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PHYTOPLANKTON-ENVIRONMENTAL INTERACTIONS IN RESERVOIRS

Volume I

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10-12 APRIL 1979,
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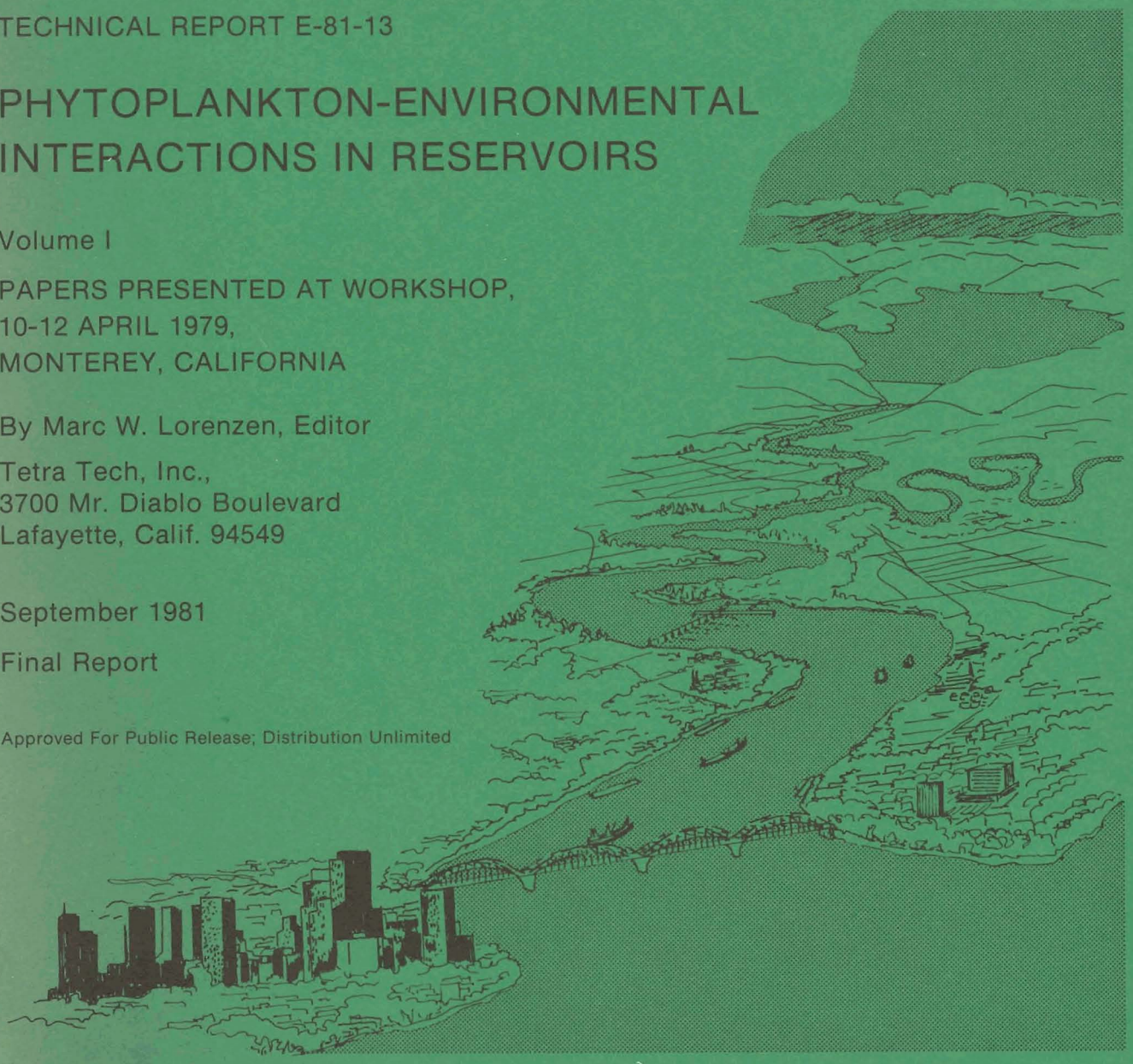

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The formal papers (Volume I of this report) include an introduction describing the purpose and scope of the Waterways Experiment Station

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Environmental and Water Quality Operational Studies (EWQOS) research program, followed by technical papers. Volume II of this report includes a discussion of the workshop papers and open literature.

The first paper, by Bierman, provides a review of processes and formulations related to nutrient kinetics with emphasis on the comparison between fixed and variable stoichiometry models. The next paper, by Goldman, reviews current knowledge and practice related to the effects of temperature on phytoplankton behavior. The third paper, by Lehman, provides a discussion of current and suggested approaches to modeling zooplankton-phytoplankton interactions. The relative importance of mass transport as compared to kinetic factors using both theoretical concepts and field data is discussed by Di Toro. Megard discusses the importance of light and its relation to mixed depth in controlling algal production. A review of current models and approaches to combining the various ecological processes is provided by Park and Collins. A paper by Scavia then provides some important perspectives on the use and interpretation of model results. Particular attention is given to transfer rates between state variables.

The remaining papers provide background on reservoir behavior and use of bioassay techniques. Harris relates the importance of physical and nutrient conditions to phytoplankton production in Hamilton Harbour. Nitrogen fixation rates in two southwestern reservoirs are described by Lawley. Kimmel and White provide an initial evaluation of DCMU-enhanced chlorophyll fluorescence as an indicator of phytoplankton physiological status. Poppe et al. provide a brief review of phytoplankton effects on reservoir use and Porcella and Cleave provide a review and comments on the use of algal bioassays.

Taylor et al., Lambou et al., and Hern et al. provide a description and analysis of data from the U. S. Environmental Protection Agency National Eutrophication Survey related to phytoplankton and temperature, nutrients, and light attenuation.

Taken as a whole, the workshop papers provide a perspective on the current state of the art in reservoir phytoplankton evaluations.

PREFACE

The compilation of papers presented herein represents the formal contributions of participants in the workshop on phytoplankton-reservoir interactions held 10-12 April 1979 in Monterey, Calif. The workshop was sponsored by the U. S. Army Engineer Waterways Experiment Station (WES) and conducted by Tetra Tech, Inc.

The purpose of the workshop was to provide current discussion related to:

a. understanding the important or key phytoplankton-reservoir interactions

b. determining whether these factors are incorporated in existing phytoplankton algorithms, and

c. identifying areas requiring additional research.

The formal papers (Volume I of this report) include an introduction describing the purpose and scope of the Waterways Experiment Station Environmental and Water Quality Operational Studies (EWQOS) research program, followed by technical papers. Volume II of this report includes a discussion of the workshop papers and open literature.

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During the conduct of this study and preparation of the report Commanders and Directors of WES were COL J. L. Cannon, CE, and COL N. P. Conover, CE. Technical Director was Mr. F. R. Brown.

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INTRODUCTION

Kent W. Thornton
Environmental Laboratory
USAE Waterways Experiment Station

Reservoirs have historically been constructed to store water for flood control, water supply, irrigation, power production, or other purposes requiring water storage. Design and management criteria have generally been directed toward determining reservoir yield, reservoir capacity, sediment trap efficiency, and other procedures designed to provide for better water quantity management.

Reservoir water quality has also become important in recent years for recreational and aesthetic reasons, reduced water treatment costs, improved reservoir releases, the requirements of legislative acts, and other reasons. In October 1977, the U. S. Army Corps of Engineers (CE) initiated Environmental and Water Quality Operational Studies (EWQOS) under the sponsorship of the Office, Chief of Engineers, and management of the U.S. Army Engineer Waterways Experiment Station (WES). EWQOS is a six-year, $30 million program of applied research designed to address many of the water quality problems associated with CE water resources projects, including both reservoirs and waterways. The fundamental objective of EWQOS is to provide new or improved technology to solve selected environmental quality problems associated with CE Civil Works activities in a manner compatible with authorized project purposes.

EWQOS ORGANIZATION

EWQOS is divided into two major interactive components--research projects and field studies. Six research project areas are supported

by reservoir or waterway field studies (Table 1). Projects I-III interact with the reservoir field studies while Projects IV-VI interact with the waterways field studies. Theoretical, developmental, and laboratory research will be conducted in the research project areas to address specific environmental quality problems such as resolubilization of phosphorus under anoxic conditions, denuded shorelines due to fluctuating water levels, or the impact of bendway cutoffs on fish productivity. The field experiments are designed to supplement, test, and corroborate research project results, and provide a system for testing various control or management techniques such as destratification or hypolimnetic aeration.

This workshop focused primarily on the reservoir portion of EWQOS and Projects I and II. There are three objectives of EWQOS reservoir research: (a) to improve the understanding and description of important ecological processes in CE impoundments including the cause-effect relations between the design and operation of reservoirs and water quality; (b) use this increased understanding of ecological processes to develop, improve, and verify predictive techniques such as mathematical reservoir ecological models; and (c) develop and modify methods to manage various water quality constituents or processes such as nuisance algae blooms or anoxic hypolimnia.

PHYTOPLANKTON-ENVIRONMENTAL INTERACTIONS IN RESERVOIRS

Since many of the water quality and environmental problems occurring in CE reservoirs result directly or indirectly from phytoplankton blooms, it is important to understand the factors and interactions responsible for the onset, duration, and magnitude of phytoplankton blooms. It is also important to understand some of the interactions among species and environmental factors producing successional changes

Table 1. EWQOS Summary

PROJECT TITLE	TASK AREA TITLE	PROJECT/TASK AREA OBJECTIVE
I. Predictive Techniques for Determining Environmental Effects		Provide reliable methods for predicting environmental effects and evaluating water quality objectives of planning, design, and operational alternatives of CE projects.
	IA. Reservoir Hydrodynamics	Develop, improve, and verify methods for describing and predicting the hydrodynamics of reservoirs to provide a basis for improved understanding of water quality and ecological variables affecting environmental quality objectives.
	IB. Improved Description of Ecological and Water Quality Processes	Develop improved understanding and techniques for determining important biological and chemical processes in reservoirs and rivers.
	IC. Mathematical Water Quality and Ecological Predictive Techniques	Develop and verify techniques incorporating biological, chemical and hydrodynamic descriptions for application to predict and evaluate environmental quality problems.
	ID. Determination of Loadings to Reservoirs	Develop and evaluate techniques for predicting loadings to CE reservoirs.
	IE. Simplified Techniques for Predicting Reservoir Water Quality and Eutrophication Potential	Evaluate existing simplified and empirical techniques for predicting water quality and eutrophication potential to determine their applicability to reservoirs and provide a basis for adaptation for CE reservoir applications.
II. Reservoir Operational and Management Techniques to Meet Environmental Quality Objectives		Provide new or improved reservoir operation and management procedures for the attainment of environmental quality objectives.
	IIA. Management of Nuisance Algal Blooms in Reservoirs	Determine the factors responsible for nuisance algal growths in CE reservoirs and develop operational and management techniques for control of nuisance algal growths.

Table 1. EWQOS Summary (Continued)

PROJECT TITLE	TASK AREA TITLE	PROJECT/TASK AREA OBJECTIVE
	IIB. Guidelines for Determining Reservoir Releases to Meet Environmental Quality Objectives	Develop and evaluate environmental criteria and operational methods to achieve reservoir releases required to maintain desirable downstream aquatic habitat.
	IIC. Operational and Management Strategies for Reservoir Contaminants	Develop and evaluate operational and management techniques to minimize adverse environmental effects of major contaminants on reservoir project purposes.
	IID. Reservoir Regulation Techniques for Water Quality Management	Develop and evaluate general operational techniques for reservoir regulation.
	IIE. Environmental Effects of Fluctuating Reservoir Water Levels	Develop planning and operational guidance to minimize adverse environmental effects of fluctuating reservoir water levels.
	IIF. Reservoir Site Prepatation	Determine the most environmentally compatible strategies for reservoir site preparation, clearing, and initial filling.
III. Engineering Techniques for Meeting Reservoir Water Quality Objectives		Provide new or improved design guidance and engineering technology for reservoir projects to meet environmental quality objectives.
	IIIA. Techniques to Meet Environmental Quality Objectives for Reservoir Releases	Develop improved mixing, reaeration, and selective withdrawal techniques to achieve reservoir release water quality objectives.
	IIIB. In-Reservoir Techniques for Improvement of Environmental Quality	Develop improved techniques for enhancing reservoir water quality through mixing, aeration/oxygenation, destratification, and selected lake rehabilitation methods.
	IIIC. Techniques for Inflow Management and Control of Loadings to Reservoirs	Develop engineering technology and design guidance for inflow management and control of contaminant loadings to reservoirs.

Table 1. EWQOS summary (Continued)

PROJECT TITLE	TASK AREA TITLE	PROJECT/TASK AREA OBJECTIVE
IV. Environmental Assessment Techniques for Project Planning and Operational Requirements		Improve procedures for environmental assessment related to planning and operational requirements of CE activities.
	IVA. Evaluation and Improvement of Environmental Assessment Techniques	Improve techniques required for performing environmental assessments.
	IVB. Data Management and Indices for Environmental Assessments	Provide planning and operational guidance on data requirements and management systems for environmental assessments and impact statements.
V. Environmental Impacts of Waterway Activities		Develop and refine techniques to adequately assess and quantify the environmental impacts resulting from selected CE waterway activities.
	VA. Environmental Impact of Selected Channel Alignment and Bank Revetment Alternatives on Waterways	To quantify the environmental effects of projects for channel alignment and bank revetment in major river systems regarding the alternation of aquatic habitats, fish populations, and water quality, and to provide recommendations for enhancing the environmental quality aspects of these projects.
	VB. Impacts of Navigations Activities on Waterways	To evaluate the environmental impacts of selected navigation projects, and to provide recommendations for resource management at these projects.
VI. Waterway Project Design and Operation for Meeting Environmental Objectives		Provide new or improved guidance for design, construction, and operation of waterway projects to achieve environmental quality objectives.

Table 1. EWQOS summary (Continued)

PROJECT TITLE	TASK AREA TITLE	PROJECT/TASK AREA OBJECTIVE
	VIA. Operational Procedures for Waterway Projects to Attain Environmental Quality Objectives	Evaluate and improve operational procedures for waterway projects.
	VIB. Design and Construction Techniques for Waterway Projects to Attain Environmental Quality Objectives	Provide new or improved guidance for design and construction of waterway projects.

in the plankton assemblage. Visual surface accumulations of phytoplankton, taste and odor problems following the senescence of a bloom, and other conditions perceived by the public to be problems must be understood before realistic and cost-effective control techniques can be developed and applied.

Many mathematical formulations and computer algorithms presently exist to simulate the complex biological, chemical, and physical interactions involved in phytoplankton dynamics, yet the predictive capability of most algorithms, under a variety of conditions, is minimal. This is a function of at least two factors: the diffuse nature of information on these interactions and the general insufficiency of knowledge in reservoir phytoplankton ecology.

WORKSHOP OBJECTIVES

The specific objectives of the Workshop on Phytoplankton-Environmental Interactions in Reservoirs were:

a. To discuss current research on phytoplankton ecology

b. To identify the important phytoplankton-environmental interactions in reservoirs

c. To determine if these factors or interactions are incorporated in existing phytoplankton algorithms

d. To identify areas requiring additional research

POTENTIAL APPLICATIONS OF WORKSHOP INFORMATION

Information obtained in the workshop will be used in designing laboratory and field experiments. These experiments will investigate those processes and interactions that workshop participants believe are central to a better understanding of phytoplankton dynamics and the factors regulating phytoplankton populations. Furthermore, the experimental results will be incorporated in the EWQOS research projects developing improved predictive techniques and environmentally compatible control procedures and influence research in related areas.

The CE must prepare an assessment of environmental impact associated with proposed operational changes in all existing reservoirs and in the creation of new reservoirs. In this regard, questions posed by regulatory agencies generally concern the potential for increased eutrophication and nuisance phytoplankton blooms. Techniques are required to predict the potential magnitude, frequency, and timing of algal blooms. This information is required to evaluate the detrimental effects on project purposes such as recreation, water supply, fish and wildlife enhancement, and other purposes. Since the results of these predictions will influence decisions concerning the desirability of multimillion dollar projects, it is also important to know the accuracy, precision, and validity of these estimates. Current models may not have a resolution greater than the prediction of seasonal succession for plankton divisions or a magnitude of $\pm$ 100% of observed plankton concentrations. However, it is important that decisionmakers have an accurate and realistic assessment of modeling capabilities.

It is hoped the workshop has initiated a continuing dialogue among participants on phytoplankton-environmental interactions in reservoirs.

PHYTOPLANKTON-NUTRIENT KINETICS MECHANISMS IN MATHEMATICAL SIMULATION MODELS, WITH SPECIAL ATTENTION TO RESERVOIRS AND IMPOUNDMENTS

by

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INTRODUCTION

Accelerated rates of eutrophication in reservoirs and impoundments have become a major water quality issue (Ackermann et al. 1973). Excessive phytoplankton growth interferes with the uses of these water bodies as sources for drinking water and water recreation. Nutrient sources can include, but are not limited to, agricultural runoff, runoff from livestock feeding activities, and discharges from wastewater treatment plants. Some of the consequences of excessive nutrient enrichment include filter-clogging and taste and odor problems in water treatment plants and thick algal scums and fish kills which interfere with recreational uses.

To develop management strategies for dealing with the problems caused by nutrient enrichment, a quantitative connection must be made between causes (external loads) and effects (concentrations of nutrients and phytoplankton in the water body). Mathematical simulation models have been developed for this purpose and have been applied to a wide variety of water bodies, including reservoirs and impoundments (Bierman et al. 1973, 1979; DiToro and Matystik 1979; Anderson et al. 1976; Canale et al. 1976; Hydroscience 1976; Thomann et al. 1975; Baca et al. 1974; O'Connor et al. 1973; Larsen et al. 1973; Chen and Orlob 1972). All of these models include dynamic mass balance equations for phytoplankton concentration which contain individual terms for phytoplankton production rates and phytoplankton loss rates in the water column. Phytoplankton production rate is a function of the ambient temperature, light, and nutrient levels.

The purpose of this paper is to review the various formulations that have been used to describe phytoplankton-nutrient kinetics in deterministic simulation models. The rationale and assumptions of each formulation are discussed, along with the data required to implement each formulation. Special attention is given to the nutrient

recycle characteristics of the various formulations and to nutrient interaction effects in cases where there is more than one potential limiting nutrient.

SCOPE

The scope of this review is restricted to phytoplankton-nutrient kinetics under optimum temperature and light conditions. Most of the discussion involves phosphorus and nitrogen because of their overwhelming importance to the issue of eutrophication. Silicon is briefly discussed because of its role as a potential limiting nutrient to diatoms. Although carbon constitutes a larger proportion of phytoplankton biomass than either phosphorus or nitrogen, phytoplankton-carbon kinetics are not discussed. The *in situ* results by Schindler *et al*. (1973a, 1973b) in the Canadian Shield and the laboratory results by Goldman *et al*. (1974) indicate that only under conditions of extreme nutrient enrichment will carbon be important in limiting phytoplankton growth rates.

PHYTOPLANKTON-NUTRIENT KINETIC MECHANISMS: PHOSPHORUS AND NITROGEN

Fixed Stoichiometry Models

The most widely used mechanism for calculating specific growth rates in phytoplankton simulation models is the hyperbolic equation by Monod (1949)

$$\mu_{sp} = \mu_{max} \frac{S}{K_s + S} \tag{1}$$

where μ_{sp} is specific growth rate, μ_{max} is maximum growth rate, S is the nutrient concentration in the water column, and K_s is the half-saturation constant. The basis for the development of this mechanism

was the observation that specific growth rates for bacteria could be related to the concentration of a carbon substrate by a hyperbolic function. This mechanism was later adopted for describing the specific growth rates of phytoplankton as a function of phosphorus and nitrogen concentrations. The Monod equation has been used in many different simulation models (Canale et al. 1976; Scavia et al. 1976; Thomann et al. 1975; Larsen et al. 1973; Chen and Orlob 1972), as well as for the interpretation of laboratory kinetics data (Middlebrooks and Porcella 1971; Schelske et al. 1974). 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 the stoichiometric composition of the phytoplankton cells remains constant as the concentration of the limiting nutrient changes in the external medium. A corollary to this assumption is that specific growth rate is directly coupled to this external concentration. The processes of nutrient uptake and cell growth are assumed to be coupled over the entire range of nutrient concentrations. An instantaneous change in external concentration corresponds to the production of phytoplankton biomass in a fixed ratio, or yield.

The principal advantage of the Monod equation is its simplicity. It is strictly an empirical equation which does not explicitly include any of the complex physiological processes occurring at the cellular level. Only two coefficients need to be determined to apply the Monod equation: μ_{max} and K_s. In practice, values for these coefficients are usually determined from bioassays on the system of interest or by simply starting with a range of reported values from the literature and then calibrating the model to the available field data.

Variable Stoichiometry, Cell Quota Models

Over the past ten years, results from an increasingly large body

of experimental evidence have challenged the basic assumptions of the Monod equation as applied to phosphorus and nitrogen limited phytoplankton growth. It is now generally recognized that the processes of nutrient uptake and cell growth are actually quite distinct and that growth rates are controlled by intracellular nutrient levels instead of by external concentrations (Rhee 1973, 1974, 1978; Droop 1968, 1973, 1974; Caperon and Meyer 1972a, 1973b; Fuhs 1969; Fuhs et al. 1972; Eppley and Thomas 1969; Azad and Borchardt 1970). These results have led to the development of so-called cell quota models.

