p.

Boyd, C.E. and J.M. Lawrence. 1967. The mineral composition of several freshwater algae. Proceedings of the Twentieth Annual Conference, Southeastern Association of Game and Fish Commissioners. pp. 413-424.

Bratzel, M.P., M.E. Thompson and R.J. Bowden (Eds.). 1977. The waters of Lake Huron and Lake Superior. Vol. II (Part A). Lake Huron, Georgian Bay, and the North Channel. Report to the International Joint Commission by the Upper Lakes Reference Group. Windsor, Ontario. 292 p.

Bush, R.M. and E.F. Welch. 1972. Plankton associations and related factors in a hypereutrophic lake. Water, Air, and Soil Pollution. 1: 257-274.

Button, D.K., S.S. Dunker and M.L. Morse. 1973. Continuous culture of Rhodotorula rubra: kinetics of phosphate-arsenate uptake, inhibition, and phosphate-limited growth. Journal of Bacteriology. 113(2): 599-611.

Canale, R.P. and A.H. Vogel. 1974. Effects of temperature on phytoplankton growth. Journal of the Environmental Engineering Division. Proceedings of the American Society of Civil Engineers. 100(EE1): 234-241.

Canale, R.P., L.M. DePalma and A.H. Vogel. 1976. A plankton-based food web model for Lake Michigan. In: Modeling Biochemical Processes in Aquatic Ecosystems. R.P. Canale (ed.). Ann Arbor Science Publishers, Ann Arbor, Michigan. pp. 33-74.

Caperon, J. and J. Meyer. 1972a. Nitrogen-limited growth of marine phytoplankton - I. Changes in population characteristics with steady-state growth rate. Deep Sea Research. 19(9): 601-618.

Caperon, J. and J. Meyer. 1972b. Nitrogen-limited growth of marine phytoplankton - II. Uptake kinetics and their role in nutrient limited growth of phytoplankton. Deep Sea Research. 19(9): 619-632.

Carpenter, E.J. and R.L. Guillard. 1971. Intraspecific differences in nitrate half-saturation constants for three species of marine phytoplankton. Ecology. 52(1): 183-185.

Chartrand, T.A. 1973. A report on the taste and odor in relation to the Saginaw-Midland supply at Whitestone Point in Lake Huron. Saginaw Water Treatment Plant, Saginaw, Michigan.

Chen, C.W. and G.T. Orlob. 1972. Ecologic simulation for aquatic environments. Water Resources Engineers, Inc., Walnut Creek, California. Report prepared for the Office of Water Resources Research, U.S. Department of the Interior. 156 p.

Conway, H.L., P.J. Harrison and C.O. Davis. 1976. Marine diatoms grown in chemostats under silicate or ammonium limitation. II. Transient response of Skeletonema costatum to a single addition of the limiting nutrient. Marine Biology. 35: 187-199.

Cowen, W.F. and G.F. Lee. 1976. Algal nutrient availability and limitation in Lake Ontario during IFYGL. Part I. Available phosphorus in urban runoff and Lake Ontario tributary waters. Environmental Protection Agency Ecological Research Series. EPA-600/3-76-094a. 218 p.

Danek, L.J. and J.H. Saylor. 1977. Measurements of the summer currents in Saginaw Bay, Michigan. Journal of Great Lakes Research. 3(1-2): 65-71.

Davis, C.O. 1976. Continuous culture of marine diatoms under silicate limitation. II. Effect of light intensity on growth and nutrient uptake of Skeletonema costatum. Journal of Phycology. 12(3): 291-300.

Davis, C.O., N.F. Breitner and P.J. Harrison. 1978. Continuous culture of marine diatoms under silicon limitation. 3. A model of Si-limited diatom growth. Limnology and Oceanography. 23(1): 41-52.

DePinto, J.V. 1974. Studies on phosphorus and nitrogen regeneration: the effect of aerobic bacteria on phytoplankton decomposition and succession in freshwater lakes. Ph.D. Dissertation. University of Notre Dame, Notre Dame, Indiana.

DePinto, J.V., V.J. Bierman, Jr. and F.H. Verhoff. 1976. Seasonal phytoplankton succession as a function of phosphorus and nitrogen levels. In: Modeling Biochemical Processes in Aquatic Ecosystems. R.P. Canale (ed.). Ann Arbor Science Publishers, Ann Arbor, Michigan. pp. 141-169.

DePinto, J.V. and F.H. Verhoff. 1977. Nutrient regeneration from aerobic decomposition of green algae. Environmental Science and Technology. 11(4): 371-377.

DiToro, D.M. and W.F. Matystik, Jr. 1979. Mathematical models of water quality in large lakes. Part I: Lake Huron and Saginaw Bay model development, verification, and simulations. In press in U.S. Environmental Protection Agency Ecological Research Series.

Dolan, D.M. 1977. Memorandum on Whitestone Point odor reductions as a function of total phosphorus loads. Large Lakes Research Station, U.S. Environmental Protection Agency. Grosse Ile, Michigan. September 12, 1977.

Dolan, D.M., V.J. Bierman, Jr., M.H. Dipert and R.D. Geist. 1978. Statistical analysis of the spatial and temporal variability of the ratio chlorophyll a to phytoplankton cell volume in Saginaw Bay, Lake Huron. Journal of Great Lakes Research. 4(1): 75-83.

Droop, M.R. 1973. Some thoughts on nutrient limitation in algae. Journal of Phycology. 9: 264-272.

Droop, M.R. 1974. The nutrient status of algal cells in continuous culture. Journal of the Marine Biological Association of the United Kingdom. 54: 825-855.

Eppley, R.W., J.N. Rogers and J.J. McCarthy. 1969. Half-saturation constants for uptake of nitrate and ammonium by marine phytoplankton. Limnology and Oceanography. 14: 912-920.

Eppley, R.W. and W.H. Thomas. 1969. Comparison of half-saturation constants for growth and nitrate uptake of marine phytoplankton. Journal of Phycology. 5: 375-379 (1969).

Fee, E.J. 1974. The importance of diurnal variation of photosynthesis vs. eight curves to estimates of integral primary production. Verh. Internat. Verein. Limnol. 19: 39-46.

Fitzgerald, G.P. and T.C. Nelson. 1966. Extractive and enzymatic analyses for limiting or surplus phosphorus in algae. Journal of Phycology. 2: 32-37.

Fitzgerald, G.P. 1969a. Field and laboratory evaluations of bioassay for nitrogen and phosphorus with algae and aquatic weeds. Limnology and Oceanography. 14: 206-212.

Fitzgerald, G.P. 1969b. Some factors in the competition or antagonism among bacteria, algae and aquatic weeds. Journal of Phycology. 5: 351-359.

Foree, E.G., W.J. Jewell and P.L. McCarty. 1970. The extent of nitrogen and phosphorus regeneration from decomposing algae. In: Advances in Water Pollution Research. Vol. 2. Pergamon Press. III-27.

Freedman, P.L. 1974. Saginaw Bay: An evaluation of existing and historical conditions. Environmental Protection Agency, Region V Enforcement Division. Great Lakes Initiative Contract Program Report No. EPA-905/9-74-003. 137 p.

Fuhs, G.W. 1969. Phosphorus content and rate of growth in the diatoms Cyclotella nana and Thalassiosira fluviatilis. Journal of Phycology. 5: 312-321.

Fuhs, G.W., S.D. Demmerle, E. Canelli and M. Chen. 1972. Characterization of phosphorus-limited plankton algae with reflections on the limiting-nutrient concept. In: Nutrients and Eutrophication: The Limiting Nutrient Controversy. Proceedings of a Symposium held at the W.K. Kellogg Biological Station, Michigan State University, February 11-12, 1971. pp. 113-133.