From the results of the various preceding studies, it has been found that specific growth rate is related to the internal level of the limiting nutrient by a hyperbolic function

$$\mu_{sp} = \mu_{max} \frac{(q - q_o)}{K_q + (q - q_o)} \tag{2}$$

where q is the total cellular level of the limiting nutrient, q_o is the minimum stoichiometric requirement, or cell quota, and K_q is a half-saturation constant. For phosphrous and nitrogen, Rhee (1973, 1978) has shown that $K_q = q_o$. In this case $\mu_{sp} = \mu_{max}/2$ when $q = 2q_o$ and Eq. 2 similifies to

$$\mu_{sp} = \mu_{max} \left(1 - \frac{Kq}{q}\right) \tag{3}$$

This equation is generally referred to as the Droop cell quota model after the original results by Droop (1968) on vitamin B_{12} limitation on *Monochrysis lutheri*.

In contrast to the Monod equation, the basic assumption of cell quota models is that the stoichiometric composition of the phytoplankton cells varies as a function of the balance between nutrient uptake rate and cell growth rate. In cell quota 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. This so-called "luxury uptake" phenomenon can occur because the time constants for nutrient uptake are on a scale of hours and the time constants for phytoplankton growth are on a scale of days.

The principal advantage of cell quota models is that they realistically describe the experimentally observed mode of cell growth without including any of the actual biochemical complexity. As with the Monod equation, only two coefficients need to be determined to apply the Droop cell quota model: μ_{max} and K_q (= q_o). In practice, values for these coefficients can be determined in a manner similar to the coefficients for the Monod equation.

Cell quota models cannot be used directly in phytoplankton simulation models because they do not describe the functional relationship between specific growth rate and external nutrient concentration. Furthermore, cell quota models are only valid under steady-state conditions and simulation models must be capable of describing dynamic conditions.

Cell quota models can be adapted for use in phytoplankton simulation models by first considering the relationship between internal nutrient levels and nutrient uptake rates. At steady-state, nutrient uptake rate is equal to cell growth rate because the value of q is constant. This equivalence can be expressed by the equation

$$V_{sp} = \mu_{sp}\, q \qquad (4)$$

where V_{sp} (mass $\cdot$ cell^{-1} $\cdot$ time^{-1}) is the specific nutrient uptake rate. Also at steady-state, the relationship between specific nutrient uptake rate and the external nutrient concentration has been observed to follow Michaelis-Menten kinetics (Rhee 1973; Eppley et al. 1969; Dugdale 1967)

$$V_{sp} = V_{max} \frac{S}{K_M + S} \tag{5}$$

where V_{max} (mass $\cdot$ cell^{-1} $\cdot$ time^{-1}) is the maximum uptake rate and K_M is the Michaelis constant or half-saturation concentration.

It is important to recognize that Eq. 5 will describe the correct relationship between V_{sp} and S only if q is held constant. Corresponding to each value of q, that is, to each steady-state, a unique hyperbolic relationship will be obtained. A family of different hyperbolae can be obtained, each corresponding to one of the possible steady-states for a given system. Rhee (1973) has shown that for the case of phosphorus uptake by *Scenedesmus,* cells at various steady-states have a common half-saturation concentration, K_M, and different maximum uptake rates, V_{max}. V_{max} was observed to decrease with increasing internal phosphorus, q. In the limit as q approaches the minimum cell quota, q_o, V_{max} approaches the true physiological maximum uptake rate. In the opposite limit as q approaches its maximum physiological limit for the particular system, V_{max} approaches its minimum values.

The notion of V_{max} as a variable which corresponds to local maxima instead of to a unique physiological rate is a point of some confusion. It is perhaps convenient to define an operational V_{max} which corresponds to the maximum uptake rate which can occur under a given set of experimental conditions. In the context of phytoplankton simulation models, however, it is more useful to consider the true physiological maximum uptake rate because such models must be capable of describing conditions over the entire range of all possible steady-states.

A relationship between specific growth rate and external nutrient concentration can now be established by combining Eqs. 3-5; however, the result will only be valid for constant q, that is at steady-state. Some method must be devised to account for the observed variation in

V_{max} as the internal nutrient level changes. Droop (1974) has discussed this problem with the use of Michaelis-Menten kinetics for nutrient uptake and has pointed out that some form of feedback or "product control" is necessary. Since the Michaelis-Menten equation describes a unidirectional reaction with no equilibrium state, uptake rate is a function only of the external nutrient concentration and there is no provision for nutrient control. One consequence of using Eq. 5 for nutrient uptake would be the infinite accumulation of non-limiting nutrients in the phytoplankton cells. Clearly, this is not physiologically possible.

Variable Stoichiometry, Internal Pool Models

Recently there have been several attempts to combine the cell quota concept for steady-state conditions with modified dynamic equations for nutrient uptake. The resulting so-called internal pool models are capable of correctly describing the limiting behavior of nutrient uptake rates as a function of changes in internal nutrient levels. Various internal pool models have been used in theoretical as well as applied phytoplankton simulation models (Koonce and Hasler 1972; Bierman *et al.* 1973, 1979; Bierman 1976; Lehman *et al.* 1975; Jorgensen 1976; Nyholm 1978; Desormeau 1978). These formulations differ primarily in the feedback mechanisms used to adjust the maximum nutrient uptake rates in response to changes in internal nutrient levels.

Koonce and Hasler (1972) proposed a modification of Michaelis-Menten kinetics using a linear correction factor

$$V_{sp} = V_{max} (q_m - q) \frac{S}{K_M + S} \qquad (6)$$

where q_m is the maximum internal nutrient level. Lehman *et al.* (1975) proposed a different modification of Michaelis-Menten kinetics using a ratio correction factor

$$V_{sp} = V_{max} \frac{(q_m - q)}{(q_m - q_o)} \frac{S}{K_M + s} \tag{7}$$

Eq. 7 was also used by Jorgensen (1976). Nyholm (1978) arbitrarily specified an uptake rate as a function of the transition range between limiting and non-limiting conditions. He used either discontinuous or continuous functions, depending on the particular application. All of these nutrient uptake mechanisms are primarily empirical because they are not based directly on knowledge of the physiological processes involved.

Several workers have proposed nutrient uptake mechanisms which are based on knowledge of the physiological processes involved. Rhee (1973) has suggested that phosphorus uptake rate could be described by an equation used for non-competitive enzyme inhibition

$$V_{sp} = \frac{V_{max}}{(1 + K_M/S)\ (1 + i/K_i)} \tag{8}$$

where i is the inhibition concentration and K_i is a constant expressing the degree of inhibition. Desormeau (1978) has adopted this mechanism for use in a refinement to the aquatic ecosystem model CLEANER. Lehman et al. (1975) rejected this mechanism because data are generally not available for the required inhibition coefficients. Bierman et al. (1973, 1979) have proposed a nutrient uptake mechanism which involves carrier-mediated transport using reaction-diffusion kinetics

$$V_{sp} = V_{max} \left[\frac{1}{1 + (PK1)\ (S_{int})} - \frac{1}{1 + (PK1)\ (S_{ext})} \right] \tag{9a}$$

$$S_{int} = S_{min}\ e^{(q/q_o - 1)} \tag{9b}$$

where S_{int} is the internal nutrient concentration, S_{ext} is the exter-

nal nutrient concentration, S_{min} is the minimum internal nutrient concentration and PK1 is an affinity coefficient. The quantity PK1 has physical significance because it is the equilibrium constant for the reaction between the nutrient 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).

The principal advantage of using internal pool models is that the experimentally observed modes of phytoplankton nutrient uptake and growth can be described over the full range of dynamic conditions that occur in the natural environment. An obvious disadvantage is additional complexity in terms of data requirements and computation. Not including the coefficients which must be determined for the growth components of the preceding models, three independent coefficients must be determined to use Eqs. 6, 7, and 9, and four independent coefficients must be determined to use Eq. 8. Since most phytoplankton simulation models already contain coefficients for which direct measurements are not available, the additional degrees of freedom imposed by the use of internal pool models can confound the interpretation of the model results.

Criteria for choosing between the Monod equation and internal pool models are not well-established because only a few internal pool models have been used in actual applications. Jorgensen (1976) compared the results of a simulation model based on Monod kinetics to the results of a simulation model based on internal pools using data from a Danish lake. He concluded that the internal pool model gave a more accurate description of the system dynamics. DiToro and Connolly (1979) pointed out that one of the problems with fixed stoichiometry models is that it is not always possible to obtain a good fit to the data for phytoplankton biomass and the concentration of a limiting nutrient simultaneously over the entire annual cycle. This occurs because if the phytoplankton nutrient stoichiometry is specified to

correspond to the minimum cell quota, then a good fit will be ensured only during periods of nutrient limitation. During periods when the nutrient is non-limiting, the phytoplankton biomass will tend to be overestimated. Canale et al. (1976) experienced this difficulty for phosphorus in the application of a fixed stoichiometry model to Grand Traverse Bay, Lake Michigan. The dissolved phosphorus concentration varied by a factor of four over the annual cycle in the bay. Healey and Hendzel (1976) reported that internal phosphorus levels varied from 1-8 μg P/mg algae in response to a variation from 10-50 μg/ℓ of dissolved phosphorus in several Canadian prairie lakes. Variations in dissolved phosphorus concentrations of even greater magnitudes are common occurrences in reservoirs and impoundments (e.g., Huang et al. 1973; Baca et al. 1974). It would appear that large seasonal variations in limiting nutrient concentrations are an important criterion in the selection of an appropriate phytoplankton kinetics mechanism.

RECYCLE KINETICS MECHANISMS: PHOSPHORUS AND NITROGEN

Consideration of nutrient recycle kinetics is an often overlooked, yet extremely important, criterion for choosing between fixed and variable stoichiometry models. It should be recognized that the choice of a phytoplankton growth kinetics mechanism always includes an implicit choice of a mechanism for nutrient recycle.

Upon cell death due to grazing, decomposition, cell lysis, etc., nutrients can be recycled within the water column and made available for the growth of new phytoplankton. In phytoplankton simulation models, dynamic mass balance equations are usually included for unavailable as well as for available nutrient forms.

In fixed stoichiometry models, recycled nutrients are usually routed to the unavailable nutrient compartment and then converted to available nutrient forms by a temperature-dependent, first-order kinetics mechanism. In variable stoichiometry models, nutrient recycle

consists of two separate components: a component associated with the minimum cell quota and a component associated with the internal nutrient in excess of the minimum cell quota. Such a two-component recycle phenomenon has been observed experimentally for both phosphorus and nitrogen (Foree et al. 1970; DePinto 1974; Rhee 1973). In a variable stoichiometry model, the nutrient component associated with the minimum cell quota is recycled to the unavailable compartment and the nutrient component associated with the excess internal level is recycled directly to the available compartment. This is consistent with evidence that the latter component consists of available nutrient forms and loosely bound compounds which rapidly convert to available forms (Rhee 1973).

Bierman et al. (1979) have applied a multi-class internal pool kinetics model to a comprehensive set of field data from Saginaw Bay, Lake Huron. The results showed that nutrient recycle from the internal pools contributed up to 70 percent of the phosphorus requirements of summer blue-green crops. The peak contribution occurred during the period of minimum external phosphorus loading and minimum available phosphorus concentration in the water column. Using an earlier version of the same model, DePinto et al. (1976) showed that nitrogen recycle from the internal pools of N_2-fixing blue-green algae contributed a substantial portion of the phytoplankton requirements in Stone Lake after the initial spring nitrogen level became depleted. This latter result has particular significance for the situations in enriched reservoirs and impoundments. If fixed stoichiometry models are applied to such systems without including some provision for nitrogen fixation and subsequent recycle, then the interpretation of the model results will be confounded (Baca et al. 1974; Hydroscience 1976).

It might be argued that a fixed stoichiometry model with a single recycle component to the unavailable nutrient compartment could adequately account for the above recycle processes by compensating with a faster conversion rate from unavailable to available forms. Notwithstanding the fact that this is inconsistent with the physiological

processes that are known to be occurring, such an approach can lead to serious difficulties. Phytoplankton-related detritus is only one of the many components which comprise the unavailable nutrient compartments. These compartments 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 is 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 unphysical results for the distribution of the individual nutrient components (Bierman 1977).

A refinement to nutrient recycle kinetics for fixed stoichiometry models was recently proposed by DiToro and Matystik (1979). In this model, nutrient recycle is partitioned into two separate components at a specified constant ratio. As in an internal pool model, one of these components is routed to the unavailable nutrient compartment and the other component is routed to the available nutrient compartment. In addition, the conversion rate from unavailable to available nutrient forms is made a function of total phytoplankton biomass. These modifications have the effect of increasing the recycle rate only during off-peak periods. A problem that still exists with this approach is that there is no mechanism for quantifying changes in internal nutrient levels and, hence, there is no consistent way to specify changes in the ratio of the two recycle components. The dynamic solution of separate uptake and growth equations in an internal pool model avoids these problems, albeit at the expense of additional model complexity.

DiToro and Connolly (1979) have more recently proposed a variable stoichiometry model based on cellular equilibrium partitioning instead of on the solutions to the full dynamic equations. This approximation reduces the computational complexity of the full dynamic equations, yet still retains the features of separate recycle components and

changes in internal nutrient levels in response to changes in external nutrient concentrations.

SILICON KINETICS MECHANISMS

Most of the available data for phytoplankton-silicon kinetics indicate that the Monod equation is valid for relating specific growth rate to external concentrations of silicon. Guillard et al. (1973) and Kilham (1975) reported that the growth rates of silicon-limited diatoms are related to the silicon concentration in the external medium by a hyperbolic equation. Paasche (1973) found a similar hyperbolic relationship, but only after a correction had been made to the dissolved reactive silicon concentration that could apparently not be used by the diatoms tested. Kilham also reported such a "threshold effect"; however, she pointed out that this effect is 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 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, appears to be internally controlled. Davis et al. (1978) have actually proposed an internal pool model to describe their experimental results for a silicon-limited diatom under steady-state and transient conditions.

MULTIPLE LIMITING NUTRIENTS

Growth Kinetics

In models which include more than one potential limiting nutrient, a mechanism must be devised for calculating phytoplankton growth rates

when the levels for both nutrients are non-optimum. The two most widely used approaches have been the multiplicative hypothesis and the threshold hypothesis. These hypotheses are stated in the following manner for the case where growth rate can be limited by either phosphorus or nitrogen

I. Multiplicative

$$\frac{\mu_{sp}}{\mu_{max}} = \frac{(q_p - q_{po})}{K_p + (q_p - q_{po})} \cdot \frac{(q_n - q_{no})}{K_N + (q_n - q_{no})} \tag{10}$$

II. Threshold

$$\frac{\mu_{sp}}{\mu_{max}} = \frac{(q_p - q_{po})}{K_p + (q_p - q_{po})} \qquad \text{when } \frac{q_p}{q_{po}} < \frac{q_n}{q_{no}} \tag{11a}$$

$$\frac{\mu_{sp}}{\mu_{max}} = \frac{(q_p - q_{no})}{K_N + (q_n - q_{no})} \qquad \text{when } \frac{q_n}{q_{no}} < \frac{q_n}{q_{po}} \tag{11b}$$

The question of which hypothesis to use has long been an open one in the literature, although the multiplicative hypothesis has probably been the more popular of the two. Recently, the results of two independent studies have given strong support to the threshold hypothesis (Droop 1974; Rhee 1978). In both of these studies, use of rigorous statistical techniques confirmed that the threshold hypothesis correctly described the data and that the multiplicative hypothesis should be rejected. A third hypothesis based on electrical resistors in parallel has been used by Scavia and Park (1976); however, the validity of this hypothesis has not been tested against experimental data.

Nutrient Uptake Kinetics

An unresolved problem is the interaction among nutrients during the uptake process which has been reported by several workers (Ketchum 1939; Droop 1974; Conway *et al*. 1976). A more general version of the

nutrient uptake mechanism used by Bierman et al. (1979) has been used to investigate several different types of interactions among substrates, including competition for a single carrier molecule (Verhoff and Sundaresan 1972; Verhoff et al. 1973). Presently, there are sufficient data to fully test these hypotheses for phytoplankton-nutrient interactions.

RESEARCH NEEDS

Some of the important unresolved research questions in the area of phytoplankton-nutrient kinetics involve nutrient recycle, nitrogen fixation, silicon kinetics, and nutrient uptake kinetics. More research is needed on the nature of the recycle processes for phosphorus and nitrogen that occur as a result of both predatory and nonpredatory phytoplankton death in the water column. A closely related need is for more research on the factors controlling nitrogen fixation and subsequent recycle of available nitrogen. These recycle processes can supply a substantial portion of the nutrient requirements for summer blooms of nuisance blue-green algae in enriched reservoirs and impoundments. Without adequate knowledge of recycle processes, it is difficult to relate the occurrence of such blooms to external nutrient loadings and ambient nutrient concentrations.

More research is needed on silicon kinetics because systems in which silicon limitation of diatom growth is important can respond differently to phosphorus and nitrogen loads than systems which are not silicon limited. This can occur because the temperature optima and successional patterns for diatoms are generally different than for other phytoplankton types.

More research is needed on the kinetic mechanisms involved in nutrient uptake. Of particular importance is the process of feedback control. Most of the existing models for nutrient uptake are strictly

empirical. Some of the existing models are based on more detailed physiological information. None of these models, however, have been adequately tested on experimental data.

In the general sense, the most urgent research need in the subject area is more experience in the application of phytoplankton simulation models to extensive sets of field data for different types of physical systems. This is the only means of establishing definitive criteria for choosing an appropriate set of phytoplankton-nutrient kinetic mechanisms for a given application. It should be recognized that the practical constraints of budget and time frame will frequently preclude the application of the most sophisticated kinetic models. Accordingly, emphasis should be placed on the further development of kinetic mechanisms which avoid unrealistic data requirements and computational complexity, yet still constitute reasonable approximations of the major dynamic features of the system. Objectives need to be well defined at the outset of a particular application and the inherent assumptions and limitations of the kinetics model used must be respected. Even the simplest kinetic models can be of great value in providing a conceptual framework for experimental design and data interpretation.

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INFLUENCE OF TEMPERATURE ON PHYTOPLANKTON GROWTH AND NUTRIENT UPTAKE

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INTRODUCTION

The role of nutrient limitation in controlling the growth of phytoplankton has been the subject of exhaustive study, dating back to the classical experiments of Ketchum (1939a, b) on phosphorus and nitrogen limitation in the diatom *Nitzschia closterium*. Since that time tremendous progress has been made in our understanding of the nutritional requirements of phytoplankton, particularly the dynamics of nutrient uptake and resulting growth, both at the biochemical and cellular levels.

In nature primary productivity and the distribution of phytoplankton species are controlled, not singularly by nutrient availability, but by a complex web of interacting environmental factors (Braarud 1962). The most obvious of these influencing factors along with nutrients are sunlight and temperature. Both factors strongly influence photosynthetic activity and the former parameter has been relatively well studied. Yet, it is rather amazing that little attention has been given to the role of temperature in regulating photosynthetic and other metabolic activities of primary producers (see p. 86-87 in Parsons and Takahashi 1977). In this regard, the recent review on temperature effects by Eppley (1972) stands out as the only serious attempt to synthesize our knowledge on this subject and to address, with the meager temperature data available, the importance of this environmental parameter in phytoplankton ecology.

In both the oceans and fresh waters, temperature varies over a wide range (-2° to 30+°C), from average surface temperatures of 1°C at latitudes of 60-70°S to >25°C at the equator (Sverdrup et al. 1963). In temperate latitudes of certain coastal regions and in many lakes it is not uncommon to have a 25-30°C variation in temperature over a yearly cycle (e.g., in Vineyard Sound, Cape Cod, Massachusetts, surface water temperatures vary from ∿0° in winter to close to ∿27-28°C in summer - Woods Hole Oceanographic Institution records). What is truly amazing about these geographical and seasonal variations in temperature

is that primary productivity does not seem to be greatly affected by this wide temperature variation (Eppley 1972) and species common to particular geographical environments and seasons have little difficulty in growing, providing nutrients are available (Smayda 1958). For example, blooms of the common neritic diatom *Skeletonema costatum* are typical in temperate coastal waters during the winter when temperatures are between 0°-5°C (Curl and McLeod 1961; Smayda 1973). Similarly, numerous neritic diatoms are common in the northern latitudes, having been classified as coldwater species by Hasle (1976). At the other end of the spectrum, many tropical species exist that appear only when water temperatures rise above 25°C (e.g., *Nannochloris* sp.).

Traditionally, the major problem in studying temperature effects in natural waters is that it is virtually impossible to isolate temperature as a sole influencing factor. This is because, not only does light intensity and duration vary simultaneously with temperature changes, but also because nutrient availability is very closely connected to the structure and intensity of thermoclines. Hence, the objectives of this review are to outline the role of temperature in influencing the cellular processes of photosynthesis, respiration, growth, and nutrient assimilation primarily from existing laboratory experiments, and to synthesize these data with data collected from previous field studies. Hopefully, this review provides clues as to the importance of temperature in regulating biogeographical variations in species composition and primary productivity.

GROWTH RATE KINETICS

Eppley (1972) in his temperature review postulated that "temperature does not seem to be very important in the production of phytoplankton in the sea." He suggested that a reason for this seeming nondependence on temperature is that phytoplankton growth rates in nature are typically well below maximum potential rates, so that temperature

effects are essentially blotted out by other limiting factors. To support this concept he compiled data from the literature on growth rate-temperature responses for many species of marine phytoplankton grown in the laboratory under a variety of batch culture conditions. An enveloping curve representing the highest observed growth rates over a temperature range 0°-40°C was drawn and the empirical equation:

$$\mu_{10} = 0.851\ (1.066)^{t} \qquad (1)$$

was determined in which μ_{10} was the growth rate in doubling/day (base 2) and t was the temperature in °C. The argument was advanced that this curve described an upper growth rate limit of marine phytoplankton that was far greater than typical growth rates found in natural waters at corresponding temperatures (Fig. 1). Thus, for the first time it was possible to quantify the potential growth rate response of marine phytoplankton to temperature and establish upper boundaries for growth rates in natural waters from observations of only temperature. That a single curve was established from data representing experiments with about 130 species or clones lent support to the idea that there is a common or universal effect of temperature on phytoplankton growth rates.

Eppley's concept of describing temperature effects as a response of maximum growth rate was expanded upon by Goldman and Carpenter (1974). We collected data from the literature of $\hat{\mu}$ (maximum growth rate) vs temperature from continuous culture studies and formed the Arrenhius plot (Fig. 2):

$$\hat{\mu}_e = (5.4 \times 10^9)\ e^{-6472/T} \qquad (2)$$

in which $\hat{\mu}_e$ was the maximum specific growth rate in 1/day (base e) and T was the absolute temperature in °K. The maximum growth rate is independent of nutrient concentration and simply represents the maximum possible growth rate of an organism for a given set of light and temperature conditions; hence, we could then conveniently insert equation

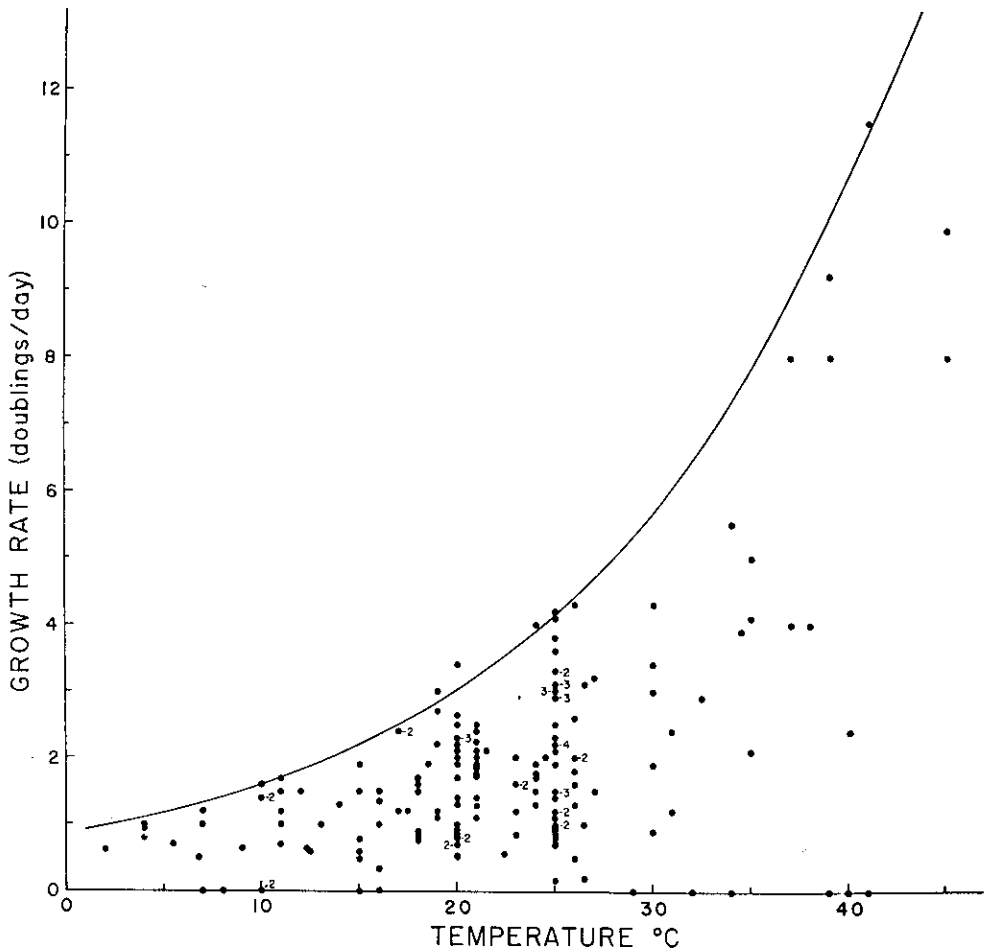

FIGURE 1. Variation in the growth rate (μ_{10}) in doublings/day of photo-autotrophic unicellular algae with temperature. Data are all for laboratory cultures. From Eppley (1972). Redrawn from Eppley (1972).

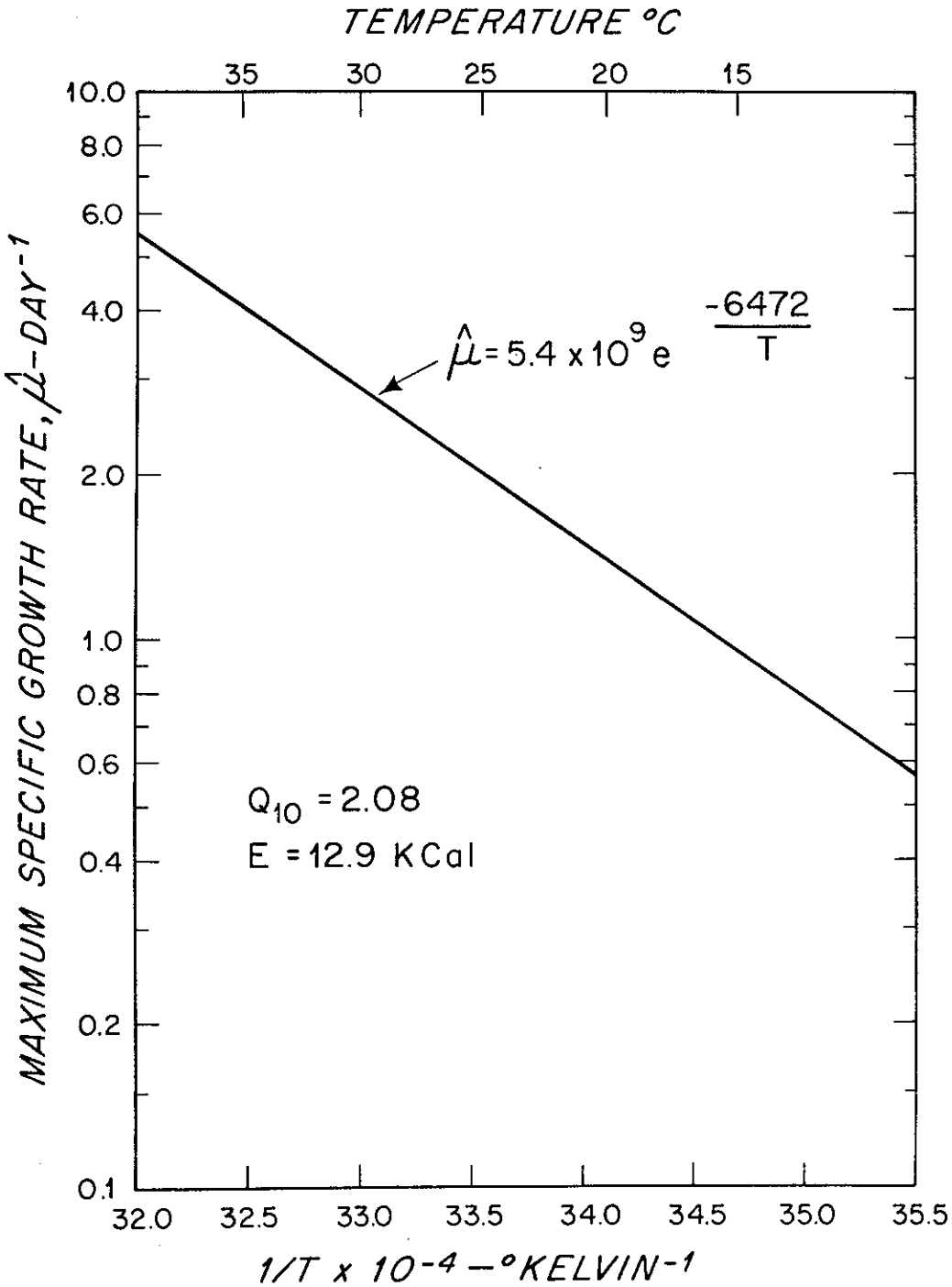

FIGURE 2. Effect of temperature on the maximum specific growth rate ($\hat{\mu}_e$) of marine and freshwater algae grown in continuous culture. Composite curve is based on studies with 12 different algal species described in Goldman and Carpenter (1974). Redrawn from Goldman and Carpenter (1974).

2 in the Monod equation, which describes the effect of external limiting nutrient concentration on growth rate, so that:

$$\mu = (5.4 \times 10^9)\ e^{-6472/T}\ \left(\frac{S}{K_s + S}\right) \qquad (3)$$

in which S was the concentration of limiting nutrient and K_s was the half saturation coefficient for growth. With equation 3 we could describe the response of growth rate to the simultaneous effects of limiting nutrient concentration and temperature. Using this equation, we constructed several hypothetical situations describing conditions under which competition between phytoplankton species could be strongly influenced by temperature. A complicating factor to the above approach is that K_s is probably as much temperature dependent as $\hat{\mu}$. Unfortunately, there are virtually no data in the literature on the temperature dependency of K_s.

In later studies with large-scale outdoor mass cultures of marine phytoplankton grown on saturating nutrients (Goldman and Ryther 1976), I observed that over a several-year period there was a systematic change in species composition with season that could be attributed directly to temperature (Figs. 3 and 4): *Skeletonema costatum* dominated when water temperatures were below 10°C; *Phaeodactylum tricornatum*, a pennate diatom, prevailed between 10°-20°C; and above 25°C one of several species, including *Amphora* sp., *Nitzschia closterium*,and *Stichoccus* sp., was dominant at a given time. The ability of the above species along with several other species to win out in competition in well-defined temperature regions was demonstrated under exacting laboratory conditions with continuous cultures for which temperature was isolated as the only variable (Fig. 5).

The overall effect of temperature on phytoplankton growth rates is clearly established. As shown by the curves of Eppley (1972) and Goldman and Carpenter (1974), for a given species and in a defined

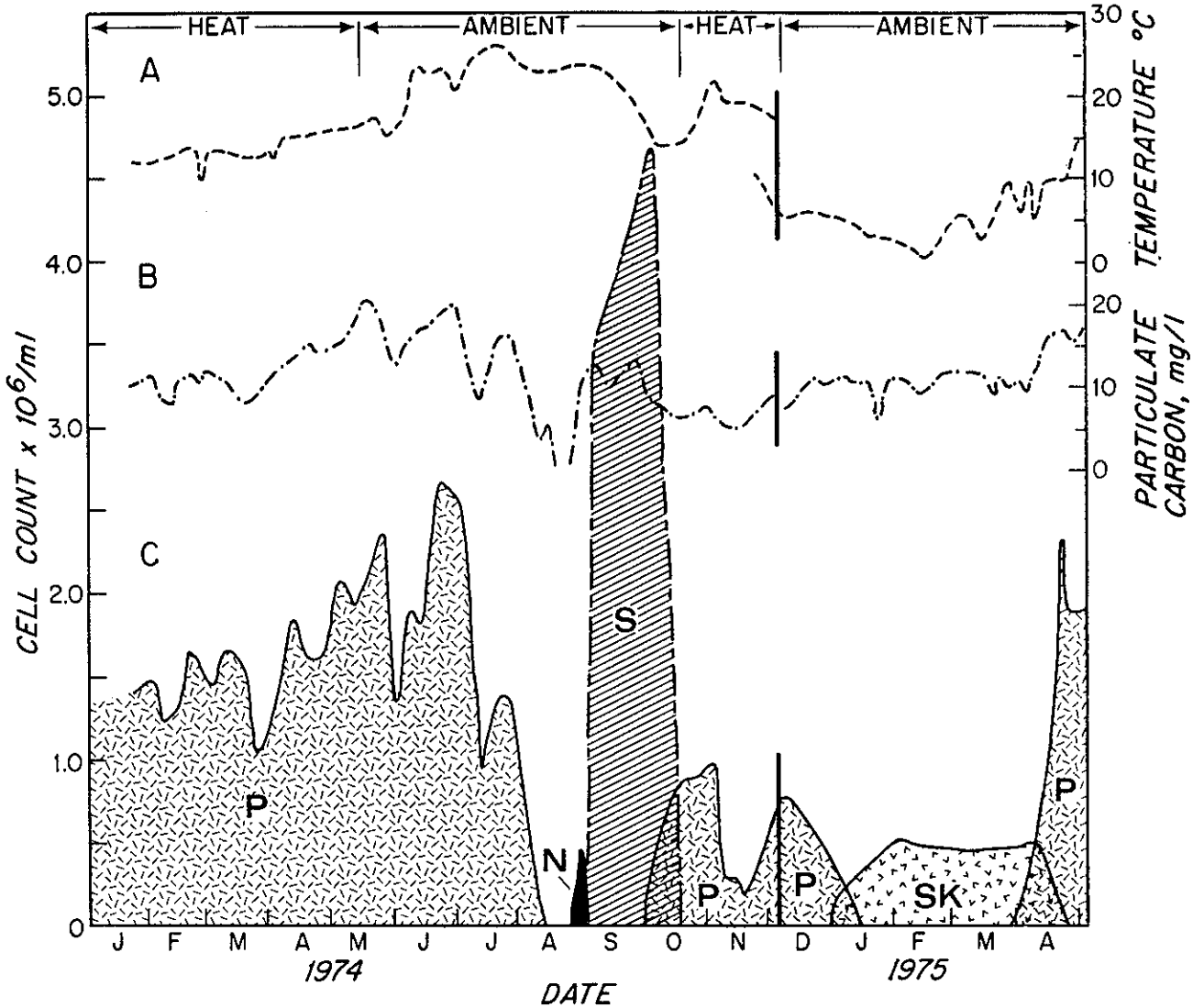

FIGURE 3. Summary of data collected in outdoor ponds at Environmental Systems Laboratory of Woods Hole Oceanographic Institution from January 1974 through April 1975. A - Pond temperature data; B - Particulate carbon data; C - Species data (P = *Phaeodactylum tricornutum*, N = *Nitzschia closterium*, S = *Stichococcus* sp., SK = *Skeletonema costatum*). From Goldman and Ryther (1976). Redrawn from Goldman and Ryther (1976).

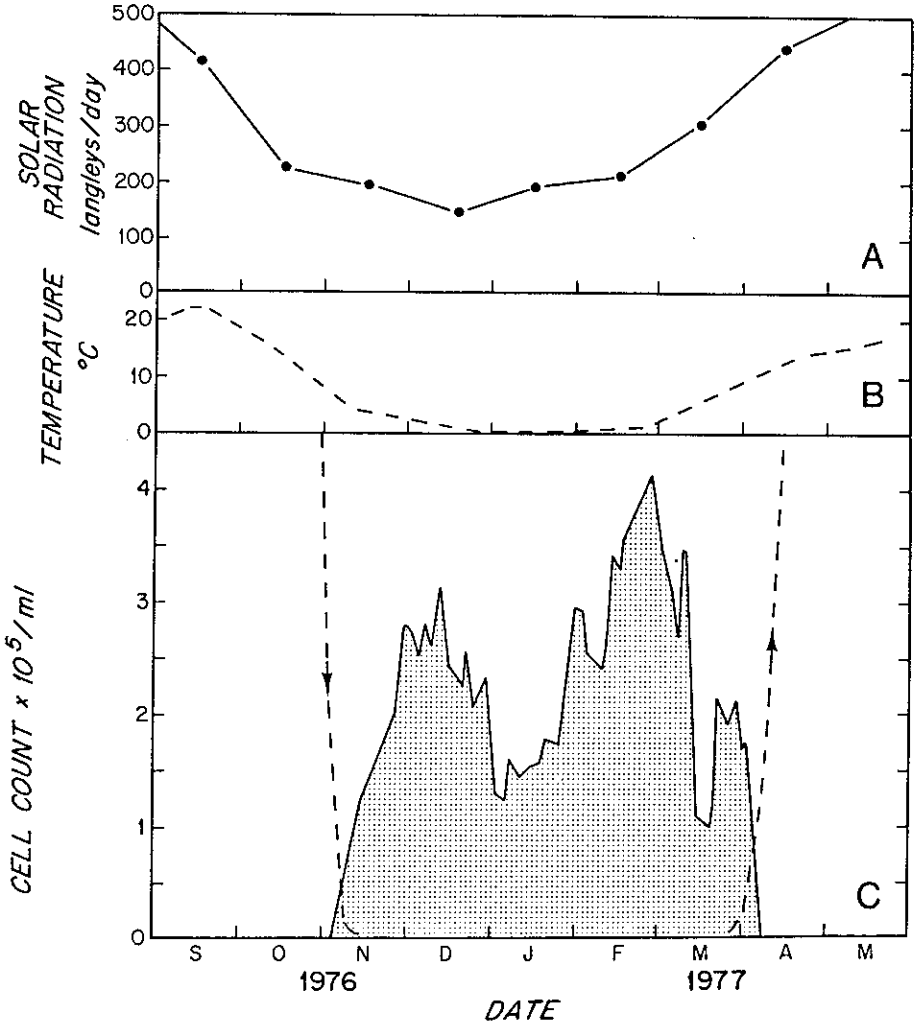

FIGURE 4. Summary of data collected in an outdoor pond at Environmental Systems Laboratory of Woods Hole Oceanographic Institution from September 1976 through May 1977. A - Solar radiation data; B - Pond temperature data; C - Species data (dashed lines = *Phaeodactylum tricornutum*; shaded area = *Skeletonema costatum*). Unpublished data.

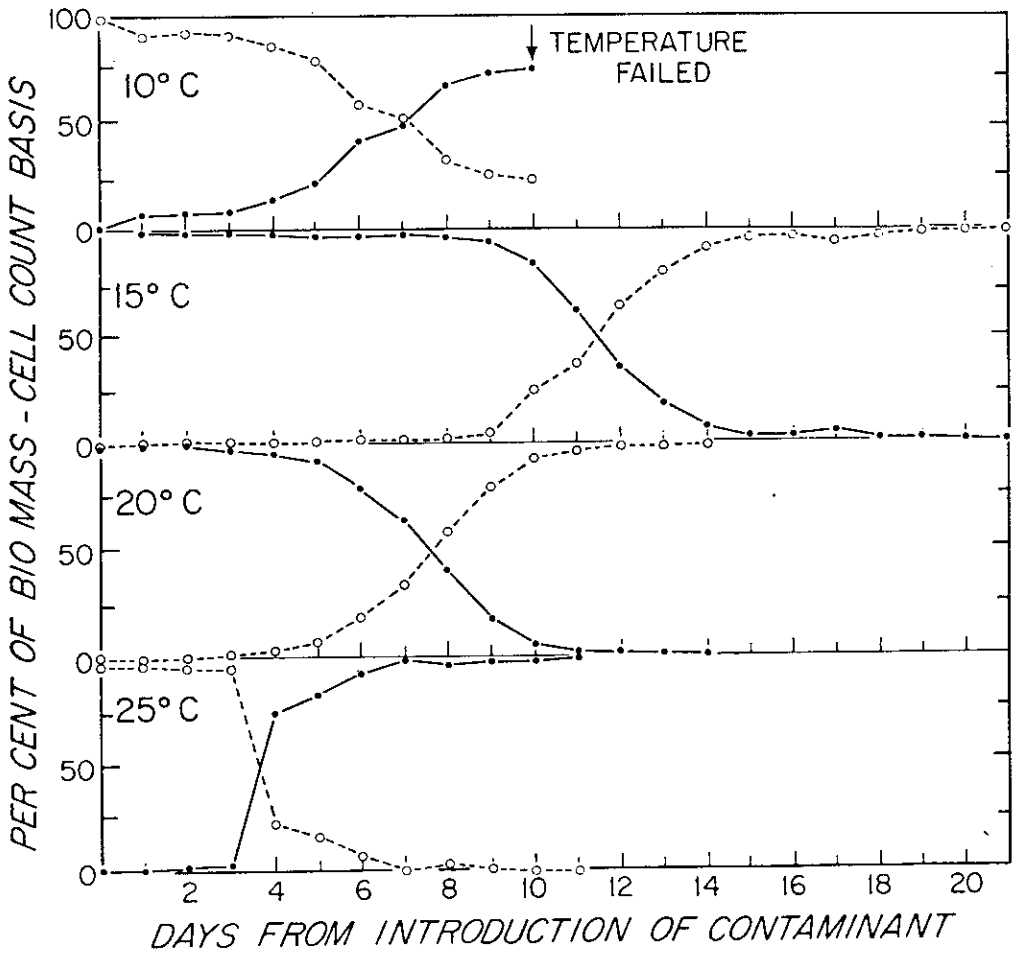

FIGURE 5. Competition between *Thalassiosira pseudonana* (solid lines) and *Phaeodactylum tricornutum* (dashed lines) at 10, 15, 20, and 25°C in laboratory continuous cultures. *T. pseudonana* at 10 and 25°C and *P. tricornutum* at 15 and 20°C were the contaminants. From Goldman and Ryther (1976). Redrawn from Goldman and Ryther (1976).

temperature region there is a direct correlation between temperature and growth rate, i.e., increasing temperatures lead to increasing growth rates. Each species may respond to temperature in this fashion only in an unique temperature range, which then characterizes the organism as belonging to a particular class based on its thermal-response characteristics. Although the growth rate curves of Eppley (1972) and Goldman and Carpenter (1974) suggest a universal type of response of phytoplankton species to temperature, it is evident from the competition situations depicted in Fig. 3 of Goldman and Carpenter (1974), that the slope of the temperature curve is as important as the range for which the curve applies in determining a given species' ability to compete with other species. For example, based on my temperature curve, at 10°C the maximum growth rate should be ∿-0.58/day. This implies that under continuous culture conditions it should be impossible to maintain a steady-state population of a particular species. Yet, at this temperature and growth rate it was possible to maintain healthy and significant steady-state populations of *Skeletonema costatum* and *Thalassiosira pseudonana* 3H (Goldman and Ryther 1976). In later continuous culture studies with *T. pseudonana* 3H under NH_4^+ limitation, $\hat{\mu}$ was found to be 3.06/day at 19°C (Goldman and McCarthy 1978), a datum point falling significantly above my temperature curve. Clearly then, there are species that display quite atypical growth rate-temperature responses, and it must be concluded that the approach of Eppley and myself only tells a portion of the story.