Gannon, J.E. and K.S. Bricker. 1979. The crustacean plankton of Saginaw Bay, Lake Huron: Spatial and seasonal community structure in relation to water quality. In preparation for U.S. Environmental Protection Agency Ecological Research Series.

Glooschenko, W.A. and J.E. Moore. 1973. Surface distribution of chlorophyll a and primary production in Lake Huron, 1971. Technical Report No. 406. Fisheries Research Board of Canada.

Goldman, C.R. 1972. The role of minor nutrients in limiting the productivity of aquatic ecosystems. In: Nutrients and Eutrophication: The Limiting-Nutrient Controversy. Proceedings of a Symposium held at the W.K. Kellogg Biological Station, Michigan State University, February 11-12, 1971. pp. 21-33.

Goldman, J.C., W.J. Oswald and D. Jenkins. 1974. The kinetics of inorganic carbon limited algal growth. Journal of the Water Pollution Control Federation. 46: 554-574.

Great Lakes Water Quality Fifth Annual Report - Appendix B. 1977. Annual Report of the Surveillance Subcommittee to the Implementation Committee of the Great Lakes Water Quality Board, International Joint Commission. Windsor, Ontario. 134 p.

Grenney, W.J., D.A. Bella, and H.C. Curl, Jr. 1974. Effects of intracellular nutrient pools on growth dynamics of phytoplankton. Journal of the Water Pollution Control Federation. 46(7): 1751-1760.

Guillard, R.R.L., P. Kilham and T.A. Jackson. 1973. Kinetics of silicon-limited growth in the marine diatom Thalassiosira pseudonana. Hasle and Heimdal (= Cyclotella nana Hustedt). Journal of Phycology. 9(3): 233-237.

Gunnison, D. and M. Alexander. 1975. Resistance and susceptibility of algae to decomposition by natural microbial communities. Limnology and Oceanography. 20(1): 64-70.

Hammer, V.T. 1964. The succession of "bloom" species of blue-green algae and some causal factors. International Association of Theoretical and Applied Limnology. 15: 829-836.

Healey, F.P. 1973. Characteristics of phosphorus deficiency in Anabaena. Journal of Phycology. 9: 383-394.

Healey, F.P. 1975. Physiological indicators of nutrient deficiency in algae. Technical Report No. 585. Fisheries and Marine Service. Environment Canada.

Hefner, M.R. 1978. Measurement of phosphorus bioavailability in river waters. M.S. Thesis. West Virginia University, Morgantown, West Virginia. 54 p.

Huang, V.H., J.R. Mase and E.G. Fruh. 1973. Nutrient studies in Texas impoundments. Journal of the Water Pollution Control Federation. 45: 105-118.

Jassby, A.D. and C.R. Goldman. 1974. Loss rates from a lake phytoplankton community. Limnology and Oceanography. 19(4): 618-627.

Jewell, W.J. and P.L. McCarty. 1971. Aerobic decomposition of algae. Environmental Science and Technology. 5(10): 1023-1031.

Jorgensen, S.E. 1976. A eutrophication model for a lake. Ecological Modelling. 2: 147-165.

Ketchum, B.H. 1939a. The absorption of phosphate and nitrate by illuminated cultures of Nitzschia closterium. American Journal of Botany. 26: 399-407.

Ketchum, B.H. 1939b. The development and restoration of deficiencies in the phosphorus and nitrogen composition of unicellular plants. Journal of Cellular and Comparative Physiology. 13: 373-381.

Kilham, S.S. 1975. Kinetics of silicon-limited growth in the freshwater diatom Asterionella formosa. Journal of Phycology. 11: 396-399.

Kilham, S.S., C.L. Kott and D. Tilman. 1977. Phosphate and silicate kinetics for the Lake Michigan diatom Diatoma elongatum. Journal of Great Lakes Research. 3(1-2): 93-99.

Koonce, J.F. and A.D. Hasler. 1972. Phytoplankton succession and a dynamic model of algal growth and nutrient uptake. Laboratory of Limnology, University of Wisconsin, Madison, Wisconsin. Eastern Deciduous Forest Biome Memo Report No. 72-114. 112 p.

Kuenzler, E.J. and B.H. Ketchum. 1962. Rate of phosphorus uptake by Phaeodactylum tricornutum. Biological Bulletin. 123: 134-145.

Larsen, D.P., H.T. Mercier and K.W. Malueg. 1973. Modeling algal growth dynamics in Shagawa Lake, Minnesota, with comments concerning projected restoration of the lake. In: Modeling the Eutrophication Process. Proceedings of a Symposium held at the Utah Water Research Laboratory. Utah State University, Logan, Utah, September 5-7, 1973. pp. 15-31.

Lehman, J.T., D.B. Botkin and G.E. Likens. 1975. The assumptions and rationales of a computer model of phytoplankton population dynamics. Limnology and Oceanography. 20(3): 343-364.

Lewin, J.C. 1962. Silicification. In: Physiology and Biochemistry of Algae. R.A. Lewin (ed.). Academic Press. Chapter 27.

Lin, C.K. and C.L. Schelske. 1978. Effects of nutrient enrichments, light intensity and temperature on growth of phytoplankton from Lake Huron. Great Lakes Research Division. Great Lakes and Marine Waters Center. University of Michigan. Special Report No. 63. 61 p.

Lund, J.W.G. 1965. The ecology of freshwater phytoplankton. Biological Reviews. 40: 231-293.

Mague, T.H. and R.H. Burris. 1973. Biological nitrogen fixation in the Great Lakes. BioScience. 23(4): 236-239.

McNaught, D.C. 1975. A hypothesis to explain the succession from calanoids to cladocerans during eutrophication. International Association for Theoretical and Applied Limnology. 19: 724-731.

McNaught, D.C., M. Buzzard, D. Griesmer and M. Kennedy. 1979. Zooplankton grazing and population dynamics relative to water quality in Southern Lake Huron. U.S. Environmental Protection Agency Ecological Research Series. EPA-600/3-80-069. 129 p.

Medveczky, N. and H. Rosenberg. 1970. The phosphate-binding protein of Escherichia coli. Biochimica et Biophysica Acta. 211: 158-168.

Medveczky, N. and H. Rosenberg. 1971. Phosphate transport in Escherichia coli. Biochimica et Biophysica Acta. 241: 494-501.

Monod, J. 1949. The growth of bacterial culture. Annual Review of Microbiology. 3: 371-394.

Mortimer, C.H. 1969. Physical factors with bearing an eutrophication in general and in large lakes in particular. In: Eutrophication, Causes, Consequences, Correctives. Proceedings of a Symposium sponsored by the National Academy of Science held at the University of Wisconsin, Madison, June 11-15, 1967. pp. 340-368.

Mullin, M.D. 1976. Atmospheric inputs of phosphorus and nitrogen to Lake Huron. Paper presented at the 19th Conference on Great Lakes Research, University of Guelph, Guelph, Ontario, May 4-6, 1976.

Mullin, M.M., P.R. Sloan and R.W. Eppley. 1966. Relationship between carbon content, cell volume, and area in phytoplankton. Limnology and Oceanography. 11: 307-311.

Nalewajko, C. 1966. Dry weight, ash, and volume data for some freshwater planktonic algae. Journal of the Fisheries Research Board of Canada. 23(8): 1285-1288.

Nalewajko, C. and D.R.S. Lean. 1978. Phosphate kinetics - algal growth relationships in batch cultures. Mitt. Internat. Verein. Limnol. 21: 184-192.

Nyholm, N. 1978. A simulation model for phytoplankton growth and nutrient cycling in eutrophic, shallow lakes. Ecological Modelling. 4: 279-310.

O'Connor, D.J., R.V. Thomann and D.M. DiToro. 1973. Dynamic water quality forecasting and management. Environmental Protection Agency Ecological Research Series. EPA-660/3-73-009. 201 p.

Ogawa, R.E. and J.F. Carr. 1969. The influence of nitrogen on heterocyst production in blue-green algae. Limnology and Oceanography. 14: 342-351.

Oksiyuk, O.P. and V.V. Yurchenko. 1971. The weight of diatoms. Hydrobiological Journal. 7(3): 106-108.

Paasche, E. 1973. Silicon and the ecology of marine plankton diatoms. II. Silicate-uptake kinetics in five diatom species. Marine Biology. 19: 262-269.

Parker, J.I., H.L. Conway and E.M. Yaguchi. 1977. Dissolution of diatom frustules and recycling of amorphous silicon in Lake Michigan. Journal of the Canadian Fisheries Research Board. 34(4): 545-551.

Paul, J.F. 1977. The water circulation in the vicinity of the Saginaw-Midland water intake station at Whitestone Point on Saginaw Bay and its effect on the taste and odor of the intake water. Report prepared for the Large Lakes Research Station, U.S. Environmental Protection Agency. Grosse Ile, Michigan. 13 p.

Pearsall, W.H. 1932. Phytoplankton in the English lakes II. The composition of phytoplankton in relation to dissolved substances. The Journal of Ecology. 20: 241-262.

Provasoli, L. 1969. Algal nutrition and eutrophication. In: Eutrophication: Causes, Consequences, Correctives. Proceedings of a Symposium sponsored by the National Academy of Science held at the University of Wisconsin, Madison, June 11-15, 1967. pp. 574-593.

Rhee, G. 1973. A continuous culture study of phosphate uptake, growth rate and polyphosphate in Scenedesmus sp. Journal of Phycology. 9: 495-506.

Rhee, G. 1974. Phosphate uptake under nitrate limitation by Scenedesmus sp. and its ecological implications. Journal of Phycology. 10(4): 470-475.

Rhee, G. 1978. Effects of N:P atomic ratios and nitrate limitation on algal growth, cell composition, and nitrate uptake. Limnology and Oceanography. 23(1): 10-25.

Richardson, W.L. 1974. Modeling chloride distribution in Saginaw Bay. Proceedings of Seventeenth Conference on Great Lakes Research. International Association for Great Lakes Research. pp. 462-470.

Richardson, W.L. 1976. An evaluation of the transport characteristics of Saginaw Bay using a mathematical model of chloride. In: Modeling Biochemical Processes in Aquatic Ecosystems. R.P. Canale (ed.). Ann Arbor Science Publishers, Ann Arbor, Michigan. pp. 113-139.

Riley, G.A. 1946. Factors controlling phytoplankton populations on Georges Bank. Journal of Marine Research. 6: 54-71.

Scavia, D. and B.J. Eadie. 1976. The use of measurable coefficients in process formulations - zooplankton grazing. Ecological Modelling. 2: 315-319.

Scavia, D., B.J. Eadie, A. Robertson. 1976. An ecological model for Lake Ontario: model formulation, calibration, and preliminary evaluation. Great Lakes Environmental Research Laboratory, Ann Arbor, Michigan. NOAA Technical Report ERL 371-GLERL 12. 63 p.

Scavia, D. and R.A. Park. 1976. Documentation of selected constructs and parameter values in the aquatic model CLEANER. Ecological Modelling. 2: 33-58.

Schelske, C.L. and E.F. Stoermer. 1971. Eutrophication, silica depletion, and predicted changes in algal quality in Lake Michigan. Science. 173: 423-424.

Schelske, C.L., E.D. Rothman and M.S. Simmons. 1978. Comparison of bioassay procedures for growth-limiting nutrients in the Laurentian Great Lakes. Mitt. Internat. Verein. Limnol. 21: 65-80.

Schindler, D.W., H. Kling, R.V. Schmidt, J. Prokopovich, V.E. Frost, R.A. Reid and M. Capel. 1973a. Eutrophication of Lake 227 by addition of phosphate and nitrate: the second, third, and fourth years of enrichment, 1970, 1971 and 1972. Journal of the Fisheries Research Board of Canada. 30: 1415-1430.

Schindler, D.W. and E.J. Fee. 1973b. Diurnal variation of dissolved inorganic carbon and its use in estimating primary production and CO invasion in Lake 227. Journal of the Fisheries Research Board of Canada. 30: 1501-1510.

Schindler, D.W. 1977. Evolution of phosphorus limitation in lakes. Science. 195: 260-262.

Shapiro, J. 1973. Blue-green algae: why they become dominant. Science. 179: 382-384.

Shuter, B.J. 1978. Size dependence of phosphorus and nitrogen subsistence quotas in unicellular organisms. Limnology and Oceanography. 23(6): 1248-1255.

Smayda, T.J. 1974. Some experiments on the sinking characteristics of two freshwater diatoms. Limnology and Oceanography. 19(4): 628-635.

Smith, V.E., K.W. Lee, J.C. Filkins, K.W. Hartwell, K.R. Rygwelski and J.M. Townsend. 1977. Survey of chemical factors in Saginaw Bay (Lake Huron). U.S. Environmental Protection Agency Ecological Research Series. EPA-600/3-77-125. 143 p.

Stoermer, E.F. and T.B. Ladewski. 1976. Apparent optimal temperatures for the occurrence of some common phytoplankton species in southern Lake Michigan. Great Lakes Research Division, University of Michigan. Publication 18. 49 p.

Stoermer, E.F., et al. 1979. In preparation for U.S. Environmental Protection Agency Ecological Research Series.

Strickland, J.D.H. 1958. Solar radiation penetrating the ocean. A review of requirements, data and methods of measurement, with particular reference to photosynthetic productivity. Journal of the Fisheries Research Board of Canada. 15(3): 453-493.

Thomann, R.V., D.M. DiToro, R.P. Winfield and D.J. O'Connor. 1975. Mathematical modeling of phytoplankton in Lake Ontario. I. Model development and verification. Environmental Protection Agency Ecological Research Series. EPA-660/3-75-005. 177 p.

Titman, D. and P. Kilham. 1976. Sinking in freshwater phytoplankton: some ecological implications of cell nutrient status and physical mixing processes. Limnology and Oceanography. 21(3): 409-417.

Toetz, D.W., L.P. Varga and E.D. Loughran. 1973. Half-saturation constants for uptake of nitrate and ammonia by reservoir plankton. Ecology. 54(4): 903-908.

U.S. Environmental Protection Agency. 1971. Algal assay procedure - bottle test. National Eutrophication Research Center. Corvallis, Oregon. 82 p.

Vallentyne, J.R. and N.A. Thomas. 1978. Fifth year review of Canada-United States Great Lakes Water Quality Agreement. Report of Task Group III, a technical group to review phosphorus loadings. U.S. Department of State. 86 p.

Vanderhoef, L.N., C. Huang, R. Musil and J. Williams. 1974. Nitrogen fixation (acetylene reduction) by phytoplankton in Green Bay, Lake Michigan, in relation to nutrient concentrations. Limnology and Oceanography. 19(1): 119-125.

Verhoff, F.H. and K.R. Sundaresan. 1972. A theory of coupled transport in cells. Biochimica et Biophysica Acta. 255: 425-441.

Verhoff, F.H., J.B. Carberry, V.J. Bierman, Jr. and M.W. Tenney. 1973. Mass transport of metabolites, especially phosphorus in cells. American Institute of Chemical Engineers Symposium Series 129. 69: 227-240.