CHEMICAL COMPOSITION AND NUTRIENT UPTAKE RATES

Temperature appears to have a dramatic effect on the physiology of phytoplankton cells. Margalef (1954) first observed that under laboratory conditions increasing temperatures led to both a decrease in cell size and an increase in cellular dark respiration in the freshwater green alga *Scenedesmus obliquus*. Jorgensen (1968) carried this observation considerably further when he showed that both the carbon

assimilated per cell in one generation period and the cellular protein content of *Skeletonema costatum* increased with decreasing temperature in the range 7°-20°C even though the growth rate increased as expected. He suggested that this increased protein content reflected a buildup of enzymes as the cell adapted to the lower temperatures so as to maintain high photosynthetic rates.

Morris and Farrell (1971) and Morris and Glover (1974) likewise showed an increase in the cellular dry weight and protein content of two other species, *Dunaliella tertiolecta* and *Phaeodactylum tricornutum*, with decreasing temperature, but could not discern any effect on the dry weight content of *Nitzschia closterium*. Morris and Glover (1974) questioned whether the cells were really adapted to growing at lower temperature because they observed variations in photosynthetic rates during batch growth. Only toward the end of batch growth were photosynthetic rates similar at a particular temperature for cells grown at different temperatures. However, two major problems with the above approach were that the cells were grown at one temperature and then immediately exposed to different temperatures for measurement of photosynthetic rates during 1½ hour incubations, and that cells from batch cultures (in which growth rate is difficult to control) were used. Adaptation to large temperature changes (that typically occur slowly in nature) may require long periods of adjustment by phytoplankton species in order for them to gear up the proper biochemical machinery to cope with the new conditions. Sudden temperature changes, in contrast, may lead to shock effects and could have biased the results of Morris and Glover (1974). In addition, relating photosynthetic capacity to growth rate is extremely difficult when batch cultures are used. Morris and Glover (1974) realized these potential pitfalls and concluded their paper with the caution that "further elucidation of the biochemical mechanism for this effect (adaptive response) must depend on the use of continuous cultures."

Eppley (1972) summarized the data available and showed that both

the carbon content per cell and the carbon/chlorophyll ratio increased with decreasing temperature for several marine phytoplankton species. Using continuous cultures, I was able to show that for a fixed growth rate of 0.6/day and over a temperature range of 10°-30°C both the cellular carbon and nitrogen contents varied with temperature for four of five species grown (Goldman and Ryther 1976; Goldman 1977b). *Skeletonema costatum*, *Phaeodactylum tricornutum*, and *Monochrysis lutheri* all displayed the characteristic increase in organic matter with decreasing temperature. *Dunaliella tertiolecta* was found to have a U-shaped response to temperature with highest cellular organic matter found at the temperature extremes 10°C and 30°C and *Thalassiosira pseudonana* 3H showed no variation in both cellular carbon and nitrogen over this temperature range (Fig. 6). Williams (1971) earlier found the same U-shaped response in a freshwater *Chlorella* species grown in continuous culture at a fixed growth rate.

Two important conclusions were drawn from the above results. First, the U-shaped response of phytoplankton organic matter to temperature may be typical of many species. For example, based on further unpublished results of mine, when the temperature range was expanded below 10°C (the lowest temperature used in my earlier study), there was a significant increase in the cellular organic matter of *Thalassiosira pseudonana* 3H (Table 1). Hence my inability to observe this U-shaped response in all the species tested may have resulted because the temperature range used was too limited and/or the temperature intervals were too large.

The second important conclusion is that because a constant growth rate (μ) was used in the above study, cellular nutrient responses to temperature could readily be translated into nutrient uptake rate responses. The cellular nutrient uptake rate is defined as:

$$\rho = \mu Q \qquad (4)$$

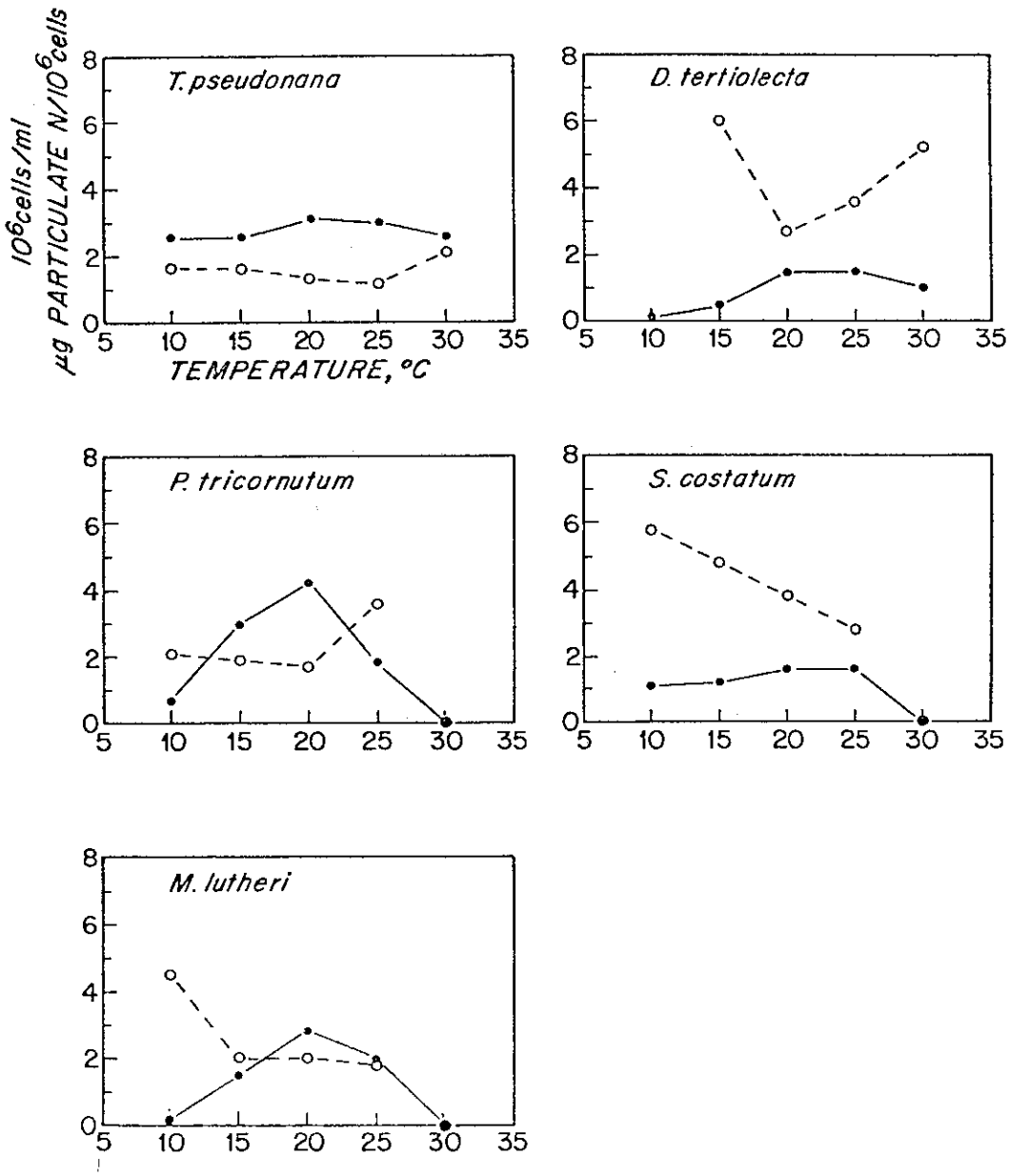

FIGURE 6. Effect of temperature on steady-state cell numbers (solid lines) and nitrogen cell quota (dashed lines) for five marine phytoplankton species grown in continuous culture at a dilution rate of 0.6/day. From Goldman (1977b). Redrawn from Goldman (1977b).

Table 1. Variation in several cell constituents for *Thalassiosira pseudonana* 3H grown in continuous culture at a growth rate of 0.3/day (unpublished data).

Temperature	Cell Constituents		
	Carbon pg/cell	Nitrogen pg/cell	Chlorophyll *a* pg/cell
7.5	7.4	1.2	0.28
11.5	4.6	0.6	0.14
14.5	4.0	0.5	0.13
18.5	4.2	0.4	0.17
23.0	3.4	0.4	0.18

in which ρ is the cellular nutrient uptake rate in nutrient/cell/time and Q is the cell quota in nutrient content/cell. Thus, for μ held constant ρ is directly proportional to Q and the data shown in Fig. 6 represent ρ when Q is multiplied by 0.6/day, the growth rate used. For a species like *Skeletonema costatum*, it is clear that ρ increases with a decrease in temperature. Such an effect is a classical example of the uncoupling of growth and nutrient uptake rates. The implications of this finding are important to our understanding of why certain species, although experiencing low growth rates at low temperatures, are able to thrive because of enhanced nutrient uptake rates. The net result is that there are fewer but larger cells at low temperatures representing potentially similar standing crops on a weight basis as at higher temperatures (Goldman 1977a).

PHYTOSYNTHETIC AND RESPIRATION RATES

The effects of temperature on photosynthetic and respiration rates in marine phytoplankton are poorly understood. Whereas, it is well established that temperature influences phytoplankton photosynthetic rates only at light saturation, this effect is clearly demonstrated only when carbon uptake per chlorophyll is considered (Steemann Nielsen and Jorgensen 1968); carbon uptake rates per cell show a temperature dependency even at low light intensities, but this dependency disappears when carbon uptake per unit of chlorophyll is used in place. The implication is that the chlorophyll content per cell decreases with decreasing temperature, as Steemann Nielsen and Jorgensen (1968) showed for *Skeletonema costatum* at 2°C. Yet, the effect of temperature on the chlorophyll content of phytoplankton cells is not nearly so clear. For example, Morris and Glover (1974) show that the chlorophyll content per cell first increases with decreasing temperatures for *Phaeodactylum tricornutum* in the range 7°-18°C and then decreases at the lowest temperature. In contrast, the chlorophyll content per cell in *Nitzschia closterium* decreases continuously with decreasing temperature. For *Dunaliella teriolecta* their results are even more puzzling:

a continuous decrease in cellular chlorophyll with decreasing temperature in the range 12°-24°C on the first day of batch growth, but an opposite effect by the fourth day.

Even more puzzling, the data of Eppley (1972) indicate a constant chlorophyll/cell ratio in the range 12°-25°C for *Dunaliella tertiolecta* and a U-shaped response for *Ditylum brightwelli* (Table 2). The same U-shaped response appears evident in my *Thalassiosira pseudonana* 3H data shown in Table 1. A major problem in trying to compare the above data is that the chlorophyll content per cell is strongly influenced by growth rate at a fixed temperature (Perry 1976). Hence, under conditions of nutrient limitation growth rate may be more influenced by available limiting nutrient than by temperature, with the result that the chlorophyll content is influenced simultaneously by both growth rate and temperature. This effect is clearly demonstrated by Perry's data showing varying chlorophyll/cell with growth rate under phosphorus limitation and constant temperature and by my data (Table 1), showing varying chlorophyll/cell with varying temperature but constant growth rate.

The continuous culture is the only growth system that can adequately be used to isolate temperature effects on various physiological parameters because growth rate is controlled directly by the dilution rate (medium flow rate/culture volume). Once a steady-state population is established, the specific growth rate is essentially equal to the dilution rate. Thus, for a fixed dilution rate, temperature can be varied and, as long as a steady-state is established, various chemical and physiological parameters can be measured.

The effect of temperature on phytoplankton respiration rates is perhaps the least understood response, and, yet, it may well be the important link to our understanding of temperature effects. Difficulties in measuring respiration rates in phytoplankton are well known, and, to date, satisfactory techniques for measuring photorespiration have yet to be developed.

Table 2. Calculated chlorophyll/cell values from carbon/cell and carbon/chlorophyll data presented by Eppley (1972) for two marine phytoplankters.

Species	Temperature °C	Carbon/Cell pg/cell	Carbon/chl.a Ratio	Chl.a/cell pg/cell
Ditylum brightwellii	5	1600	41	39
	7.5	1500	48	30
	10	1330	50	27
	15	720	25	29
	20	680	14	49
Dunalliela tertiolecta	12	41.8	38	1.1
	16	35.6	29	1.2
	19.5	25.9	25	1.0
	20	28.2	24	1.2
	21	25.3	26	1.0
	25	22.5	16	1.4

Tang and French (1933) demonstrated that dark respiration was more temperature dependent than photosynthesis. It is now known that the dark reactions of photysynthesis, which involve many enzymatic processes, are temperature dependent but that the light reactions are insensitive to temperature changes. Zelitch (1971) points out that a temperature increase of 10°C more than doubles photorespiration in a 20°-35°C range. The Q_{10} of each of the above metabolic processes is not linear over a 0-30°C range and is species specific.

With regard to marine phytoplankton, dark respiration has been well studied (see review by Lloyd 1974), but hardly any information is available on temperature effects. The studies of Steemann Nielsen and Hansen (1959) and Ryther and Guillard (1962) over 15 years ago stand out as the only attempts to measure temperature effects on dark respiration in marine phytoplankton. Steemann Neilsen and Hansen (1959) measured photosynthetic and respiration rates along with growth rates of natural marine phytoplankton and concluded that, whereas growth rates were dependent on temperature, photosynthesis and respiration were not. Ryther and Guillard (1962), in a more detailed study, showed that dark respiration rates of six marine phytoplankton clones (five species) were temperature dependent, but the degree of this dependency was species specific. The highest respiratory coefficients (g carbon respired/hr/g chlorophyll) were found in eurythermal clones and the increase with temperature was more regular. In contrast, the stenothermal clones showed varying respiratory responses to temperature; but, in general, their respiration was low and not nearly as temperature-dependent as with the eurythermal clones.

Packard et al. (1975) measured the effect of temperature on the respiratory electron transport system in natural marine phytoplankton and concluded that, although there were variations in this parameter with location, there did not appear to be a systematic variation with temperature. Falkowski (1977) measured the adenylate energy charge in *Skeletonema costatum* over a temperature range of 2°-30°C and found no

apparent variation, even though the growth rate increased tenfold. Both the data of Packard et al. (1975) and Falkowski (1977) point to the fact that temperature adaptation by marine phytoplankton may be an important mechanism for species selection in different temperature environments.

The importance of photorespiration in marine phytoplankton is unclear, although it is well established that glycolate production is an end product of the process (Tolbert 1974). The importance of glycolate formation and excretion of dissolved organics, in general, is the subject of much controversy (Sharp 1977; Fogg 1966, 1977). Sharp (1977) suggests that the excretion of dissolved organic carbon by healthy phytoplankton is minimal. Yet Fogg (1966) in his review has shown that glycolic acid excreted from phytoplankton can represent a large fraction of photoassimilated CO_2. The possible effect of temperature on this process has yet to be addressed.

FIELD STUDIES

The difficulties in isolating temperature effects from other influencing factors in field studies were stated earlier. Yet a number of researchers have attempted to sort out the influence of temperature on productivity of natural populations. Bunt's work on Antarctic phytoplankton productivity (Bunt 1964a, b; Bunt and Lee 1970) is instructive because he was able to demonstrate significant algal activity under the ice cover when temperatures were $\sim$1.5°C. In one case, a large bloom of *Phaeocystis*, a common coldwater species, was observed in January 1963, when cell numbers reached 3×10^6 cells/liter and when the ice cover began to disappear in McMurdo Sound (Bunt 1977a). He also showed that photosynthetic rates of natural populations taken from temperatures <-1.5°C showed a marked increase between 5°-15°C (Bunt 1977b), suggesting that these species were not adapted to the cold temperatures. El-Sayed (1966) noted that there were significant variations in primary

productivity in different regions of Antarctic waters even though temperatures were similar and suggested that more laboratory studies were required to isolate temperature effects.

The studies of Smayda (1973, 1975) on winter blooms of *Skeletonema costatum* in Narragansett Bay, Rhode Island, and those of Malone (1976, 1977) on productivity in the New York Bight include the most extensive and useful temperature-productivity data available. In both situations, *Skeletonema costatum* was a dominant winter species. Smayda (1973) showed that the growth rate for this species was strongly temperature dependent, with rates of <1.0/day at temperatures <5°C. When winter temperatures dropped to 0.9°C in Narragansett Bay, temperature was the main factor controlling growth rates. Yet, even though there is a strong temperature dependence at these low ambient temperatures, the dominance of *Skeletonema* is suggestive that this species has remarkable adaptive characteristics, as proposed earlier by Jorgensen (1968). Malone's data from the New York Bight shed some light on this subject. He found that the $\log_{10}$ of the assimilation number increased linearly with increasing temperatures for natural populations of phytoplankton from September 1973 through August 1974 for temperature >8°C. Below 8°C when *Skeletonema* was the dominant species, there was a dramatic rise in the assimilation number, once again suggesting the remarkable adaptive capacity of *Skeletonema*. These results were in close agreement with my own data (Goldman 1977b), in which I showed that nutrient uptake rates of *Skeletonema* increased with decreasing temperature. Malone (1977) confirmed and expanded on the above results by showing that the nano and net plankton fractions of populations from the Bight displayed the same remarkable increase in assimilation number when temperatures fell below 8°C.

The major conclusion of the above results, together with my own temperature data (Goldman 1977b), is that growth rate may not be the best parameter to judge the ability of phytoplankton populations to cope with extreme cold and warm temperatures. Rather, determination of variations in the chemical composition, chlorophyll content, cell

size, assimilation numbers, and respiration rates as a function of temperature may offer a more fruitful avenue of research.

MODELING TEMPERATURE EFFECTS

The complexity of temperature effects on phytoplankton activity--primarily the effect on the uncoupling of nutrient uptake and growth processes, makes it extremely difficult to incorporate temperature functions into phytoplankton models. Previous attempts to incorporate temperature effects into models have been limited to temperature-growth rate relationships such as described in equations 1 and 2. As more temperature-growth rate data are becoming available, it is becoming increasingly evident that such representations are, at best, crude approximations. For we now know that the temperature response of some, and perhaps many, species does not conform to existing relationships.

Moreover, it is becoming clear that the temporal and spatial scales on which phytoplankton obtain their rations of nutrients may be so small that they are impossible to measure with existing techniques. For example, we (MaCarthy and Goldman 1979) recently showed that marine phytoplankton, with a previous history of nitrogen limitation, can assimilate this nutrient at a rate significantly greater than their growth rate during short (5 min) incubation periods. Thus, a phytoplankton cell need be exposed to a high nitrogen level for only a fraction of its doubling period in order to satisfy its requirement for this nutrient. In oceanic waters where nutrients are frequently below detectable levels, such a supply of nutrients could exist on a microscale where phytoplankton cells randomly and probably frequently come in contact with minute zones of high nutrients originating from zooplankton excretions and bacterial degradation of detritus. How an environmental parameter such as temperature influences these processes is completely unknown.

From the available information on how temperature affects the uncoupling between nutrient uptake and growth rate, it appears that this phenomenon is species specific; that is, certain species such as *Skeletonema* seem to be able to cope with extreme temperatures better than others. Thus, when considering how little we know about the basic physiology of temperature effects on phytoplankton nutrient assimilation processes, it becomes an almost impossible task to develop realistic phytoplankton models that can describe accurately the impact of this parameter on the different rate processes. Clearly, considerably more research in this area is needed.

ACKNOWLEDGMENTS

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GRAZING, NUTRIENT RELEASE, AND THEIR FORMULATION IN PLANKTON MODELS

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INTRODUCTION

When I was asked to attend this conference and to speak about grazing in plankton communities, I wasn't sure if I should first defend the importance of grazing formulations in simulation models, or whether I should immediately begin defining the process constructs of interest, and debating the alternative ways of handling them mathematically. There fortunately appears to be substantial agreement among modelers on the first point. Grazing as a potentially important loss term for phytoplankton populations can be found incorporated in one form or another into every dynamic model of plankton communities from Riley's (1946) work to the present. Only gross-level models that correlate chlorophyll content or transparency of the water with rates of nutrient loading (e.g., Vollenweider 1969; Dillon and Rigler 1974; Chapra and Tarapchak 1976; Oglesby 1977a; Oglesby and Schaffner 1978) neglect the impact of zooplankton altogether. The same is true for fisheries models. Whereas correlations can be found between fishery yield and primary production or physical factors (e.g., Melack 1976; Oglesby 1977b), many dynamic representations include zooplankton as an important food resource for the fish, at least during their larval stages. This prevalence of regard for zooplankton in aquatic simulation models reflects an obvious concern for their importance in nature, and it acknowledges the swift responses of these organisms to changes in their prey and in their predators. Empirical investigations have repeatedly demonstrated that grazing can sometimes influence the composition and abundance of algal communities (Cushing 1963; Haney 1973), and these seasonal effects of grazing pressure are mimicked by simulation models (Steele 1974; Canale _et al_. 1975, 1976; Scavia 1979b; Steele and Frost 1977). The direction and substance of the modeling efforts have made it clear that representing grazing, growth, and reproduction of planktonic herbivores is vital for predicting the dynamics of the phytoplankton, so the issue shifts immediately from whether or not to

include zooplankton in simulation models of lake ecosystems to the matter of how best to represent the processes and components involved.