APPENDIX A

MODEL EQUATIONS

STATE VARIABLE EQUATIONS

For each phytoplankton type, ℓ, the rate of change of intracellular phosphorus is given by:

A.1.0 $$\frac{d(A_\ell PSA_\ell)}{dt} = \text{boundary contribution} + \text{net uptake} - \text{grazing} - \text{decomposition} - \text{respiration} - \text{sinking}$$

A.1.1 $$\text{boundary contribution} = \frac{Q}{V}\,(ABD_\ell PSABD_\ell - A_\ell PSA_\ell)$$

A.1.2 $$\text{net uptake} = A_\ell RlPM_\ell f(T)_\ell f(L)_\ell \times (0.322\times10^{-4})\ \frac{\text{moles P}}{\text{mg P}}\left[\frac{1}{1+PKl_\ell PCA_\ell} - \frac{1}{1+PKl_\ell PCM}\right]$$

A.1.3 $$\text{grazing} = PSA_\ell RAGRZD_\ell$$

A.1.4 $$\text{decomposition} = A_\ell PSA_\ell RLYS_\ell TCROP \cdot 1.08^{(T-20)}$$

A.1.5 $$\text{respiration} = A_\ell PSA_\ell RRESP_\ell f(T)_\ell$$

A.1.6 $$\text{sinking} = A_\ell PSA_\ell ASINK_\ell / DEPTH$$

Expanding by the chain rule for derivatives:

A.2.0 $$\frac{d(A_\ell PSA_\ell)}{dt} = A_\ell \frac{dPSA_\ell}{dt} + PSA_\ell \frac{dA_\ell}{dt}$$

For each phytoplankton type, ℓ, the rate of change in biomass is given by:

A.3.0 $$\frac{dA_\ell}{dt} = \text{boundary contribution} + \text{gross production} - \text{grazing} - \text{decomposition} - \text{respiration} - \text{sinking}$$

A.3.1 boundary contribution = $\frac{Q}{V}$ $(ABD_\ell - A_\ell)$

A.3.2 gross production = $A_\ell SPGR_\ell$

Specific growth rate of phytoplankton ℓ, $SPGR_\ell$, is set equal to the minimum value of the following functions:

A.3.2.1 $RAMAX_\ell\ f(T)_\ell\ f(L)_\ell\ [(P-PO)/(KPCELL + (P-PO))]$

A.3.2.2 $RAMAX_\ell\ f(T)_\ell\ f(L)_\ell [(N-NO)/(KNCELL + (N-NO))]$

A.3.2.3 $RAMAX_\ell\ f(T)_\ell\ f(L)_\ell [SCM/(KSCM + SCM)]$

A.3.3 grazing = $RAGRZD_\ell$

A.3.4 decomposition = $A_\ell RLYS_\ell TCROP \cdot 1.08^{(T-20)}$

A.3.5 respiration = $A_\ell RRESP_\ell 1.08^{(T-20)}$

A.3.6 sinking = $A_\ell ASINK_\ell / DEPTH$

In equation A.3.0, it is assumed that the contribution to the derivative due to changes in intracellular phosphorus is negligible.

Setting the right hand sides of equations A.1.0 and A.2.0 equal and substituting equation A.3.0 gives the following equation for the state variable PSA_ℓ:

A.4.0 $\frac{dPSA_\ell}{dt}$ = boundary contribution + net uptake

- gross production

A.4.1 boundary contribution = $\frac{Q}{V}$ $ABD_\ell(PSABD_\ell - PSA_\ell)/A_\ell$

A.4.2 net uptake = $RIPM_\ell f(T)_\ell f(L)_\ell (0.322 \times 10^{-4})$ $\frac{\text{moles P}}{\text{mg P}}$

$$\times \left[\frac{1}{1 + PKI_\ell PCA_\ell} - \frac{1}{1 + PKI_\ell PCM} \right]$$

A.4.3 gross production = $PSA_\ell SPGR_\ell$

A.5.0 $\frac{dPCM}{dt}$ = boundary contribution - net uptake

+ respiration + zooplankton excretion + decomposition

+ transformation + external loading

A.5.1 boundary contribution = $\frac{Q}{V}$ (PCMBD-PCM)

A.5.2 net uptake = $(0.322 \times 10^{-4}) \frac{\text{moles P}}{\text{mg P}}$

$$\times \sum_{\ell} A_{\ell} R1PM_{\ell} f(T)_{\ell} f(L) \left[\frac{1}{1 + PKT_{\ell} PCA_{\ell}} - \frac{1}{1 + PKT_{\ell} PCM} \right]$$

A.5.3 respiration = $\sum_{\ell} A_{\ell}(PSA_{\ell} - PSAMIN_{\ell}) RRESP_{\ell} 1.08^{(T-20)}$

A.5.4 zooplankton excretion = $\sum_{\ell} (PSA_{\ell} - PSAMIN_{\ell}) RAGRZD_{\ell}$

A.5.5 decomposition = $TCROP \cdot 1.08^{(T-20)} \sum_{\ell} A_{\ell}(PSA_{\ell} - PSAMIN_{\ell}) RLYS_{\ell}$

A.5.6 transformation = $RTOP \cdot TOP \cdot 1.08^{(T-20)}$

A.5.7 external loading = WPCM/V

The equation for nitrogen concentration, NCM, is functionally identical to equation A.5.0 for phosphorus concentration.

A.6.0 $\frac{dSCM}{dt}$ = boundary contribution

- gross diatom production

+ transformation + external loading

A.6.1 boundary contribution = $\frac{Q}{V}$ (SCMBD-SCM)

A.6.2 gross diatom production = $\sum_{\text{diatoms}} A_{\ell} SSA_{\ell} SPGR$

A.6.3 transformation = $RTOS \cdot TOS \cdot 1.08^{(T-20)}$

A.6.4 external loading = WSCM/V

A.7.0 $\frac{dZ_k}{dt}$ = boundary contribution + growth rate

- death rate

A.7.1 boundary contribution = $\frac{Q}{V}$ ($ZBD_k - Z_k$)

A.7.2 growth rate = $RZ_k Z_k$ (refer to A.10.0)

A.7.3 death rate = $ZDETH_k Z_k$ (refer to A.14.1 and A.14.2)

A.8.0 $\frac{dTOP}{dt}$ = boundary contribution + respiration
+ decomposition + zooplankton excretion + zooplankton death - transformation - sinking + external loading

A.8.1 boundary contribution = $\frac{Q}{V}$ (TOPBD-TOP)

A.8.2 respiration = $\sum_{\ell} A_\ell PSAMIN_\ell RRESP_\ell 1.08^{(T-20)}$

A.8.3 decomposition = $\sum_{\ell} A_\ell PSAMIN_\ell RLYS_\ell TCROP \cdot 1.08^{(T-20)}$

A.8.4 zooplankton excretion = $\sum_{k} RZPEX_k Z_k$ (refer to A.12.0)

A.8.5 zooplankton death = $\sum_{k} BDETH_k Z_k \ (0.161 \times 10^{-7}) \ \frac{\text{mole P}}{\text{mg Z}} \ 1.08^{(T-20)}$

A.8.6 transformation = RTOP·TOP·$1.08^{(T-20)}$

A.8.7 sinking = TOP·TOPSNK/DEPTH

A.8.8 external loading = WTOP/V

The equation for unavailable nitrogen, TON, is functionally identical to equation A.8.0 for unavailable phosphorus.