In contrast to the recent advances in the ways that simulation models treat algal cells, including such things as internal nutrient stores, changes in physiological condition, and interactions of growth limitations, there has been no fundamental advance in the treatment of zooplankton beyond that of Riley in 1946. This is because the zooplankton assemblage is usually characterized as a single individual, with a single feeding rate, respiration rate, growth rate, etc. The approach works well for the phytoplankton where all computations are made with respect to a characteristic cell or biomass pool, but it is not at all evident that the practice can be extended validly to populations of animal species where egg, juvenile, sub-adult, and adult stages may be subject to different constraints on their resource utilization and survivorship. Some authors have subdivided herbivorous zooplankton into general taxonomic groups, like copepods and cladocerans (Bloomfield et al. 1973), or else they have separated the community into functional groups like raptors, omnivores, herbivorous cladocera, herbivorous copepods, and even nauplii (Canale et al 1975, 1976), but most of these exercises are just minor variations on Riley's original theme. Very few authors have tried to model the size and age structure of zooplankton populations in terms of the developmental stages involved (e.g., Maguire et al. 1976), but the few models that incorporate this feature show that striking effects propagate to both lower and higher trophic levels (Hairston and Pastorok 1975; Steele and Frost 1977).

I have already indicated the substantial empirical evidence for claiming that herbivores exert controls on the overall abundance of algal populations at some times of the year, particularly during the

late spring and summer. Equally well documented is the fact that the grazers are very selective about the types of particles that they ingest (Arnold 1971; Nival and Nival 1973; Berman and Richman 1974; Richman et al. 1977). Some of the selection may be dictated purely by the mechanical properties of the filtering apparatus (Nival and Nival 1976; Boyd 1976), but there may also be a high degree of chemosensation and decisionmaking involved (Poulet and Marsot 1978). Several authors have dealt with this subject of active and passive "electivity" in their models (Park et al. 1974; Smith et al. 1975; Scavia and Park 1976) and it proves to be a major force shaping the structure of phytoplankton communities in the simulations (Steele and Frost 1977).

Closely allied to selective feeding but more subtle in its species-specific effects is the fate of nutrients released into the water by the zooplankton. These nutrients are available not only to the preferred prey of the grazers, but also to species which may not be as susceptible to grazing stress. Nutrients remineralized by zooplankton are known to be important components of internal nutrient loading in many water bodies; that is, they constitute an important autochthonous source of inorganic nutrients for algal production, which at some seasons may exceed all external supplies of N and P (Barlow and Bishop 1965; Ganf and Blažka 1975; Lehman 1979). At times the zooplankton may thus be the principal source of the nutrients that permit de novo synthesis of algal biomass, so that rates of primary production in the water column may depend upon the metabolic rates of the animals.

The processes necessary to construct a model of zooplankton grazing dynamics are very easy to identify; they constitute the elements of energy or nutrient budgets at the organismic level (e.g.,

Dagg 1976): ingestion, assimilation, respiration, excretion, egestion, and allocation of effort between reproduction and growth. All of these processes are demonstrably size, age, and species specific. The issue here is how to abstract the most important aspects of each one, and how to represent them formally. Most of the remaining text will be used to probe the empirical data that are particularly pertinent to each of these processes, and to examine alternative formulations for each one. I will restrict my attention as much as possible to the herbivorous zooplankton.

INGESTION

A discussion of feeding and feeding rates is a good starting point for this exercise because the rate at which algal food is ingested by the grazers naturally shapes the character of mortality among the phytoplankton. Empirical evaluations of feeding rates have been performed for decades, and it should be no surprise that virtually all of the mathematical formulations of the process are due to the experimentalists. The favorite procedures for measuring feeding rates rely either on direct quantification of changes in abundance of the food particles (e.g., Reeve 1963; Frost 1972), or on incorporation by the animals of a radioactively labelled food (e.g., Rigler 1961b; Geller 1975). Early workers had believed that filter-feeding zooplankton were completely automatic, in the sense that each animal would always filter a constant volume of water, regardless of the concentration or types of particles it contained (Fleming 1939; Harvey 1942), and this notion was incorporated into the earliest models (Riley 1946). Remnants of the idea still persist in some simulation efforts today (Canale _et al_. 1975, 1976; Di Toro _et al_. 1977), although the recent authors follow Riley _et al_. (1949) in specifying an upper limit to the rate at which zooplankton can

assimilate the ingested material. Studies by Ryther (1954) and Marshall and Orr (1955), however, soon made it clear that unbounded ingestion rates are not the case at all. Feeding rate (i.e., quantity of food consumed) does increase with particle abundance, but the relationship is not without bound. At high concentrations of food particles the rate of ingestion levels off to some maximum value. Subsequent work showed that this new empirical relationship had general validity for describing the behavior of both field and laboratory populations (Rigler 1961b; Reeve 1963; Burns 1966; Parsons et al. 1967). Several different formulations were advanced to describe the empirical results mathematically. In their most general forms the equations include the presumption that feeding can occur only at concentrations greater than some threshold level, $P_o \geq 0$:

$$I = I_{max} \left(\frac{P - P_o}{P_{critical} - P_o}\right) \quad \text{for } P < P_{critical}$$
$$= I_{max} \quad \text{for } P \geq P_{critical} \qquad \text{(Rectilinear)} \quad (1)$$

$$I = I_{max}[1 - e^{-k(P-P_o)}] \qquad \text{(Ivlev)} \quad (2)$$

$$I = I_{max}\left[\frac{(P-P_o)}{k + (P-P_o)}\right] \qquad \text{(Michaelis-Menten)} \quad (3)$$

where I = ingestion rate (consumption per unit time)

I_{max} = maximum ingestion rate

P = food concentration

k = a constant specific to the animal

The filtering or clearing rates of the grazers, F (volume cleared per unit time), are related to ingestion by the expression:

$$F = I/P \qquad (4)$$

The choice of which equation an author uses to represent his data appears to be completely subjective. The lack of consensus stems from the fact that no theory exists to separate a priori the several curves that might fit a given collection of data. In hope of resolving the issue, Mullin, Stewart, and Fuglister (1975) used Frost's (1972) extensive data on feeding rates of *Calanus pacificus*, a marine calanoid copepod, to try to distinguish the best empirical model by statistical means. They discovered that the data conformed to all three models with almost the same goodness of fit in each case.

Some authors have taken a less empirical approach to the issue and have tried to justify grazing models from basic assumptions about feeding behavior. Most notable in this respect are the efforts of Cushing (1959, 1968), and Crowley (1973) who derived Michaelis-Menten formulations for grazing zooplankton from the same constructs that Holling (1959) used to erect a scheme for predation rates among animals in general. Theoretical justification of this approach relies on the assumption that the predator must partition its time between searching for, handling, and digesting individual prey items. The assumption works well for raptorial predators, but the distinction between search time and handling time is lost among filter feeders which simultaneously gather and process food from suspension. An alternative approach advanced by Lam and Frost (1976) and by Lehman (1976) has been to treat grazing as an optimization process for the grazer in which effort is expended to gather food, and nutritional reward is accrued from its digestion. These recent modeling efforts were provoked by the acknowledgement that empirical models differ most substantially from each other at low particle abundances (Mullin, Stewart, and Fuglister 1975), and that the behavior of grazing at these low densities has a strong effect on the stability of model plankton communities (Steele 1974). It also happens that at the low concentrations experimental data are most difficult to

obtain, and are subject to the greatest measurement errors. Despite the experimental difficulties, Frost (1975) managed to show that *Calanus* does not cease feeding at low food abundances, nor does it filter at its maximum rate - the only two possibilities consonant with the empirical models now in use. Instead the filtering rates of the animals increase with food abundance at low particle concentrations, a feature which causes the ingestion curves to be concave upward in that same region. The behavior is consistent with the optimization hypotheses of Lam and Frost (1976) and Lehman (1976), but not with the other models commonly in use. This experimental observation still awaits confirmation from other species before one can attest to its general validity, but it already has had an impact on the formulations of recent grazing models (Steele and Frost 1977).

At present the quarrel is not over the best representation for most extant experimental data - all the proposed models clearly work almost equally well in that regard. There also seems to be no strong reason to reject current empirical models in favor of, say, an energy-optimization approach, at least until more species are examined. What really is at issue is whether or not the models erected for feeding experiments conducted on one type or collection of food can be applied to other food mixtures. Most modelers assume that they can, by an introduction of simple food-specific coefficients. The data suggest that things are a little more complex.

SELECTION OF FOOD TYPES

One customary expedient used by modelers to generate feeding rates is to express abundance of all phytoplankton in units of volume, dry weight, or carbon equivalents in order to obtain a single

"food" concentration which can be substituted into one of the equations cited above (e.g., Steele 1974; Jorgensen 1976; Jorgensen et al. 1978; Ikeda and Adachi 1978). Nyholm (1978) probably expresses the sentiments of many of these authors when he justifies this treatment with the claim that "grazing is a complex phenomenon that can only be accounted for very approximately." Of course, when the phytoplankton are modeled as a single entity, it may be hard to imagine doing anything else. Nonetheless, the introduction of species structure, size structure, or functional categories into the phytoplankton models necessitates some treatment of the selective grazing patterns which have been amply documented in nature. Several procedures have been tried, all of which involve multiplying the abundance of a food type P_i by a selection coefficient w_i in order to generate the requisite behavior. Canale et al. (1975, 1976), for instance, treat ingestion I_i on each food category as:

$$I_i = w_i \cdot f(\Sigma P_i) \tag{5}$$

The overall ingestion rate is determined by the total abundance of food, ΣP_i, a feature shared with the models mentioned above, but these authors assume that the ingested particles can be assigned to a variety of individual categories by means of w_i:

$$w_i = \frac{\alpha_i P_i}{\Sigma \alpha_i P_i} \tag{6}$$

where α_i is the proportion of the total diet that will be composed by P_i when all food categories are in equal abundance.

Vanderploeg and Scavia (1979a) have examined this use of selection coefficients as first introduced by O'Neill (1969) and they advocate using a term they call w_i', the conditional probability that

feeding will occur when food type i is encountered in a mixture. They propose

$$I_i = I_{max} \left(\frac{w_i' P_i}{K + \Sigma w_i' P_i}\right) \qquad (7)$$

as the most satisfactory representation of specific ingestion rates, a formulation which is employed in many large simulation models (Bloomfield et al. 1973; Park et al. 1974; Scavia 1979b). Their implication is that simple, measurable coefficients applied to each food source can represent both the mechanical biases of the food-gathering mechanism (passive selection, in the sense of Frost 1977), and the more active selection/rejection process based perhaps on taste (Poulet and Marsot 1978). To acquire the necessary data, Vanderploeg and Scavia (1979b) stress the need for renewed experimental efforts to tabulate values of w_i (and presumably of K as well).

This attitude of using model equations as a guide to future research has certain drawbacks, however, and this case provides an especially good example. There is absolutely no guarantee that any physical analogues exist for the coefficients w_i and K in the above equation; at least there is no guarantee that those terms can be parameterized as constants. By using such an equation one assumes that the zooplankter has no way of altering its diet vis-á-vis changes in the nutritional quality of available prey. One assumes that selection is fixed and then seeks to measure the supposed parameters. Doyle (1979) has addressed this matter experimentally for a selective deposit feeder, and he finds that the half-saturation "constant" K must be treated as a function of food quality, quite distinct from the w_i coefficients. There is every reason to suspect that the same cautionary note should be applied to filter-feeding zooplankton. Wilson (1973) and Richman et al.

(1977), for instance, showed that some copepod species change their size-specific selectivity in response to the character of the available particle spectrum. But even if one could ignore the changing selectivities, the extensive data accumulated by Geller (1975) for *Daphnia pulex* suggest that substantial errors would result from applying Equation 7 to different food sources simultaneously. Equation 7 predicts that ingestion rates will approach I_{max} for any food i, provided high enough concentrations P_i are encountered. But Geller found that I_{max} was specific to the food species, ranging from 0.05 μg C animal^{-1}h^{-1} to 0.67 μg C animal^{-1}h^{-1} for individuals 2 mm long at 15°C (Table 1). To some extent this is because the volume ingested plays a role in regulating feeding rates (McMahon and Rigler 1965; Geller 1975), and because the food species have distinctly different carbon to volume ratios. Also, there are considerable differences between species in the degree to which they are compressed into the periotrophic membrane inside the gut (Geller 1975). Lehman (1976, 1978) has proposed that one way to deal with this matter is to specify the available volume of the gut V_G as a constraint on ingestion:

$$V_G \geq t_G \Sigma I_i V_i \tag{8}$$

where I_i is the ingestion rate for food category i (μg C time^{-1}), V_i is the effective volume that each unit of food i occupies inside the gut, including packing effects, and t_G is gut passage time. If one specifies ingestion in terms of the conditional probability w_i that an item will be captured and eaten,

$$I_i = w_i F P_i \tag{9}$$

where F is filtering rate (ml time^{-1}) and P_i is the abundance of food category i (μg C ml^{-1}), then the constraints on filtering rate can be expressed as:

Table 1. Maximal rates of ingestion (μg C animal^{-1} h^{-1}) measured by Geller (1975) for 2-mm *Daphnia pulex* feeding on different food types at 15°C.

		I_{max}
Scenedesmus acutus	(green)	0.41
Stichococcus minutissimus	(green)	0.67
Staurastrum planctonicum	(green)	0.08
Nitzschia actinastreoides	(diatom)	0.30
Asterionella formosa	(diatom)	0.39
Stephanodiscus hantzschii	(diatom)	0.17
Microcystis aeruginosa	(blue-green)	0.10
Anabaena planctonica	(blue-green)	0.05

$$F \leq \frac{V_G}{t_G \Sigma w_i P_i V_i} \tag{10}$$

This equation specifies the inverse relationship between filtering rate and particle abundance that is observed in field and laboratory studies when particle concentrations are high and t_G approaches some minimum value. At low cell concentrations, the empirical data suggest that filtering rates are bounded, probably by physiological constraints on the movement of water through the filtering apparatus. Geller (1975) has shown that at low food abundances particles are retained inside the gut for long periods of time and filtering rates approach a maximum. At high food levels, gut passage time is comparatively short and filtering rate varies inversely with food concentration. Regarding the consumption process in this way has the additional advantage that temporarily elevated feeding rates of starved animals (Mullin 1963; Frost 1972) can be easily accommodated. These increased rates are evident only at high food concentrations where filtering rates would ordinarily be depressed by the constraint of a full gut (Figure 6 in Geller 1975).

Provided that t_G has a finite lower bound, as seems to be the case (Geller 1975, Figure 2), the constraints specified in this section cause predicted feeding behavior to conform to the empirical rectilinear model (Eq. 1). The "critical concentration" consequently has a clear physiological basis; it is the point at which the handling and digestive machinery just keeps pace with filtering rates, and its value changes with the character of food types included in the diet. At higher food abundances ingestion is limited only by the processing mechanisms. Because digestion and assimilation loom as such potentially important limits to ingestion, they will be considered next.

ASSIMILATION AND EGESTION

Although some authors have assumed for expediency that all material ingested by zooplankton is assimilated by them, the production of feces by the animals in nature constitutes a strong denial to that assumption. The formulation of assimilation and its converse, egestion, can influence not just secondary production in a model, but rates of nutrient cycling as well. Most authors treat assimilation as a constant fraction of ingestion rate for all food categories (e.g., Park et al. 1974) but the equations are formulated in such a way that digestion efficiencies can be assigned to each food type individually (Scavia and Park 1976). There appears to be strong experimental support to proceed in this manner (Lefévre 1942; Marshall and Orr 1955; Arnold 1971; Porter 1973), particularly in light of results like those shown in Table 2, where rates of ingestion (Geller 1975) and assimilation (Lampert 1977b) have been assembled for *Daphnia pulex* feeding on five different algal species. Rates have been normalized to *Scenedesmus* in each case to account for possible differences between experimental conditions used by the two authors. One can see that rates and assimilation efficiencies may be identical for taxonomically dissimilar organisms like *Scenedesmus*, a green alga, and *Asterionella*, a diatom, but that the relations between assimilation and ingestion for the green algae *Scenedesmus*, *Stichococcus*, and *Staurastrum* are very different. Results like these caution against attempts to identify generalities about assimilation for broad functional or taxonomic groups (e.g., Canale et al. 1975, 1976).

As indicated earlier, most of the plankton simulation models in use today follow Riley et al. (1949) by imposing an upper limit on the rate of assimilation by the zooplankton even if ingestion rates are unbounded. In these latter cases (DiToro et al. 1977;

Table 2. Maximal rates of ingestion and assimilation for different species of algae by 2-mm *Daphnia pulex* at 15°C. Rates are normalized to *Scenedesmus*.

	Ingestion[1]	Assimilation[2]
Scenedesmus	1.0	1.0
Stichococcus	1.6	0.8
Staurastrum	0.2	0.6
Nitzschia	0.7	0.5
Asterionella	1.0	1.0

[1]from Geller (1975); [2]from Lampert (1977b).

Canale et al. 1975, 1976, for "nonselective grazers") the joint assumptions lead to predictions of "superfluous feeding" (Beklemishev 1962) at high food abundances. That is, much more material is ingested than the animals can possibly assimilate. Conover (1966) has disclaimed the occurrence of superfluous feeding among herbivorous zooplankton, and Lampert (1977b) agrees that no substantial evidence exists to support it. One should not conclude, however, that assimilation efficiency is totally independent of food concentration. Schindler (1968) has demonstrated that the ratio of assimilated energy to ingested energy decreases by approximately a factor of 2 when *Daphnia magna* is fed on progressively more concentrated diets. In other words, when food is very abundant and processing rates are rapid, digestion is less complete than when food is rare. This seems to correspond to Geller's (1975) observations about variable gut passage times. At low food abundances, ingested material may be retained for more than an hour inside the gut, but when external concentrations are high, food is egested within 10 minutes.

The optimal length of time that food items ought to be retained inside the gut of an herbivorous zooplankter can be derived fairly easily from Equation 10 and from the additional consideration that the nutritive value Q obtained from the food can be written

$$Q = F \Sigma w_i P_i E_i \tag{11}$$

where E_i is the nutritive reward obtained from each unit of food type i that is ingested. The optimal solution for fixed values of P_i occurs where $dQ/dF = 0$:

$$\Sigma w_i P_i E_i + F \Sigma w_i P_i (dE_i/dF) = 0 \tag{12}$$

By writing dE_i/dF as $(dE_i/dt_G)(dt_G/dF)$ and using Equation 10, one finds that the optimal gut passage time is given by

$$t_G = \frac{\Sigma w_i P_i E_i}{\Sigma w_i P_i (dE_i/dt_G)} \tag{13}$$

in the general case, and by

$$t_G = \frac{E}{dE/dt_G} \tag{14}$$

when only one food type is involved. A graphical interpretation of this result is shown in Figure 1. The optimal length of time that food should be retained inside the gut corresponds to the point where a tangent to the function E passes through the origin. This point is denoted t_{min} because it is the minimal length of time that food should be digested; under some conditions the gut contents can be retained much longer.