A.9.0 $\frac{dTOS}{dt}$ = boundary contribution + respiration
+ decomposition + zooplankton excretion
- transformation - sinking
+ external loading

A.9.1 boundary contribution = $\frac{Q}{V}$ (TOSBD-TOS)

A.9.2 respiration = $\sum_{\text{diatoms}} A_\ell SSA_\ell RRESP_\ell 1.08^{(T-20)}$

A.9.3 decomposition = $\sum_{\text{diatoms}} A_\ell SSA_\ell RLYS_\ell TCROP \cdot 1.08^{(T-20)}$

A.9.4 zooplankton excretion = $\sum_{\text{diatoms}} RAGRZD_\ell \, SSA_\ell$ (refer to A.11.0)

A.9.5 transformation = $RTOS \cdot TOS \cdot 1.08^{(T-20)}$

A.9.6 sinking = $TOS \cdot TOSSNK/DEPTH$

A.9.7 external loading = $WTOS/DEPTH$

PROCESS RATE EQUATIONS

Specific growth rate for zooplankton k:

A.10.0 $$RZ_k = RZMAX_k ZASSIM_k 1.08^{(T-20)} \left[\frac{\sum_\ell ZEFF_{k\ell} A_\ell - AZMIN_k}{ZKDUM_k + \sum_\ell ZEFF_{k\ell} A_\ell - AZMIN_k} \right]$$

A.10.1 $$ZKDUM_k = \left[\frac{\sum_\ell ZEFF_{k\ell} A_\ell - AZMIN_k}{\sum_\ell ZEFF_{k\ell} A_\ell} \right] KZSAT_k$$

Rate at which phytoplankton ℓ is grazed by zooplankton:

A.11.0 $$RAGRZD_\ell = 1.08^{(T-20)} \sum_k \left[\frac{RZMAX_k Z_k (ZEFF_{k\ell} A_\ell - ADUM_{k\ell})}{ZKDUM_k + \sum_\ell ZEFF_{k\ell} A_\ell - AZMIN_k} \right]$$

A.11.1 $$ADUM_{k\ell} = \frac{ZEFF_{k\ell} A_\ell}{\sum_\ell ZEFF_{k\ell} A_\ell} AZMIN_k$$

Note: $\sum_\ell ADUM_{k\ell} = AZMIN_k$

Rate at which phosphorus is excreted to the unavailable pool by zooplankton k:

A.12.0 $$RZPEX_k = (1-ZASSIM_k) RZMAX_k 1.08^{(T-20)} \left[\frac{\sum_\ell (ZEFF_{k\ell} A_\ell - ADUM_{k\ell}) PSAMIN_\ell}{ZKDUM_k + \sum_\ell ZEFF_{k\ell} A_\ell - AZMIN_k} \right]$$

The process rate equation for nitrogen excretion is functionally identical to equation A.12.0 for phosphorus.

Rate at which silicon is excreted to the unavailable pool by zooplankton k:

$$\text{A.13.0} \qquad RZSEX_k = RZMAX_k \; 1.08^{(T-20)} \left[\frac{\sum_{\text{diatoms}} (ZEFF_{k\ell} A_\ell - ADUM_{k\ell}) SSA_\ell}{ZKDUM_k + \sum_\ell ZEFF_{k\ell} A_\ell - AZMIN_k} \right]$$

Zooplankton death rate is given by:

$$\text{A.14.1} \qquad ZDETH_k = BDETH_k \; 1.08^{(T-20)} \qquad Z_k \leq ZSAFE_k$$

$$\text{A.14.2} \qquad ZDETH_k = (BDETH_k + PDETH_k Z_k) \; 1.08^{(T-20)} \qquad PSAT_k \geq Z_k > ZSAFE_k$$

MISCELLANEOUS FUNCTIONS

$$\text{A.15.0} \qquad PSAMIN_\ell = PO_\ell / FACT_\ell$$

$$\text{A.15.1} \qquad PCAMIN_\ell = PSAMIN_\ell (0.25 \times 10^6) / CONCP_\ell$$

$$\text{A.15.2} \qquad f(L) = \frac{(2.718)PHOTO}{K_e \cdot DEPTH} \left[e^{-\alpha_1} - e^{-\alpha_0} \right]$$

$$\text{A.15.2.1} \qquad PHOTO = 0.64 \{0.78 - 0.22 \left[SINE(6.28*(TIME + 90)/365) \right] \}$$

$$\text{A.15.2.2} \qquad \alpha_0 = RADINC / RADSAT_\ell$$

$$\text{A.15.2.3} \qquad \alpha_1 = \alpha_0 \, e^{-K_e \cdot DEPTH}$$

$$\text{A.15.2.4} \qquad K_e = 1.195 / \text{Secchi Depth} + 0.159$$

RADINC, Secchi Depth and T were specified externally on a daily basis using linear interpolation between measured values.

PHYTOPLANKTON TEMPERATURE REDUCTION FACTORS

$$\text{A.16.0} \qquad f(T)_{\text{diatoms}} = \begin{cases} 0.2(T-2)/1.6 & T \leq 10 \\ 1 & 10 < T \leq 14 \\ (1.6 - 0.2(T-14))/1.6 & T > 14 \end{cases}$$

$$\text{A.16.1} \qquad f(T)_{\text{greens}} = 0.0824(T-3)/1.4$$

$$\text{A.16.2} \qquad f(T)_{\text{others}} = 0.0706(T-3)/1.2$$

A.16.3 $f(T)_{\text{non-heterocystous blue-greens}} = 0.03125(T-3)$ $T \leq 11$

$= (0.25 + 0.0833(T-11))$ $T > 11$

A.16.4 $f(T)_{\text{heterocystous blue-greens}} = 0.01875(T-3)/0.7$ $T \leq 11$

$= (0.15 + 0.0611(T-11))/0.7$ $T > 11$

Note: The minimum value for f(T) for each species is arbitrarily specified at 0.01 day^{-1}.

TABLE B-1. SUMMARY OF PHYTOPLANKTON COEFFICIENTS

Coefficients	Units	Phytoplankton Type				
		Diatoms	Greens	Others	Blue-Greens (non-N_2)	Blue-Greens (N_2)
R1PM	day^{-1}	0.500	0.500	0.500	0.500	0.500
PK1	liters/mole	0.518×10^{6}	0.167×10^{7}	0.518×10^{6}	0.200×10^{7}	0.518×10^{6}
PO	mole P/cell	0.724×10^{-13}	0.312×10^{-14}	0.148×10^{-13}	0.566×10^{-14}	0.488×10^{-14}
CONCP	-	0.250×10^{6}	0.250×10^{6}	0.250×10^{6}	0.356×10^{6}	0.356×10^{6}
KPCELL	mole P/cell	0.724×10^{-13}	0.312×10^{-14}	0.148×10^{-13}	0.566×10^{-14}	0.488×10^{-14}
R1NM	day^{-1}	0.125	0.125	0.125	0.125	0.125
NK1	liters/mole	0.100×10^{7}	0.100×10^{7}	0.100×10^{7}	0.100×10^{7}	0.100×10^{7}
NO	mole N/cell	0.801×10^{-11}	0.345×10^{-12}	0.163×10^{-11}	0.438×10^{-12}	0.377×10^{-12}
CONCN	-	0.208×10^{7}	0.208×10^{7}	0.208×10^{7}	0.208×10^{7}	0.208×10^{7}
KNCELL	mole N/cell	0.801×10^{-11}	0.345×10^{-12}	0.163×10^{-11}	0.438×10^{-12}	0.377×10^{-12}
SSA	mole Si/mg	0.334×10^{-5}	-	-	-	-
KSCM	mole Si/liter	0.357×10^{-5}	-	-	-	-
RAMAX	day^{-1}	1.6	1.4	1.2	1.0	0.70
ASINK	meter/day	0.05	0.05	0.05	0.05	0.05
RLYS	liters/mg day	0.004	0.004	0.004	0.012	0.012
FACT	mg/cell	0.450×10^{-5}	0.194×10^{-6}	0.918×10^{-6}	0.246×10^{-6}	0.212×10^{-6}
RADSAT	langleys/day	100	100	100	50	50
RRESP	day^{-1}	0.05	0.05	0.05	0.05	0.05

TABLE B-2. SUMMARY OF ZOOPLANKTON COEFFICIENTS

Coefficient	Unit	Zooplankton Type	
		Fast Ingester	Slow Ingester
RZMAX	day^{-1}	0.70	0.10
ZASSIM	-	0.60	0.60
KZSAT	mg/liter	1.0	1.0
AZMIN	mg/liter	0.20	0.20
BDETH	day^{-1}	0.05	0.01
PDETH	day^{-1}	0.50	0.10
ZSAFE	mg/liter	0.01	0.01
PSAT	mg/liter	1.0	1.0

TABLE B-3. SUMMARY OF COEFFICIENTS FOR UNAVAILABLE NUTRIENTS

Coefficient	Units	Value
RTOP, RTON, RTOS	day^{-1}	0.005
TOPSNK, TONSNK, TOSSNK	meters/day	0.05

TABLE C-1. INITIAL PHYTOPLANKTON CONCENTRATIONS

Parameter	Unit	Phytoplankton Type				
		Diatoms	Greens	Others	Blue-Greens (non-N_2)	Blue-Greens (N_2)
A	mg/liter	1.22	0.013	0.03	0.07	0.0002
PSA	moles P/mg	0.644×10^{-7}	0.644×10^{-7}	0.644×10^{-7}	0.920×10^{-7}	0.920×10^{-7}
NSA	moles N/mg	0.356×10^{-5}	0.356×10^{-5}	0.356×10^{-5}	0.356×10^{-5}	0.356×10^{-5}

TABLE C-2. INITIAL ZOOPLANKTON CONCENTRATIONS

Parameter	Unit	Zooplankton type	
		Fast ingester	Slow ingester
Z	mg/ℓ	0.0924	0.0436

TABLE C-3. INITIAL NUTRIENT CONCENTRATIONS.

Parameter	Concentration µg/liter
PCA	5.8
NCM	300
SCM	300
TOP	20.
TON	200
TOS	300

APPENDIX D

FORCING FUNCTIONS: EXTERNAL LOADS, BOUNDARY CONDITIONS, NET EXCHANGE FLOWS, TEMPERATURE, AND LIGHT

TABLE D-1. TIME SERIES VALUES FOR SAGINAW RIVER LOAD FOR CHLORIDE IN 1974.

Julian Day	Load in Kilograms
1	1.05×10^6
15	0.315
18	0.798
23	5.21
25	1.76
28	2.93
29	1.65
37	0.652
51	1.27
53	0.291
56	1.77
60	1.45
65	2.29
73	1.08
74	1.97
88	0.567
91	1.90
92	3.30
94	2.40
95	2.91
99	1.38
101	1.16
105	1.88
109	0.993
116	0.761
128	1.02
134	0.920
137	4.50
141	1.17
147	0.627
151	1.34
155	0.755

TABLE D-1. CONTINUED

Julian Day	Load in Kilograms
158	0.627×10^6
162	1.68
165	0.943
172	0.822
179	0.379
190	0.596
213	0.422
272	0.464
274	0.847
280	0.638
295	0.854
311	0.971
325	0.408
337	0.208
353	0.309
365	0.379

TABLE D-2. TIME SERIES VALUES FOR SAGINAW RIVER LOAD FOR TOTAL PHOSPHORUS IN 1974.

Julian Day	Load in Kilograms
1	3069
16	1581
24	8649
29	27125
32	7037
34	2908
49	1265
56	5208
59	5828
66	32240
67	11625
74	4030
90	2585
95	11718
99	5456
114	4743
134	3286
141	17298
142	7254
147	3001
154	1965
162	6293
165	2709
206	1262
295	1169
337	530
365	1277

TABLE D-3. TIME SERIES VALUES FOR SAGINAW RIVER LOAD FOR DISSOLVED ORTHO-PHOSPHORUS IN 1974.

Julian Day	Load in Kilograms
1	1228
3	1228
18	289
21	1138
22	1609
24	1950
25	2226
28	4061
30	976
32	1519
36	834
49	434
56	1500
59	1327
64	4216
67	1888
78	636
99	372
100	4340
101	1088
106	316
109	1147
126	440
134	1485
135	290
141	240
142	775
153	165
155	701
158	276
162	1218
165	499
171	1538
176	293
193	499
226	319
262	394
274	946
280	601
295	818
305	846
311	216
317	825
325	918
337	415
353	493
365	527

TABLE D-4. TIME SERIES VALUES FOR SAGINAW RIVER LOAD FOR TOTAL KJELDAHL NITROGEN IN 1974.

Julian Day	Load in Kilograms
1	11620
14	3822
21	49560
25	19460
30	37660
38	8750
52	18900
59	11648
66	184800
72	21980
89	21980
95	41720
101	18060
105	25200
116	8008
123	10486
135	21840
141	48020
147	13902
158	8288
162	16100
165	8862
179	3654
279	5852
353	4354
365	4354

TABLE D-5. TIME SERIES VALUES FOR SAGINAW RIVER LOAD FOR NITRATE PLUS NITRITE NITROGEN IN 1974

Julian Day	Load in Kilograms
1	20440
18	11074
24	93940
28	233800
30	117180
39	30240
53	33460
59	42000
65	184800
74	57960
90	29960
95	136920
101	57680
106	54740
112	20160
137	31220
141	53620
142	25060
169	21140
179	4536
189	4214
207	1355
225	1144
261	168
280	2268
353	1918
365	1918

TABLE D-6. TIME SERIES VALUES FOR SAGINAW RIVER LOAD FOR DISSOLVED AMMONIA NITROGEN IN 1974

Julian Day	Load in Kilograms
1	1764
2	1764
18	861
21	3472
28	9996
32	5446
38	1918
49	1033
52	1792
56	4690
59	3836
65	17220
73	4984
80	4214
87	2114
92	13720
95	890
101	1876
105	3654
109	902
119	1680
123	3234
134	2422
135	5012
141	480
142	4886
143	515
155	1400
162	3136
165	1792
172	1442
176	743
226	461
261	2226
352	2590
365	2590

TABLE D-7. TIME SERIES VALUES FOR SAGINAW RIVER LOAD FOR DISSOLVED SILICATE SILICON IN 1974

Julian Day	Load in Kilograms
1	19880
18	9884
21	23464
23	71680
25	45640
28	68600
29	145320
32	34720
38	16212
39	24388
50	10024
53	48720
59	35560
65	162400
74	52920
78	39760
93	56000
95	93800
101	46200
105	57120
114	1599
120	15372
130	19572
134	14840
137	52080
147	19264
158	9072
162	27636
176	11256
179	6804
186	17640
193	5068
274	8820
295	6552
311	13916
325	7588
353	7364
365	7364

TABLE D-8. CHEMICAL BOUNDARY CONDITIONS USED BETWEEN INNER AND OUTER PORTIONS OF SAGINAW BAY

Julian Day	Total P	Dissolved PO -P	Dissolved $(NO_3 + NO_2)$-N	Dissolved NH_3-N	Total Kjeldahl N	Dissolved SiO_2-Si
51	-	1.0	300.	7.0	-	374.
84	-	4.0	400.	14.0	-	513.
110	-	2.0	500.	15.5	-	467.
118	4.7	3.2	300.	18.6	227.	420.
137	10.0	3.6	340.	8.2	173.	534.
154	19.3	4.7	325.	30.7	163.	275.
170	7.4	5.0	300.	36.2	148.	336.
189	6.6	4.4	220.	32.0	172.	494.
206	20.8	5.2	100.	43.2	366.	541.
225	11.0	3.0	125.	49.0	323.	455.
261	14.7	6.2	100.	33.8	233.	541.
279	12.6	3.8	140.	20.6	176.	411.
315	9.2	3.2	160.	24.0	152.	439.
352	18.0	4.0	300.	33.0	410.	420.