Equations 13 and 14 were derived by assuming that filtering rate was unbounded, so that

$$F = \frac{V_G}{t_G \ \Sigma w_i P_i V_i} \tag{15}$$

at all food abundances. At very low food densities, however, F is constrained to some maximum value F_{max}, as I have already indicated. This means that ingestion rates will be below saturation and t_G could conceivably increase. For a single food type, the critical concentration where these constraints become operative is

$$P_{critical} = \frac{V_G}{F_{max} t_{min} V} \tag{16}$$

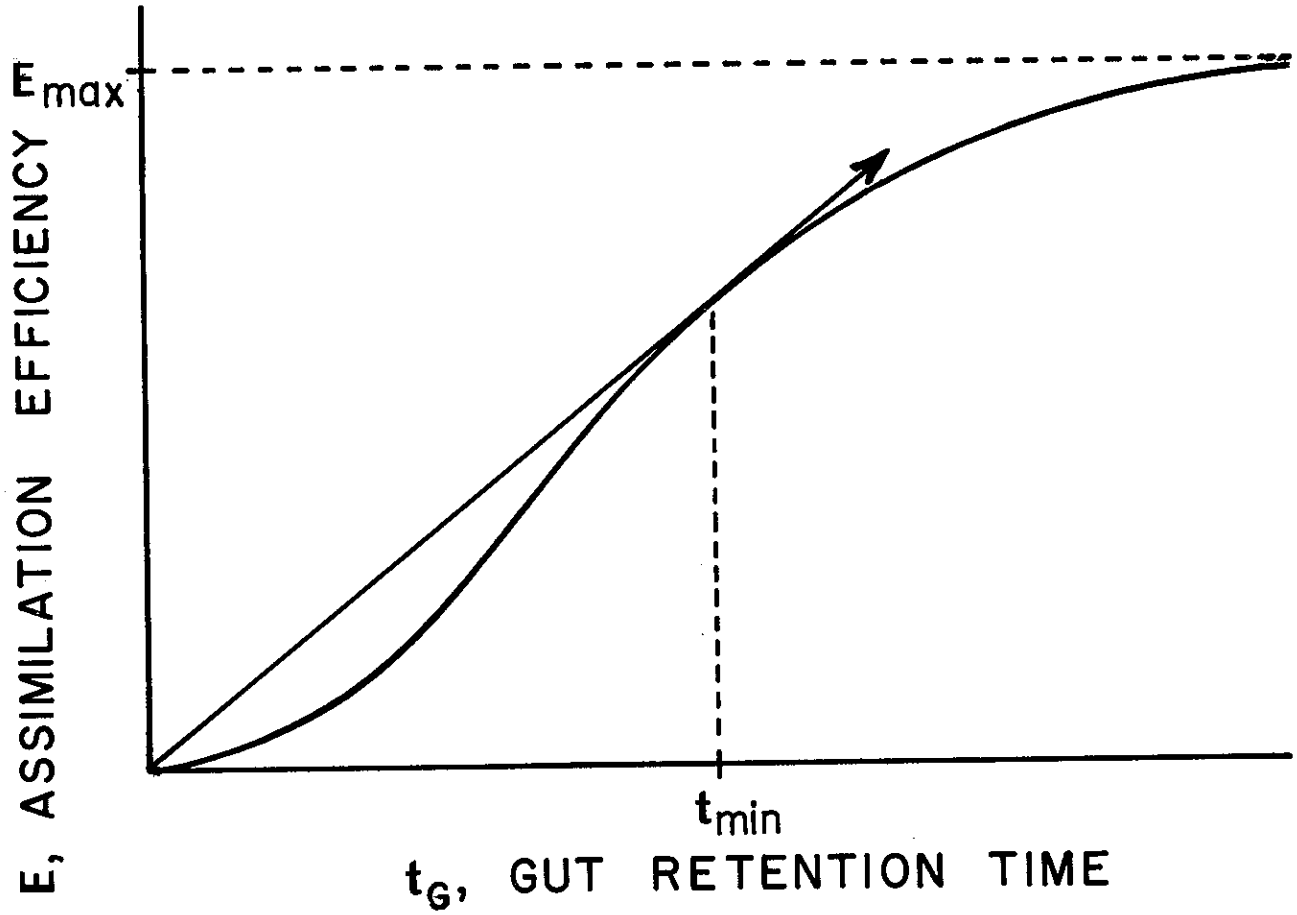

FIGURE 1. The relationship between digestion rates and the optimal length of time that food should be retained in the gut. The optimal time t_{min} is the point where a line through the origin is just tangent to the digestion function E.

For $P < P_{critical}$, $dF/dP = 0$ and ingestion increases linearly (Figure 2). When $P > P_{critical}$, ingestion is constant, $t_G = t_{min}$, and thus $dQ/dP = 0$ (i.e., assimilation is constant, in accord with Lampert [1977b]). It is likewise clear that $\lim_{P \to 0} Q = 0$, so the only remaining uncertainty concerns the behavior of assimilation, Q, in the region $(0, P_{critical})$. Using Equations 11 and 15, simplified to a single prey type, one can show that

$$\frac{d^2Q}{dP^2} = \frac{Ft_G^2}{P} \cdot \frac{d^2E}{dt_G^2} \qquad (\text{for } t_G \geq t_{min}) \qquad (17)$$

This second-derivative is everywhere negative and continuous on the interval because it is the product of positive coefficients and a negative term (d^2E/dt_G^2, see Figure 1), which means that the assimilation curve is convex upward for $P < P_{critical}$ (Figure 2). This explains why Lampert (1977b) found that a curvilinear model best fit his data for assimilation rates, even though Geller (1975) had shown that ingestion seemed to fit the rectilinear model using the same animals and food species.

The preceding analysis suggests that large differences in assimilation efficiency as a function of food concentrations are unlikely. Differences of a factor of 2 (Schindler 1968) or less (Lampert 1977b) are probably the full range that occur in natural populations. Efforts to improve the ways that assimilation efficiencies are treated in models probably would not have great effects on the simulated growth rates of the animals for this reason. The picture is a little different when one considers the fate of materials that are ingested but not assimilated by the animals. The fact that Schindler (1968) reported assimilation efficiencies between 90% and a little more than 40% means that between 10% and 60% of the ingested matter may be returned to the water unassimilated. Regarded in this way,

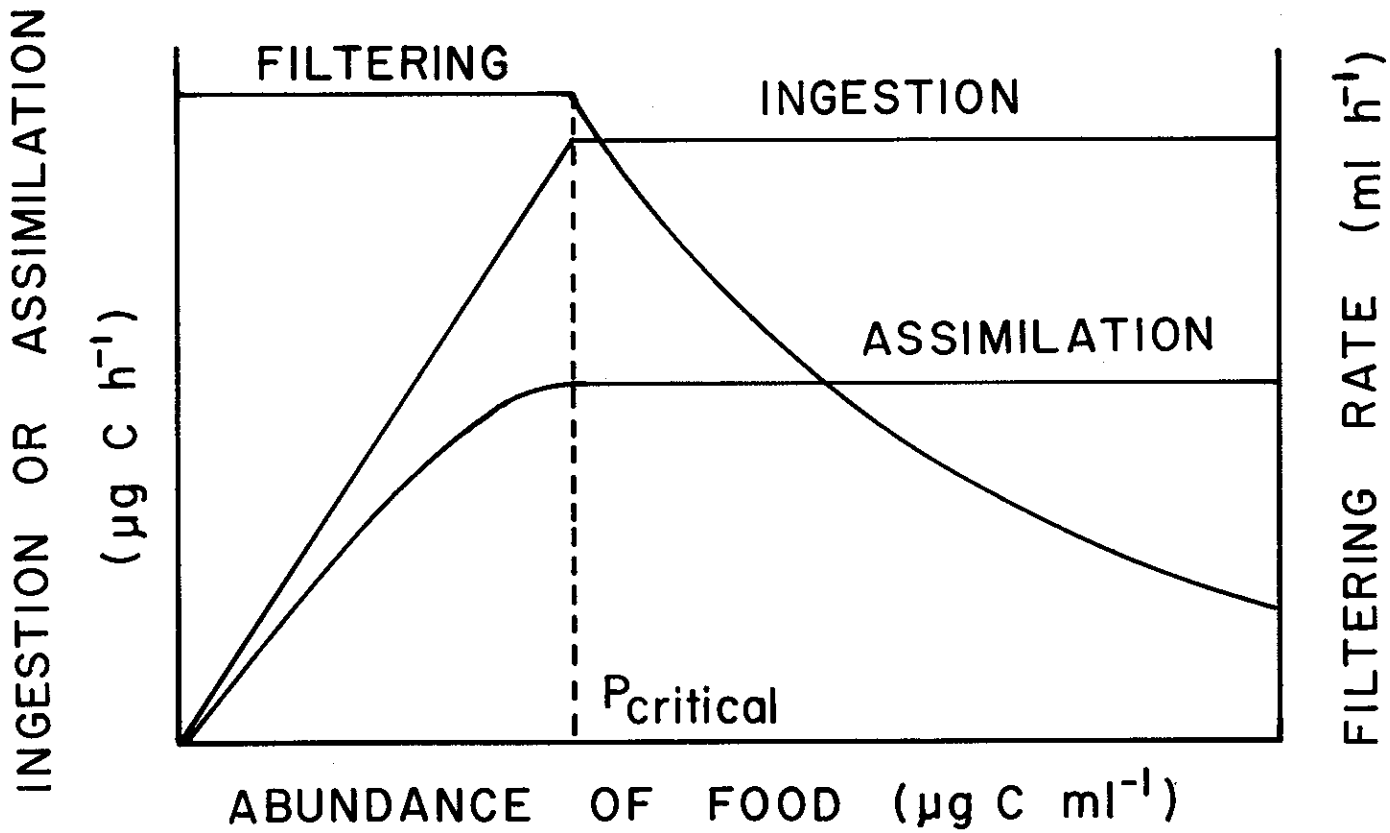

FIGURE 2. The relationships between abundance of food and values for filtering rate, ingestion rate, and assimilation predicted by the gut passage model described in the text. Ingestion conforms to the empirical rectilinear model, but assimilation is curvilinear for food concentrations less than $P_{critical}$.

the variability of the egested portion is much larger than that of the assimilated portion on a relative basis. The nutrients associated with this egested material are either released to inorganic pools immediately or are subsequently remineralized by microbial decomposers. Failure to properly account for these variable rates in simulation models means that a large and influential nutrient flux is in error. Releases of nutrients caused by inefficient feeding are not confined to egestion, either. Lampert (1978) has demonstrated that uningested cells that are broken or damaged during filtering may leach dissolved organic carbon to the water, and one can safely assume that nutrients like P and N are released as well. These various fluxes associated with imperfect feeding efficiencies may loom very large in calculations of nutrient recycling at some times of the year. Their magnitudes must be added to those of the nutrients that are excreted to the water during the normal metabolism of assimilated compounds, a process that will be explored next.

RESPIRATION AND EXCRETION

Most of the information currently available about assimilation rates and assimilation efficiencies of herbivorous zooplankton deals exclusively with the metabolism of carbon. The extent to which the data can be applied to other elements is open to some question. Clearly this presents no problems in models where constant stoichiometries are assumed for all plant and animal matter (e.g., Canale et al. 1975, 1976; Scavia 1979b; DiToro et al. 1977; Walsh 1977), but as soon as the option of variable cell nutrient quotas (Droop 1968, 1973) is introduced, it is no longer valid to use equal assimilation efficiencies for different elements. Empirical guides are substantially lacking on this point, but the stoichiometry of the animals probably does not vary nearly as much as that of the algae

(Cowgill and Burns 1975), and values may be similar among different species (Vijverberg and Frank 1976). Inorganic nutrient stores in the algae (e.g., luxury consumed stores of P) are probably not assimilated by the zooplankton, and the constituents would be selectively egested. This means that nutrient ratios in the egested material may be substantially different from the ratios that are ingested. Regardless of whether constant or variable stoichiometry is used to describe the phytoplankton, the best procedure at present seems to be to treat the zooplankton as having fixed elemental composition. This way net assimilation (assimilation minus catabolic losses) can be calculated in terms of C and then scaled to all other elements.

Efforts to characterize metabolic excretion of N and P by zooplankton in terms of their respiration rates are very common for both marine and fresh waters (e.g., Conover and Corner 1968; Satomi and Pomeroy 1968; Ganf and Blažka 1975). The published O:P and O:N ratios are subject to considerable variability, which may be due to variability in the nutritional condition of the animals (Ikeda 1977; Mayzaud 1973). The requisite information may be much more difficult to decipher than was originally anticipated. Lampert (1975), for instance, showed that much of the carbon assimilated by *Daphnia pulex* is metabolized almost immediately. He (Lampert 1977a) suggests that a sizable portion of the metabolic demands of herbivorous zooplankton is met by the immediate use of newly digested food, rather than by catabolism of body constituents. This means that the stoichiometry of excreted P and N may not bear any simple relation to the elemental ratios of the animal tissue.

Apart from these uncertainties over the proportions of C, N, and P that are metabolized by the zooplankton, there is some disagreement regarding the fractions of total P and total N that are released to the water in organic and inorganic form. Johannes and Webb

(1965) indicated that release of organic N was substantial for natural plankton, and others working with concentrated natural collections have sometimes found the same (Le Borgne 1973). Corner and Newell (1967), on the other hand, reported that *Calanus helgolandicus* consistently released about 75% of its N as ammonia, and that release of organic N was only substantial when the animals were crowded. Mullin, Perry, Renger and Evans (1975) have criticized the use of concentrated and unsorted net samples to estimate excretion rates because of compounds that leak from dead and injured animals. In general, the most cautious studies demonstrate that most of the N is released to the water as NH_3-N (e.g., Butler et al. 1969; Jawed 1969), but that a measurable fraction, usually less than 25%, consists of other compounds (e.g., Mayzaud 1973; Mayzaud and Dallot 1973). A similar disagreement exists over the relative rates of release of inorganic and organic P. Although concentrated net plankton may release as much as half of the P in organic form (Satomi and Pomeroy 1968; Le Borgne 1973), careful laboratory studies with undamaged animals find that most of the release in short-term assays is PO_4-P (Rigler 1961a; Butler et al. 1969; Peters and Lean 1973).

Much of the preceding work was performed with marine zooplankton, but the generalization that PO_4-P and NH_3-N are the dominant release products seems to hold for the freshwater plankton as well (Peters and Lean 1973; Jacobsen and Comita 1976). The compounds are very reactive biologically, and they are reabsorbed swiftly by the phytoplankton. The picture that emerges is one of very rapid cycling of nutrients within the biotic community at some times of the year. The distinction between egestion and excretion is a necessary one because rates of nutrient release decline quickly when zooplankton are separated from their food supply (Mayzaud 1976) and egestion is halted. Nonetheless, Scavia (1979a) has

reviewed some of the formulations used to model rates of respiration and nutrient excretion by zooplankton, and he acknowledges the need to make those processes functions of feeding rates, too. The experimental data unfortunately don't yet provide a good guide for this work, and a lot more needs to be done. Results of further studies are bound to influence our attitudes about all aspects of recycling fluxes in lakes and reservoirs. Many current models make a distinction, for instance, between the proportions of recycling fluxes that can be assigned to zooplankton and to the microbial community. Materials egested by the zooplankton may form a sizable fraction of the substrate available to the microbes, however, and thus the importance of identifying the fate of release products becomes evident.

GROWTH AND REPRODUCTION

One of the main reasons that the treatment of zooplankton in simulation models has failed to make any significant advances over the last 30 years is that very little attention has been paid to processes of growth and reproduction in these animals. Most of the effort has gone into formulating ingestion, assimilation, and even excretion more succinctly for the animals, all the while assuming that the population could be formalized as a single characteristic individual. The result in most cases has been that zooplankton populations are modeled as a single biomass pool (Bloomfield *et al.* 1973; Park *et al.* 1974; Steele 1974; Jorgensen 1976; Jorgensen *et al.* 1978), characterized by single functions for feeding, respiration, etc. The problem with this approach is that the experimental evidence is unequivocal on the point that these metabolic and behavioral processes definitely do not vary linearly with the biomass of an individual (Mullin and Brooks 1970; Paffenhöfer 1971, 1976; Poulet 1977). Each process can usually be scaled to an animal's

mass by the formula aW^b, where W is weight, carbon content, or other similar metric, and b is a coefficient that often lies between 0.67 and 1.0. For feeding terms like F_{max} and I_{max}, the precise value of b may depend on whether food abundance is above or below the critical concentration (Geller 1975; Lampert 1977b). For respiration, the value of b is generally recognized as about 0.75 (see Scavia 1979a for a discussion of how this value conforms to the experimental and modeling literature). As a consequence of this disproportionate scaling between biomass and activity rates, changes in the size and age structure of zooplankton communities cause effects that are usually ignored in simulation models. Equal biomass of juveniles and adults feed, assimilate, respire and grow at much different rates (Paffenhöfer 1976; Lampert 1977b). Often the model simplifications are carried to even further extremes. Cloern (1978), for instance, suspected that grazing by zooplankton was a cause of mortality on the alga *Cryptomonas*, but to estimate that mortality he applied a single filtering rate to every individual zooplankter in the lake, regardless of species, size, or developmental stage. This approach even exceeds the usual assumption that all zooplankton biomass behaves identically, regardless of how it is packaged.

Few models have tried to deal with age structure in the context of larger simulations. Maguire et al. (1976) modeled the life history and developmental stages of the calanoid copepod *Diaptomus* in elaborate detail, but the simulations were not interactive with the physical or biotic environment. The model used a projection matrix like that first introduced by Leslie (1945, 1948) to model discrete stages in which all transition probabilities, development times, and mortality rates were constant. Most authors who try to introduce age or size structure in their models do so in a very superficial way. Scavia and Park (1976) and McNaught and Scavia (1976), for instance, modeled age structure as an explicit linear function

of population size. They assumed that populations at low densities were composed primarily of immatures, and that at high densities they were exclusively adults. The efforts evince a concern for the importance of age structure in the populations, but the weakness of the approach is evident when the constructs are evaluated in light of detailed population studies (e.g., Rigler and Cooley 1974). Even though an adult copepod may outweigh its early naupliar stages by a factor of 50 or more, maximal biomass does not always occur when only adults are present. In fact, populations composed exclusively of adults are often very low in abundance, particularly during the winter (Eichhorn 1957). In the freshwater cladoceran *Daphnia*, large adult populations are usually associated with many juveniles (Hall 1964), and there is certainly no evidence that proportions of adults to juveniles change as a simple function of total population abundance (Prepas and Rigler 1978).

Proper formulations of zooplankton life histories in simulation models can be expected to have implications that extend beyond the level of simple descriptions of the communities. Patterns of mortality and resource utilization presumed to affect small species will probably affect the juveniles of large species as well (Neill 1975a, b) and will influence not just population abundances, but probably rates of nutrient cycling, too (Bartell and Koonce 1978). The only model to date that has attempted a comprehensive welding of phytoplankton production with the life histories of zooplankton species is that of Steele and Frost (1977). The model includes many simplifying assumptions in order to deal with feeding, growth, reproduction, and recruitment through the developmental stages, but the results are sobering, nonetheless. The authors conclude that "size structure is at least as important and probably more significant than total biomass of a population, in understanding the exchange of energy between trophic levels." The effects extend from

feeding and production to rates of nutrient recycling by herbivores. The Steele and Frost model was designed for a marine system, where copepods are the dominant zooplankton, so effects might be even greater in lakes where many of the common species release not fecal pellets but uncompacted feces that would be more easily retained in the water column as suspended detritus. What is apparent from the empirical data, and from a comprehensive model like that of Steele and Frost, is that we need a better index than just the total biomass of herbivorous zooplankton in a water mass in order to simulate their effects on the composition and abundances of algal populations.

DISCUSSION AND CONCLUSIONS

The principal motivation for including the dynamics of zooplankton in current simulation models seems to have been to account for important and variable loss rates among the phytoplankton. Given the source of the motivation it is not surprising that the modelers have tried to apply the methods, concepts, and equations that they used for the algae directly to the herbivores with very few changes. This is one reason why the models specify a "half-saturation constant" for feeding or for growth, even though there may be no strict analogue for this constant in nature. The models are consequently artificial constructs with limited utility in any ecosystem simulation. The persistent danger is that model designers can forget the origins and limitations of their constructions. Thus one finds statements that a model "contains a very complex construct for predator-prey interaction..., and one might expect it to be quite realistic" (Park et al. 1979). In fact, the model equations lauded there (Park et al. 1979) are not fully consistent with empirical data.

Because comprehensive models of the zooplankton are so rare at present it is difficult to know how large an error is introduced when one ignores size structure and other life history constraints. The same can be said about vertical migration, diurnal feeding rhythms, production of resting stages, and any other behavioral processes not discussed in this review which may have sizable impacts on the plankton community. Most of us believe that skillfully designed models are a good means to abstract the subset of important processes from the class of all possible ones, but we are reminded (Mortimer 1975) that modeling "cannot create data, and except within a strict and continuous verification framework, cannot distinguish good input from bad, cannot judge the validity of assumptions, and cannot generate original concepts." The model is handmaiden to the experimentalist, not the reverse.

We are at a stage where our ability to model the effects of zooplankton on phytoplankton communities will profit from easily identified experiments and continued simulation efforts, too. First, mechanisms and adaptations for feeding need to be evaluated in light of the discovery by Mayzaud and Poulet (1978) that the filter feeders change their digestive physiology in response to their food supply. Efforts are needed to quantify the actual determinants of feeding rates, and to examine how the animals respond to changes in the quality of their food supply. This avenue will prove far more useful than research directed toward finding values for the fictitious parameters of most current models. Rates of assimilation should be measured for mixtures of foods as well as for single food types to provide the guides for more realistic models. If ingestion really is controlled by volumetric constraints, then experiments will show it, and model formulations will be improved. Most importantly, rates of nutrient remineralization due to the activities of the zooplankton must be quantified for animals fed on diets of different quality and abundance. Experimental design is critical,

because uptake and release of nutrients proceed simultaneously and inseparably, but this is one area where models and empiricism work together very well (Lehman 1979).

New models can take advantage of the experimental findings, but more importantly, they can be used to discover how the complicated allometric relationships between size structure and size-specific activity rates can be simplified without sacrificing realism at the levels of interest (e.g., algal production). Can the gross behavior of a size-structured population be parameterized in terms of respiration rates, for instance? If so, those rates can be measured. The key to this approach is to simplify complex models in a way that keeps resultant errors to a minimum, but which also yields a set of constructs that can be applied generally. This is in contrast to the current practice of erecting assumptions of convenience without regard to the limitations on accuracy that they immediately impose. If we are going to continue to use simplistic unstructured representations of the zooplankton in our models, we at least ought to know how far the results will diverge from more complex models that are now within our ability to construct. Steele and Frost (1977) maintain that the differences are fundamental, and of equal consequence to any other element of the model, so the issue should no longer be ignored.

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EFFECTS OF VERTICAL AND HORIZONTAL TRANSPORT ON PHYTOPLANKTON POPULATION GROWTH AND DISTRIBUTION

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INTRODUCTION

The seasonal distribution of phytoplankton biomass in natural waters is the result of an interplay between the transport and kinetic factors to which the population is subject. It is the purpose of this paper to review a portion of the available theoretical and computational information, in order to provide background and guidance in assessing the relative importance of these two classes of phenomena.

Two types of analyses are presented. The first is based on a simplified vertical one-dimensional case which applies during the period of exponential growth of the population. For this case analytical solutions are available which can be used to determine the relative importance of kinetic and transport factors, particularly phytoplankton settling and vertical dispersion.

The second approach is based on computational experience with phytoplankton calculations in a variety of natural waters which illustrate the effects of vertical and horizontal transport. These have been chosen from calculations with which the author has personal experience and for which the relevant effects have been investigated. The review is not meant to be exhaustive but rather to present a series of cases which illustrate the various factors that have been found to be important.

MASS CONSERVATION EQUATION

The application of a conservation of mass equation to phytoplankton biomass has a long history beginning with the investigations of Riley *et al.* (1949). The general three-dimensional form of the equation is:

$$\frac{\partial P}{\partial t} + \frac{u\partial P}{\partial x} + \frac{v\partial P}{\partial y} + \frac{w\partial P}{\partial z} - \frac{\partial}{\partial x}\left(E_x\frac{\partial P}{\partial x}\right) - \frac{\partial}{\partial y}\left(E_y\frac{\partial P}{\partial y}\right) - \frac{\partial}{\partial z}\left(E_z\frac{\partial P}{\partial z}\right) = (G-D)P \quad (1)$$

where P is the concentration of phytoplankton biomass (chlorophyll, or dry weight, for example); u,v,w are the velocities in the three coordinate directions x,y,z; E_x,E_y,E_z are the dispersion coefficients in the three directions which parameterize the mixing motions not included in the advective field specification; G is the population growth rate; and D is the population death rate. The latter two parameters specify the kinetics of the population: its response to light, temperature, nutrient concentration, and predation. The proper specification of these expressions is the subject of other presentations. The subject of this presentation is primarily the effect of the transport field and its interaction with the kinetics, although methods of establishing the transport parameters will be discussed as well.

The difficulty with a direct analysis of the conservation equation (1) is that, even for the simplified case of constant transport and kinetic parameters, the mathematical complexities prevent a comprehensive analysis. Therefore a simplified analysis of the one-dimensional vertical approximation will be used to investigate the interactions with respect to the dimensionless parameters groups.

VERTICAL ONE-DIMENSIONAL ANALYSIS

The analysis of a simplified vertical one-dimensional phytoplankton conservation equation based on the asymptotic properties of the solution has been reported elsewhere (Di Toro 1974). This section and the computed results are based on that analysis which contains the mathematical details.

Consider an idealized lake or reservoir for which the horizontal gradients are negligible in comparison to the vertical and temporal gradients and for which the geometry is such that the horizontal cross-sectional area is constant in depth. The resulting one-dimensional conservation of mass equation is:

$$\frac{\partial P}{\partial t} - \frac{\partial}{\partial z}\left(E \frac{\partial P}{\partial z}\right) + \frac{\partial}{\partial z}(wP) = (G - D)\, P \qquad (2)$$

In the absence of vertical transport, the population at each depth would either grow exponentially if $G(z) > D(z)$ or decay exponentially if $G(z) < D(z)$. For $E = w = 0$ the solution is of the form:

$$P(z,t) \sim \exp\,[G(z) - D(z)]\, t \qquad (3)$$

so that G-D is the net growth or decay rate of the population in a kinetic reactor with conditions comparable to those at depth z. The magnitude of G is quite well known (Di Toro et al. 1971; Eppley 1972) from numerous short-term growth experiments. For the case of excess nutrients and constant optimal light intensity, G is in the range of 1.5-2.5 day^{-1} at 20°C. The decay rate, D, for a population isolated from a light source is on the order of 0.05 to 0.2 day^{-1} at 20°C (Riley et al. 1949). Thus, in the absence of vertical transport and with excess nutrients present, there should exist a depth at which the population is growing at a rate on the order of 1.0 day^{-1} so that in ten days the population at this depth increases by approximately 22,000 times. At large depths, however, the population should, in ten days, decrease to approximately 37% of its initial concentration. Such explosive growth does occasionally occur (patch blooms), but the more normal course of events is a much slower growth of the entire population until either nutrient exhaustion, zooplankton predation, or self-shading reduces G-D to a point at which population growth

ceases. The question of interest is how does the population growth rate depend on the kinetic parameters, G and D, and the transport parameters, E and w.

If conditions are such that the population does increase with time, and for that period the transport and kinetic parameters are constant in time, then there are mathematical reasons (DiToro 1974) to expect that after a relatively short time, the population distribution will be of the form

$$P(z,t) \simeq P(z)e^{\mu t} \tag{4}$$

That is, the entire population will be growing at an asymptotic population log growth rate, μ, <u>independent of depth</u>. The asymptotic population growth rate, μ, and the asymptotic population distribution as a function of depth, P(z), aside from a constant multiple, are independent of the initial biomass. They depend only on the kinetic and transport parameters which characterize the period of population growth.

To establish that, in fact, phytoplankton biomass behaves as predicted by the mathematical analysis, plots of log P(z,t) vs. time at various depths are presented in Figures 1 and 2.

During the intensive Project Hypo study of Central Lake Erie (Burns and Ross 1972), the phytoplankton population increased approximately fivefold in 35 days. As shown in Figure 1, the asymptotic population growth rate was $\mu \simeq 0.043$ day^{-1} and the population increased at this exponential rate at 1, 12, and 17-20 m, with the population in the deeper layers (21-25 m) acquiring this growth rate near the end of the sampling period. The time to achieve the asymptotic distribution is $\sim 1/\mu$ which in this case is on the order of 25 days.

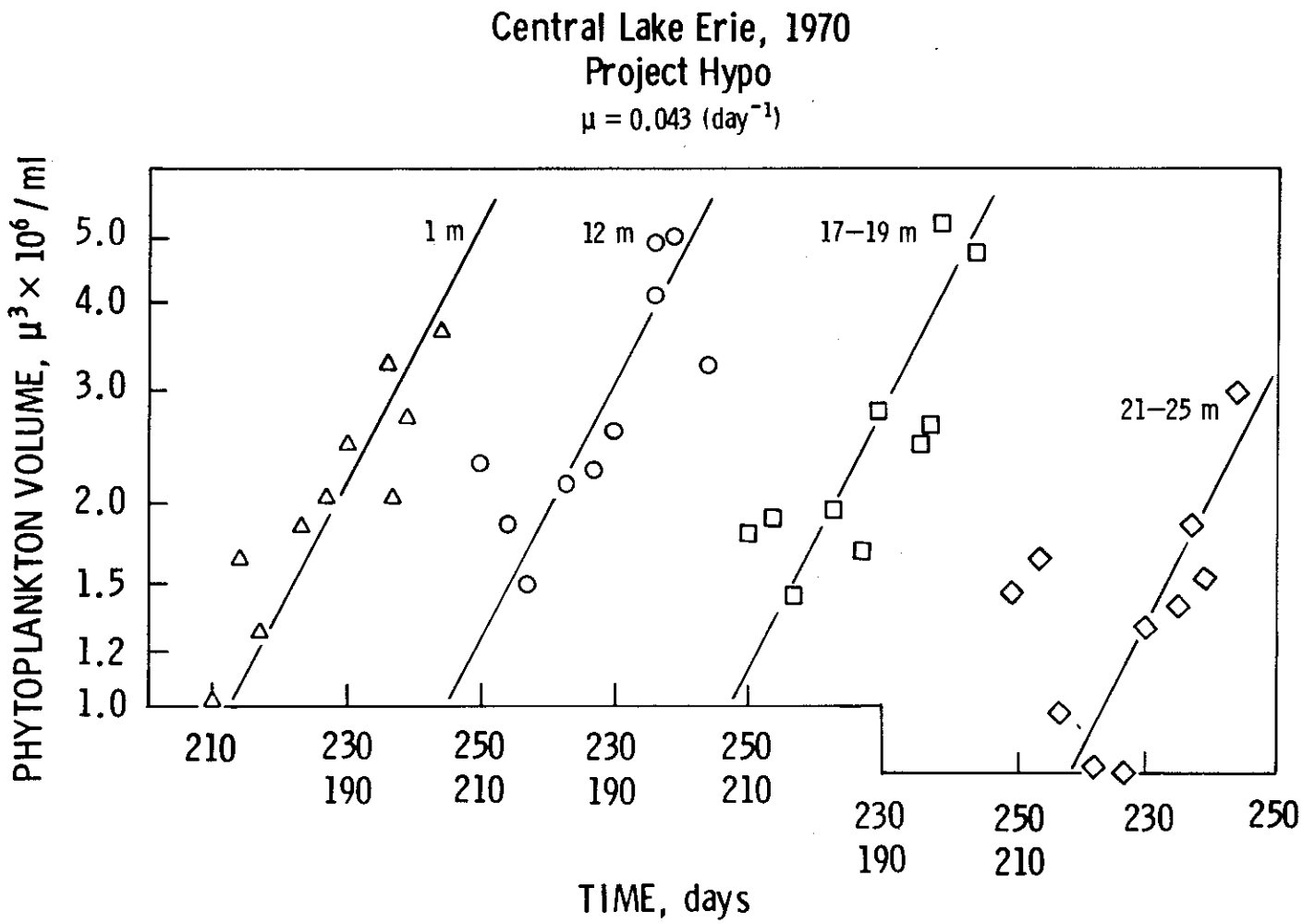


FIGURE 1. Central Lake Erie phytoplankton biovolume, four station log averages, 1970 (Project HYPO), logarithm of phytoplankton biomass versus time at depths of 1, 12, 17-19, and 21-25 meters. The time scales for each depth are displaced to the right and labeled below each other for clarity, as indicated (Di Toro 1974).

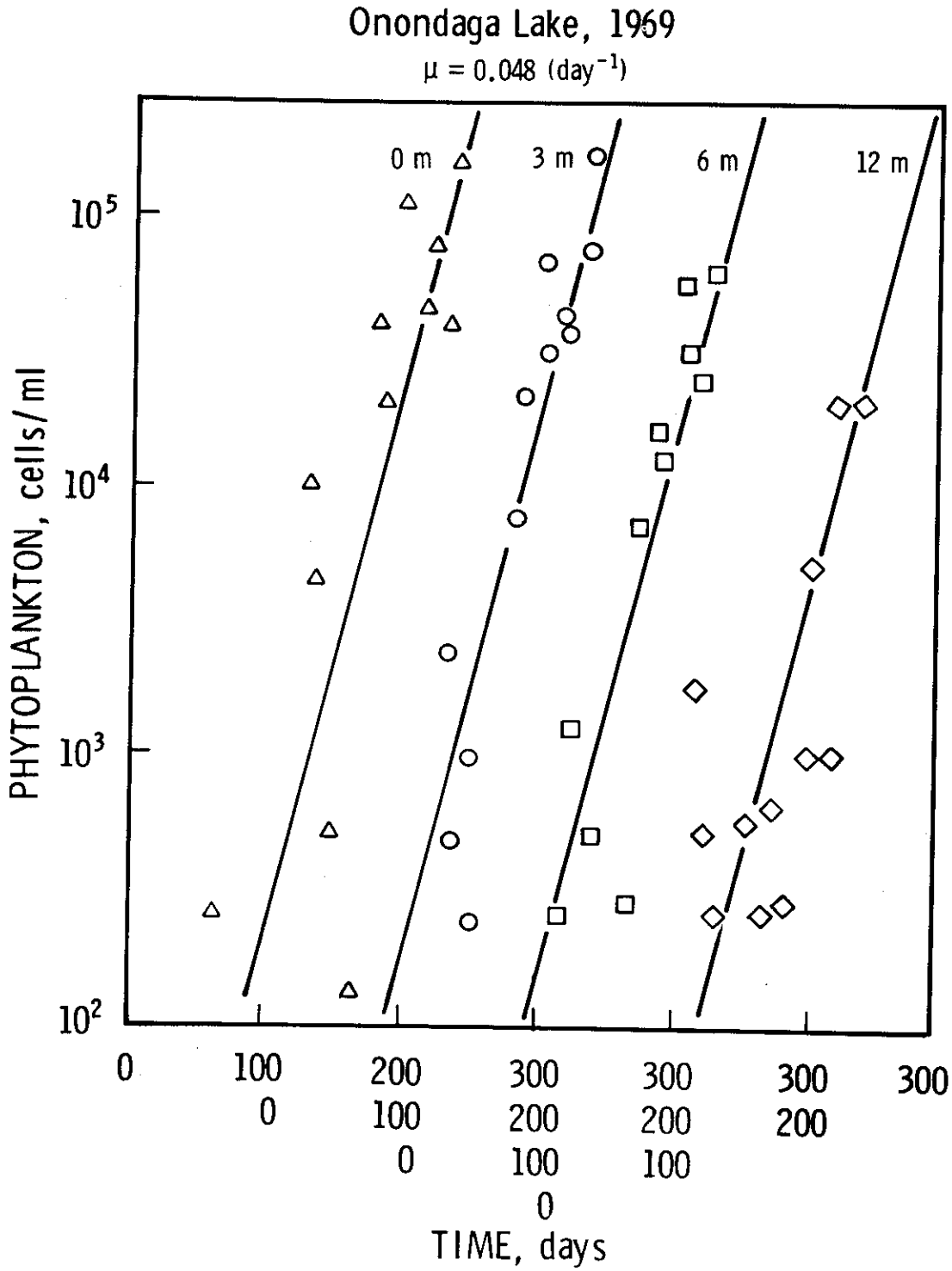


FIGURE 2. Onondaga Lake, two stations, 1969. Logarithm of phytoplankton total cell counts versus time at depths of 0, 3, 6, and 12 meters. The time scales for each depth are displaced to the right and labeled below each other for clarity, as indicated (Di Toro 1974).

Onondaga Lake is a small (12 km^2 surface area, 20 m maximum depth), highly eutrophic lake in New York State (O'Brien and Gere 1971). The duration of the growth period for the phytoplankton population is 150 days during which the population increases one thousandfold to concentrations of 10^5 cells/ml corresponding to a population growth rate of μ=0.048 day^{-1}. As shown in Figure 2, the population growth rate is approximately the same at the four depths sampled even though there is almost an order of magnitude less biomass in the deeper layers.

Taken as a whole, the data presented here and elsewhere (Di Toro 1974) strongly suggest that during the exponential growth of a population, if the kinetic and transport parameters are constant, an asymptotic population growth rate occurs which characterizes the growth of the entire population, which is independent of position.

SOLUTION FOR A SPECIFIC CASE

The existence of an asymptotic population growth rate, independent of depth for temporally constant parameters, is a consequence of the properties of the general mass balance equation. In order to investigate the relationship between this growth rate and the parameters of the equation, it is necessary to make certain assumptions concerning the variations in depth of the kinetic and transport parameters. In particular, assume (not very realistically for some cases) that all the parameters, save the growth rate, are constant. For the growth rate, a form which leads to an analytical solution is an exponentially decreasing approximation:

$$G(z) = G\ e^{-z/L} \tag{5}$$

where L is the reciprocal of the light extinction coefficient.

The solution proceeds directly from the conservation of mass equation (2) together with the boundary condition at the water surface which requires that no biomass cross the air-water interface, and the boundary condition at infinite depths, for which we require that the biomass remain finite. The result is an eigenvalue problem which has a solution

$$P(z) = e^{\pi z/2L} J_\nu(2\lambda e^{-z/2L}) \tag{6}$$

where $\nu = \sqrt{\pi^2 + 4\lambda^2/\kappa}$

$\kappa = G/(D+\mu)$

$\pi = wL/E$

$\lambda = L\sqrt{G/E}$

and $J_\nu(Z)$ is a Bessel function of the first kind. The eigenvalue equation is obtained from the boundary condition at $z = 0$:

$$J_\nu(2\lambda)(1 + \frac{\nu}{\pi}) \frac{\pi}{2\lambda} = J_{\nu+1}(2\lambda) \tag{7}$$

A multiplicity of μ's are solutions for this equation; the one of interest is that which is largest and, more important, positive since it is the asymptotic population log growth rate. For certain sets of π and λ, no positive μ exists. For such situations no population increase is possible.

In order to investigate the interplay of transport and kinetic factors on the population growth rate, μ, a series of numerical solutions of the eigenvalue equation as a function of relevant parameter groups have been generated. Consider the results in Figure 3 which present the population growth rate plus decay rate normalized by the maximum growth rate as a function of normalized settling velocity $w/\sqrt{G/E}$. Assume for the sake of simplicity that the growth rate, G,

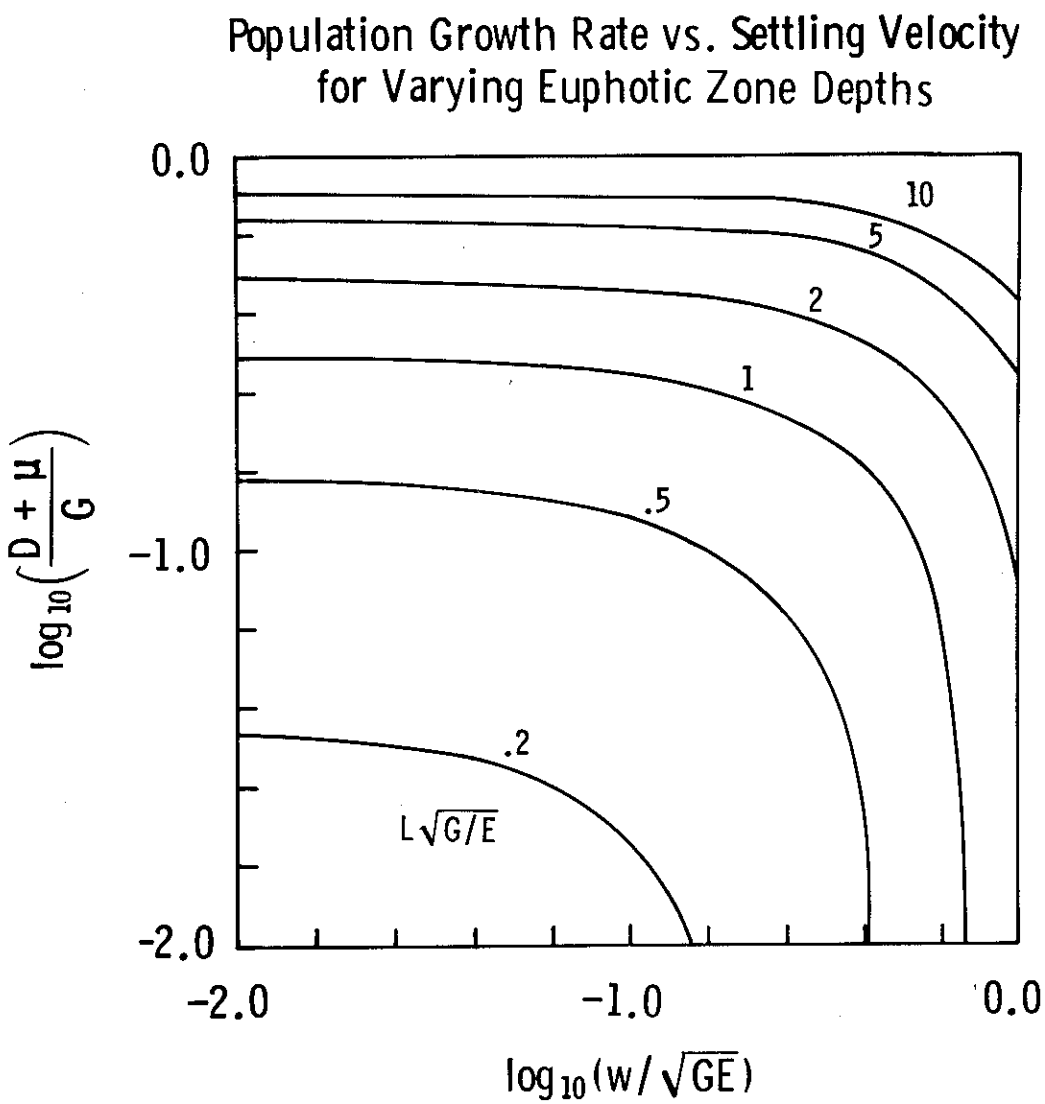


FIGURE 3. Normalized population net growth rate versus normalized algal settling velocity for various normalized euphotic zone depths. The plot illustrates the effects of these parameter variations if it is assumed that growth rate and dispersion coefficients are constant (Di Toro 1974).

and the dispersion coefficient, E, are constant with values G = 1 day^{-1} and E = 1 m^2/day. Then the plot relates normalized population growth rate to changes in sinking velocity in m/day for various euphotic zone depths in meters. A reasonable value of D/G is 0.1 so that if the transport parameters result in $(D + \mu)/G < 0.1$, no population growth is possible. Thus for a euphotic zone depth of L = 0.2 m no population growth is possible and the population simply decays away, even for a zero settling velocity. For this case the loss due to vertical dispersion exceeds the production in the small euphotic zone. For a euphotic zone depth of 0.5 m settling velocities of up to w = 0.1 m/day have a small effect on the population growth rate, whereas a value much in excess of 0.16 m/day cannot be tolerated by the population. Situations with deeper euphotic zones, for example L = 2 m, can sustain higher settling velocities of up to w = 0.2 m/day before the population growth rate is affected and population growth continues to be possible for settling velocities of up to w = 1.0 m/day.