TABLE D-9. BIOLOGICAL BOUNDARY CONCENTRATIONS USED BETWEEN INNER AND OUTER PORTIONS OF SAGINAW BAY

Julian Day	Concentrations in mg dry weight/liter						
	Diatoms	Greens	Others	Blue-Greens (non-N_2)	Blue-Greens (N_2)	Zooplankter 1	Zooplankter 2
84	0.422	0.142	0.304	0.006	0.000	-	-
110	1.17	0.002	0.372	0.030	0.000	-	-
118	0.794	0.002	0.033	0.014	0.000	0.002	0.015
137	5.05	0.004	0.029	0.010	0.054	0.001	0.015
154	0.182	0.008	0.029	0.036	0.170	-	-
170	0.471	0.007	0.034	0.065	0.012	0.236	0.041
189	0.007	0.007	0.002	0.000	0.000	0.445	0.045
206	0.176	0.079	0.074	0.331	0.011	0.009	0.008
225	0.100	0.128	0.012	0.279	0.052	-	-
261	0.145	0.031	0.020	0.361	0.007	0.067	0.059
279	0.745	0.057	0.044	0.229	0.005	0.018	0.038
315	0.945	0.166	0.004	0.033	0.000	0.039	0.036

Boundary conditions for PSA and NSA have been specified at twice the minimum cell quota for all five phytoplankton types; i.e., PSABD = 2 x PSAMIN and NSABD = 2 x NSAMIN.

TABLE D-10. WATER CIRCULATION RATES USED BETWEEN INNER AND OUTER PORTIONS OF SAGINAW BAY

Time Interval Julian Days	Flow Rate meter^3/second
0-74	176
75-124	499
125-149	2080
150-179	1920
180-224	900
225-350	672
350-365	83

Inner Bay Volume	0.806×10^{10} meters^3
Inner Bay Average Depth	5.83 meters

TABLE D-11. AVERAGE WATER TEMPERATURES IN INNER SAGINAW BAY IN 1974

Julian Day	Temperature °C
1	0.29
52	1.25
109	6.44
119	8.71
135	9.87
155	16.6
170	15.4
190	21.9
207	21.6
226	21.8
262	17.0
280	11.8
315	8.71
351	0.29
365	0.29

TABLE D-12. VALUES USED FOR INCIDENT SOLAR RADIATION

Julian Day	Incident Radiation langleys/day
1	100
30	70
60	100
75	125
90	300
120	440
150	600
180	660
210	625
240	540
270	390
300	210
330	115
360	100
365	100

TABLE D-13. AVERAGE SECCHI DEPTHS IN INNER SAGINAW BAY IN 1974

Julian Day	Secchi Depth meters
1	1.67
52	3.13
109	0.76
119	1.26
135	1.11
155	1.14
170	1.08
190	1.18
207	1.13
226	1.01
262	0.77
280	0.84
315	1.12
351	1.28
365	1.67

APPENDIX E

RESULTS OF SENSITIVITY ANALYSES

This Appendix contains tabulated results for all 72 sensitivity analysis runs with the calibrated model. Results are presented for individual phytoplankton groups in Tables E-1 to E-6. Table E-7 contains summary results for average phytoplankton responses to each parameter varied, in order of decreasing sensitivity. Only these average results will be discussed here.

In interpreting the results, it is important to maintain a proper perspective. The following considerations are pertinent:

1. Responses were not always symmetrical about the calibration results for equal plus and minus variations in a given parameter.

2. Some individual phytoplankton groups responded to greater degrees than other groups to variations in certain parameters.

3. Some of the parameter variations only had direct effects on certain phytoplankton groups. For example, variations in silicon-related parameters only had direct effects on the diatoms.

Mindful of these qualifications, the results can be a useful guide to the relative importance of the various mechanisms and coefficients in the model.

One of the most significant results was the extreme sensitivity of the phytoplankton to variations in the underwater light environment (XTINCO), and the relative insensitivity to variations in incident solar radiation (RADINC). This was consistent with the discussion in Section 8. Phytoplankton responses were relatively sensitive to temperature variations, but only moderately sensitive to variations in hydraulic detention time (Q). This latter result implied that the dynamic behavior of the calibration results was primarily a reflection of the biological-chemical kinetics in the model, and not of the boundary conditions.

In general, the phytoplankton were sensitive to variations in maximum growth and ingestion rates for the phytoplankton and zooplankton, respectively, and to variations in the associated half-saturation concentrations. The phytoplankton were relatively more sensitive to variations in phosphorus half-saturation concentrations than to variations in nitrogen half-saturation concentrations. The phytoplankton were more sensitive to variations in zooplankton assimilation efficiency (ZASSIM) and phytoplankton respiration rate (RRESP) than to variations in any other loss-related pa-

rameter. Consistent with the discussion in Section 8 on limiting nutrients, the diatoms were especially sensitive to variations in SSA, percent silica by dry weight. The value for this coefficient had a strong influence on the size of the spring diatom peak.

The phytoplankton were relatively insensitive to variations in net sinking rates for phytoplankton (ASINK) and unavailable nutrient forms (TOPSNK, TONSNK, TOSSNK). This was probably due to the relatively short hydraulic detention time of the bay. In addition, the values found for these coefficients in the calibration were apparently consistent with a relatively high degree of vertical dispersion in the water column.

It was significant to note that the phytoplankton were relatively insensitive to variations in conversion rates from unavailable to available nutrient forms (RTOP, RTON, RTOS). This was most probably due to the relatively short hydraulic detention time of the bay. This result was the opposite of what would be expected for systems with much longer hydraulic detention times, such as the other major basins in the Great Lakes.

TABLE E-1. RESULTS OF SENSITIVITY ANALYSES FOR EXTERNAL FORCING FUNCTIONS - PEAK CROPS

	Percent Change in Peak Crops Relative To Final Calibration						
		Diatoms					
Parameter Varied	Total Zoo	Spring	Fall	Greens	Others	Blue-Greens (Non-N_2)	Blue-Greens (N_2)
Plus 20%							
Q	-3	-4	+12	-9	-7	-6	-3
T	+2	+9	+2	-15	-17	+22	+56
RADINC	0	-2	+10	+1	+1	-1	-1
XTINCO	0	+1	-34	-29	-21	-48	-54
Plus 50%							
Q	-8	-8	+27	-21	-15	-12	-10
T	+10	-13	-36	-50	-40	+26	+43
RADINC	0	-4	+18	+1	+1	-2	-2
XTINCO	+1	-23	-58	-57	-58	-83	-84
Minus 20%							
Q	+3	+4	-15	+14	+8	+5	+1
T	-3	-6	+10	-71	-75	-66	-70
RADINC	-1	+4	-16	-3	-2	+1	0
XTINCO	0	+11	+24	+70	+56	+4	+55
Minus 50%							
Q	+9	+11	-43	+42	+21	+14	-10
T	-4	-5	-43	-95	-91	-96	-97
RADINC	0	-6	-48	-20	-12	+5	0
XTINCO	0	+2	-46	+524	+897	-90	+768

TABLE E-2. RESULTS OF SENSITIVITY ANALYSES FOR EXTERNAL FORCING FUNCTIONS - ANNUAL INTEGRATED GROSS PRODUCTION

Parameter Varied	Percent Change in Annual Integrated Gross Production Relative to Final Calibration				
	Diatoms	Greens	Others	Blue-Greens (Non-N_2)	Blue-Greens (N_2)
Plus 20%					
Q	+3	-10	-4	-6	-4
T	-4	+11	+5	+42	+120
RADINC	+2	+1	+1	-1	0
XTINCO	-11	-25	-21	-46	-55
Plus 50%					
Q	+8	-19	-8	-11	-12
T	-13	-30	+6	+106	+243
RADINC	+3	+2	+1	-1	-2
XTINCO	-23	-61	-61	-85	-84
Minus 20%					
Q	-3	+15	+6	+8	+1
T	+13	-68	-62	-74	-78
RADINC	-3	-3	-2	+1	0
XTINCO	+11	+62	+69	-12	+141
Minus 50%					
Q	-8	+51	+17	+26	-12
T	-9	-96	-92	-99	-90
RADINC	-11	-20	-12	+5	-2
XTINCO	+5	+308	+466	-94	+615

TABLE E-3. RESULTS OF SENSITIVITY ANALYSES FOR PHYTOPLANKTON GROWTH RATE COEFFICIENTS - PEAK CROPS

	Percent Change in Peak Crops Relative to Final Calibration						
		Diatoms					
Variation in RAMAX	Total Zoo	Spring	Fall	Greens	Others	Blue-Greens (Non-N_2)	Blue-Greens (N_2)
Plus 50%							
All Phytoplankton	0	+10	-10	+280	+414	-54	+604
Diatoms, Greens, Others Only	0	+10	+21	+477	+607	-84	-40
Blue-Greens only	0	0	+7	-82	-70	+70	+186
Minus 50%							
All Phytoplankton	+1	-43	-54	-77	-84	-93	-94
Diatoms, Greens, Others Only	+1	-43	-59	-88	-91	+27	-9
Blue-Greens Only	0	0	+11	+53	+32	-95	-88

TABLE E-4. RESULTS OF SENSITIVITY ANALYSES FOR PHYTOPLANKTON GROWTH RATE COEFFICIENTS - ANNUAL INTEGRATED GROSS PRODUCTION

Variations in RAMAX	Percent Change in Annual Integrated Gross Production Relative to Final Calibration				
	Diatoms	Greens	Others	Blue-Greens (Non-N_2)	Blue-Greens (N_2)
Plus 50%					
All Phytoplankton	+3	+158	+248	-68	+590
Diatoms, Greens, Others Only	+12	+311	+364	-83	-40
Blue-Greens Only	0	-76	-59	+39	+283
Minus 50%					
All Phytoplankton	-27	-82	-84	-94	-94
Diatoms, Greens, Others Only	-28	-90	-89	+26	-14
Blue-Greens Only	+2	+85	+45	-95	-93

TABLE E-5. RESULTS OF SENSITIVITY ANALYSES FOR MISCELLANEOUS COEFFICIENTS - PEAK CROPS

	Percent Change in Peak Crops Relative To Final Calibration						
		Diatoms				Blue-Greens	Blue-Greens
Coefficient Varied	Total Zoo	Spring	Fall	Greens	Others	(Non-N_2)	(N_2)
Plus 50%							
R1PM	0	0	0	0	0	0	0
R1NM	0	+13	+10	+14	-1	+6	+12
P-Uptake Half-Saturation Concentration	0	-8	-76	+66	-95	+6	-87
N-Uptake Half-Saturation Concentration	0	+10	-19	-15	-10	-12	-17
KSCM	0	0	0	+4	+5	0	+1
SSA	-9	-23	-1	+4	+4	+7	+9
RADSAT	-1	+10	-30	-7	-4	+2	0
ASINK	-2	+3	-10	-2	-1	-12	-17
RLYS	0	-4	-2	+4	-1	-25	-27
RRESP	-6	+5	-9	-12	-16	-54	-68
RZMAX	+65	-10	-39	-71	-52	+25	+24
ZASSIM	+69	+2	-27	-50	-30	+16	+16
KZSAT	-10	0	+14	+128	+126	-37	-26
AZMIN	0	+5	-11	+9	+12	-6	-4
BDETH	-12	-2	+12	+48	+38	-10	-6
PDETH	-29	-2	+6	+68	+62	-25	-22
RTOP, RTON, RTOS	+1	0	+6	+2	+2	+2	-3
TOPSNK, TONSNK, TOSSNK	0	-1	-3	0	0	-1	0
Minus 50%							
R1PM	0	0	0	0	0	0	0
R1NM	-1	+4	-37	-38	-15	-38	-33
P-Uptake Half-Saturation Concentration	0	0	0	0	0	0	0
N-Uptake Half-Saturation Concentration	0	+12	+13	+6	-7	+14	+22
KSCM	0	0	-1	-4	-5	0	-2
SSA	+12	+70	0	-17	-11	-21	-29
RADSAT	0	-4	+26	+2	+2	-3	-4
ASINK	+2	0	+11	+4	+2	+12	+17
RLYS	+2	+4	+7	-10	-4	+35	+50
RRESP	+4	+6	+7	-24	-8	+37	+116
RZMAX	-49	+11	+6	+393	+746	-96	-84
ZASSIM	-58	+8	+23	+348	+540	-88	-73
KZSAT	+13	+2	-41	-77	-64	+23	+16
AZMIN	0	+9	0	-15	-22	+9	+4
BDETH	+11	+3	-16	-38	-34	+10	+6
PDETH	+79	+4	-10	+6	-17	+14	+15
RTOP, RTON, RTOS	-1	-4	-6	0	+1	-4	+1
TOPSNK, TONSNK, TOSSNK	0	+2	+3	+1	0	+1	-1

TABLE E-6. RESULTS OF SENSITIVITY ANALYSES FOR MISCELLANEOUS COEFFICIENTS - ANNUAL INTEGRATED GROSS PRODUCTION

Coefficient Varied	Percent Change in Annual Integrated Gross Production Relative to Final Calibration				
	Diatoms	Greens	Others	Blue-Greens (Non-N_2)	Blue-Greens (N_2)
Plus 50%					
R1PM	0	0	0	0	0
R1NM	+4	+11	0	+3	+11
P-Uptake Half-Saturation Concentration	-15	+59	-91	+11	-94
N-Uptake Half-Saturation Concentration	-4	-9	-5	-7	-16
KSCM	-2	+3	+4	+1	+1
SSA	-27	+6	+5	+10	+8
RADSAT	-6	-7	-4	+1	0
ASINK	-2	-1	-1	-11	-15
RLYS	0	+14	+6	-10	-25
RRESP	-3	+9	-3	-41	-61
RZMAX	-14	-55	-44	+25	+21
ZASSIM	-9	-41	-30	+16	+15
KZSAT	+5	+102	+103	-36	-18
AZMIN	+1	+22	+18	-6	-2
BDETH	+3	+31	+25	-11	-6
PDETH	+4	+66	+70	-25	-16
RTOP, RTON, RTOS	+6	+5	+2	+6	+2
TOPSNK, TONSNK, TOSSNK	-2	-2	-2	-3	-4
Minus 50%					
R1PM	0	0	0	0	0
R1NM	-10	-34	-14	-33	-36
P-Uptake Half-Saturation Concentration	0	0	0	+1	-17
N-Uptake Half-Saturation Concentration	+4	+1	-1	+9	+19
KSCM	+4	-4	-4	-1	-2
SSA	+79	-22	-18	-26	-26
RADSAT	+4	+3	+1	-2	-3
ASINK	+2	+2	+3	+11	+15
RLYS	+1	-19	-8	+8	+43
RRESP	+2	-25	-1	+7	+106
RZMAX	+8	+277	+428	-94	-75
ZASSIM	+8	+248	+342	-87	-60
KZSAT	-12	-58	-48	+22	+12
AZMIN	-2	-25	-24	+7	+1
BDETH	-3	-28	-23	+9	+4
PDETH	-9	-35	-20	+16	+16
RTOP, RTON, RTOS	-6	-5	-1	-8	-11
TOPSNK, TONSNK, TOSSNK	+2	+3	+2	+4	+3

TABLE E-7. SUMMARY OF AVERAGE RESPONSES TO SENSITIVITY ANALYSES

Parameter Varied	Average Absolute Percent Change for all Phytoplankton Groups in Response to ± 50 Percent Variation	
XTINCO	180	
RAMAX	145	
RZMAX	104	
ZASSIM	86	
RRESP	82	
T	78	
KZSAT	42	
P-Uptake Half-Saturation Concentration	29	
PDETH	28	
SSA	22	(53 for diatoms)
Q	17	
R1NM	16	
RLYS	14	
TOPSNK, TONSNK, TOSSNK	14	
BDETH	14	
AZMIN	11	
RADSAT	8	
N-Uptake Half-Saturation Concentration	8	
KSCM	8	
ASINK	6	
RADINC	6	
RTOP, RTON, RTOS	5	
R1PM	0	