A similar presentation for the effect of dispersion coefficient is shown in Figure 4. For simplicity assume that the G = 1.0 day^{-1} as before and that w = 1 m/day. Then the plot relates normalized population growth rate to dispersion coefficient in m^2/day. A most surprising result can be seen in Figure 4. Increasing vertical dispersion from E = 1.0 m^2/day to 10.0 m^2/day actually increases the population growth rate with the effect being the most dramatic for the shallow euphotic zones with depths of less than 5 meters.

At first glance this appears to be incorrect since the mixing causes the population in the euphotic zone to be transported out of the zone, on balance, and therefore, increasing dispersion would tend to decrease population growth. However, biomass is also being advected out of the zone via the settling velocity. With a small dispersion coefficient there is very little biomass at the surface

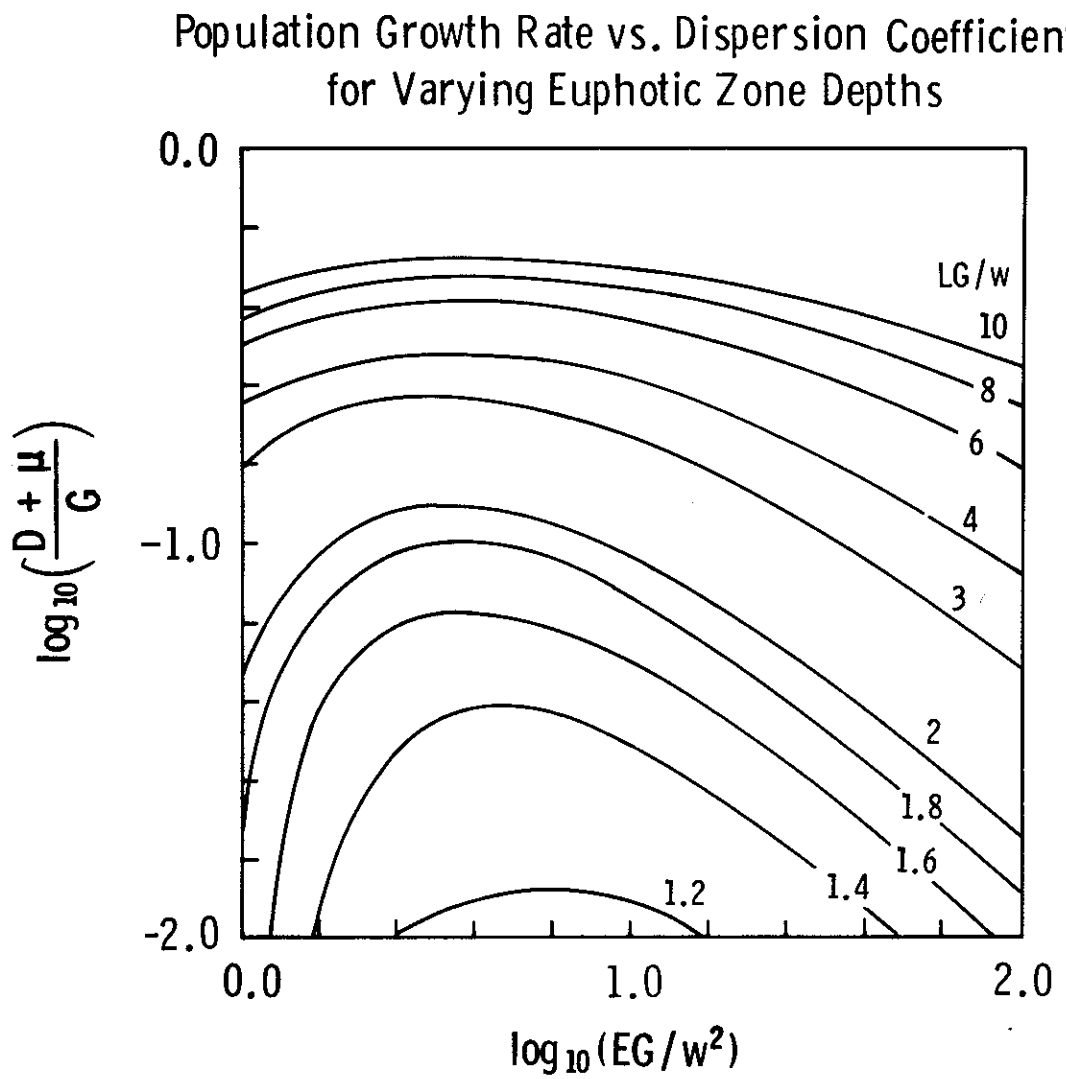


FIGURE 4. Normalized poulation net growth rate versus normalized vertical dispersion coefficient for various normalized euphotic zone depths. The plot illustrates the effects of these parameter variations if it is assumed that growth rate and settling velocity are constant (Di Toro 1974).

since there is no way for the population, which grows as it sinks, to return to the surface layers. Hence, increasing the mixing actually benefits the population by allowing more biomass to accumulate in the surface layers where the growth rates are largest. Further increases of dispersion to $E = 100\ m^2/day$ do in fact decrease population growth rate until, with too large a dispersion coefficient, the normalized population growth rate decreases below the critical value of $(D + \mu)/G = 0.1$ at which point if $D/G = 0.1$ the population net growth rate is negative and the population decreases.

PRELIMINARY APPLICATIONS

As a first step in exploring the utility of the preceding analysis, a series of representative values for the dimensionless parameters is shown in Figure 5. The majority come from the coastal ocean (Riley et al. 1949) with two lakes included. It is interesting to note that the values of $G/D+\mu$ are comparable whereas the value of $L\sqrt{G/E}$ span an order of magnitude. The major difficulty with increasing the number of points on this graph is in estimating the settling velocity. Values for G, D, and L for a given temperature, light intensity, and extinction coefficient can be approximated; μ is obtained from population observation; vertical dispersion can be obtained from vertical temperature models in which case the analysis, to within the accuracy of the assumptions of constant parameters, can provide vertical settling velocities.

It is interesting to note that these data, when plotted on the figure which investigates the effect of dispersion, are in the range of the maxima for the oceanic situations and in the decreasing regions for the shallower situations. Whether this indicates some adaptive

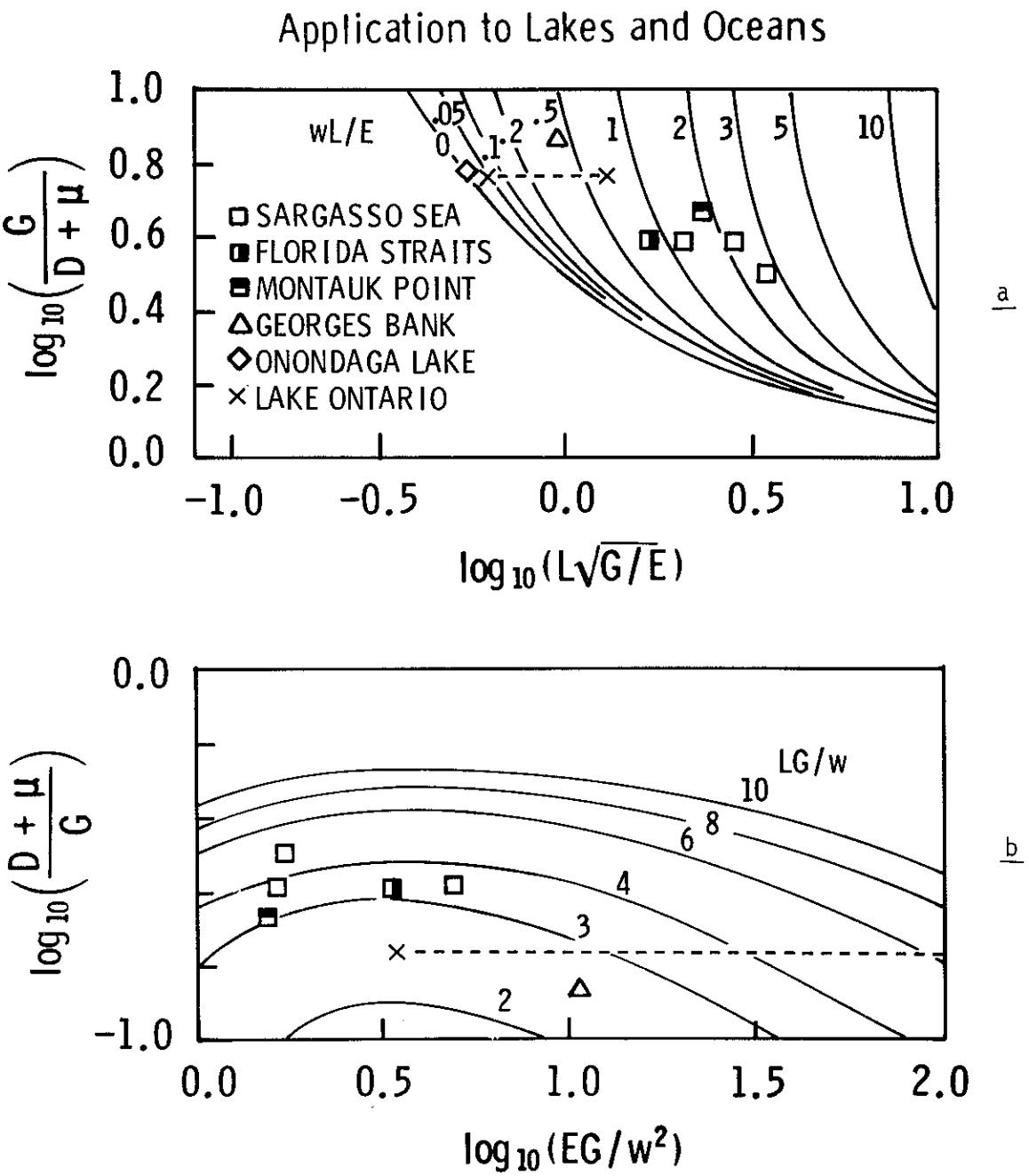


FIGURE 5. Application to lakes and oceans (a) the range of biologically and physically relevant dimensionless numbers. (b) normalized population growth rate versus normalized dispersion coefficient - a possible adaptation to the vertical dispersion in the oceans (Di Toro 1974).

mechanisms for the characteristics of the marine phytoplankton is an interesting speculation but it is probably beyond the precision of the analysis to pursue this point.

An example of the application of these equations to the determination of algal settling velocities is shown in Figure 6 (Schnoor and Di Toro 1979). Biomass and carbon-14 primary production measurements are used to estimate G and μ. The depth of the euphotic zone and vertical dispersion coefficient are obtained from light and temperature measurements, respectively. The death rate, D, is varied between 0.05 and 0.25/day. For a specific death rate, equation (7) can be solved for the relationship between net growth rate, μ, and gross growth rate, G, for various settling velocities, w. For D = 0.05 and 0.25/day these curves are shown on Figure 6 together with the data from Lake LBJ and Central Lake Erie. The comparison indicates that the blue-green algae (Lake LBJ) and phytoflagellates (Lake Erie) have low gross growth rates and correspondingly low settling velocities ($\sim$ 0.1 m/day). Green algae had the largest gross growth rate and settling velocity (1-3 m/day). Diatoms are intermediate for both parameters (0.1 - 1.0 m/day).

METHODS OF ESTIMATING TRANSPORT COEFFICIENTS

For any reasonably complicated natural setting, analytical solutions of the conservation of mass equations are not feasible and numerical integrations are necessary. If the water body is conceived of as a series of interconnected segments, then a typical conservation of mass equation for concentration c_{ij} of substance i in segment j has the general form:

$$V_j \frac{dc_{ij}}{dt} = \sum_k Q_{kj} c_{ik} + \sum_k E'_{kj}(c_{ik} - c_{ij}) + S_{ij} \qquad (8)$$

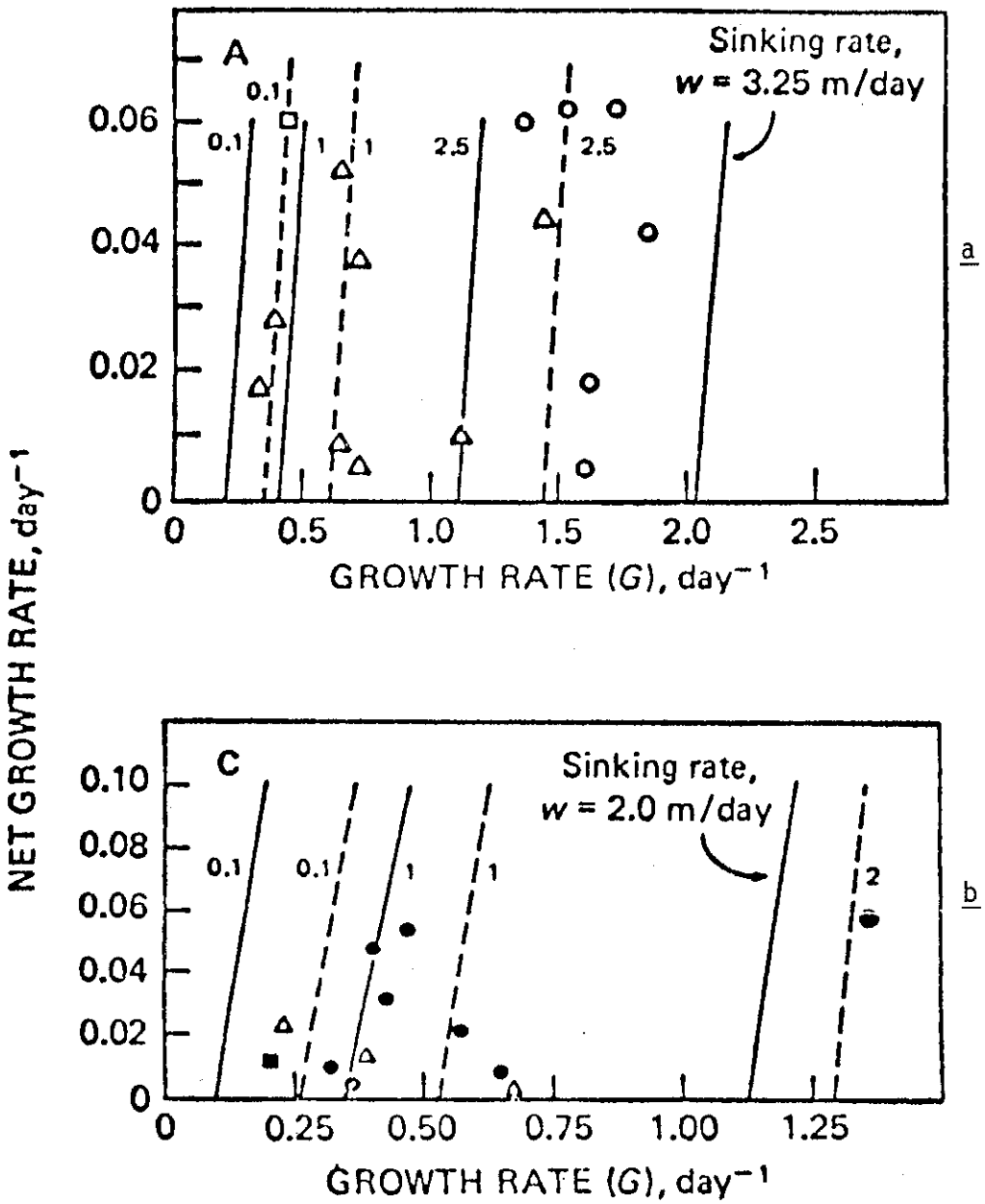


FIGURE 6. (a) Observed net growth rate versus average gross growth rate for Lake LBJ, 1973-1974. Lines of algal sinking velocity consistent with the observed euphotic zone depth and vertical dispersion. Key: Greens (open circles), Diatoms (triangles), Blue-Greens (open square), Mixed (closed circle), Flagellate dominated (closed square). Solid lines assume D = 0.05 day^{-1}; dashed lines assume D = 0.25 day^{-1}. (b) Similar to (a) for Lake Erie, 1970 (Schnoor and Di Toro 1979). Redrawn from Schnoor and Di Toro (1979).

V_j is the segment volume, S_{ij} is the net source of substance i in segment j; E'_{kj} is the bulk rate of transport of c_{ik} into and c_{ij} out of segment j by the dispersive and mixing velocities for all segments k adjacent to segment j, and Q_{kj} is the net advective flow rate between segments k and j. Numerical integration of these equations gives the temporal distribution of the concentrations in each of the spatial segments.

In order to make the calculation it is necessary that the advective and dispersive transport parameters Q_{kj} and E'_{kj} be specified. Three methods are available to obtain the advection: hydrodynamic computations, measurements, and the analysis of tracers. Only the later method is available for the estimation of dispersion coefficients. Therefore, whatever method is chosen for the estimates of the velocity field, an analysis of available tracers is a necessary step.

The vertical segmentation used for an analysis of the dissolved oxygen-phytoplankton-nutrient interactions in Lake Erie (Di Toro and Connolly 1979) consists of an epilimnion and hypolimnion segment. The vertical dispersion coefficients for the central and eastern basins were obtained from a fit of the temperature data. The results are shown in Figure 7. The decrease in vertical dispersion as stratification occurs and the increase at overturn are characteristic.

Horizontal exchanges can also be estimated from tracer data. As an example consider the exchange between Saginaw Bay and Southern Lake Huron that results from the counterclockwise large lake circulation into the northern shore and out of the southern shore of Saginaw Bay. Analysis based on the available temperature, chlorides, and phosphorus data is shown in Figure 8 (Di Toro and Matystik 1979).

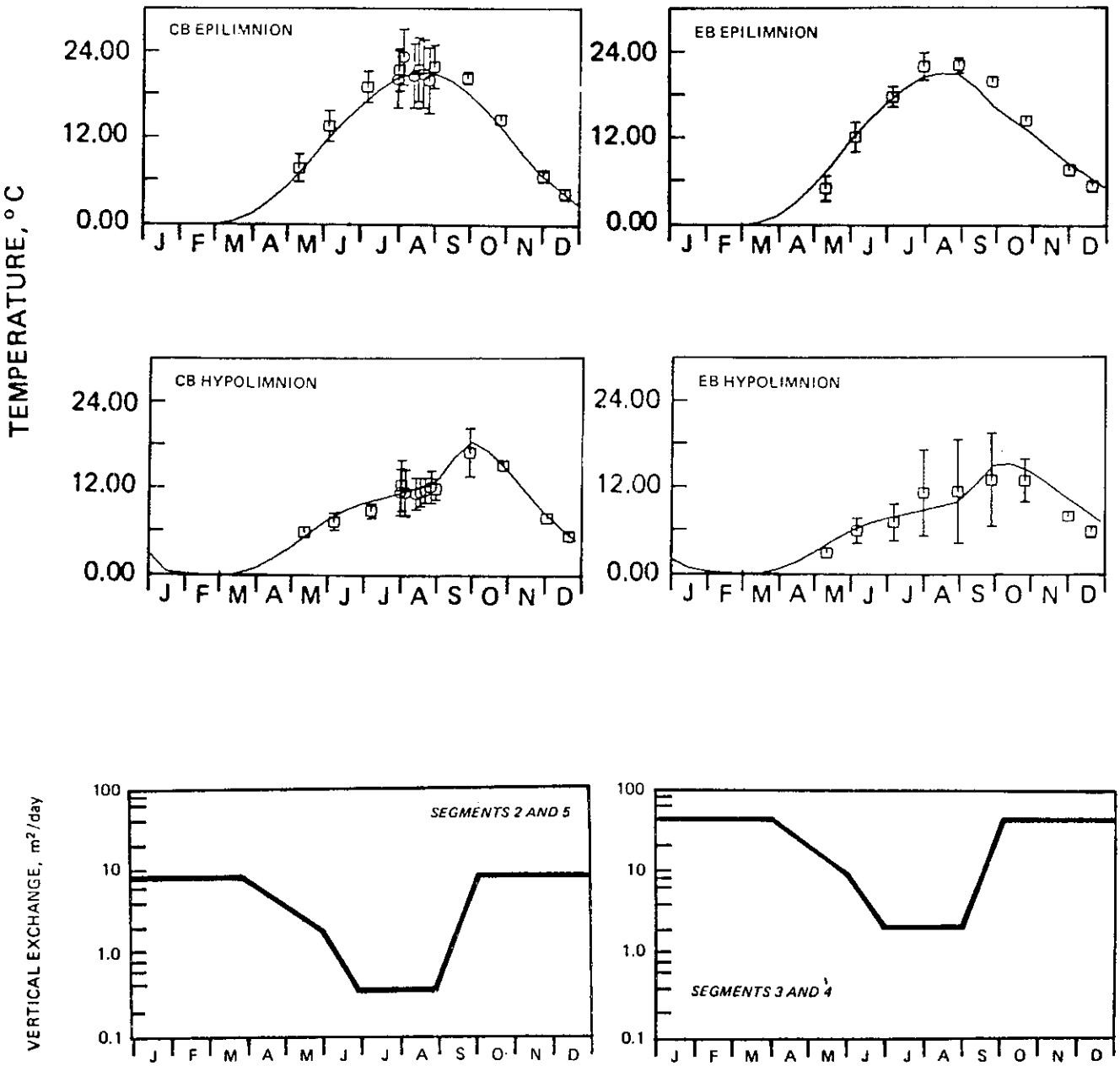


FIGURE 7. Calibration of Central Basin and Eastern Basin Lake Erie vertical dispersion, 1970. Symbols are means ± standard deviation of observed epilimnion and hypolimnion temperatures. Lines are calculated using the illustrated vertical dispersion coefficients (Di Toro and Connolly 1979).

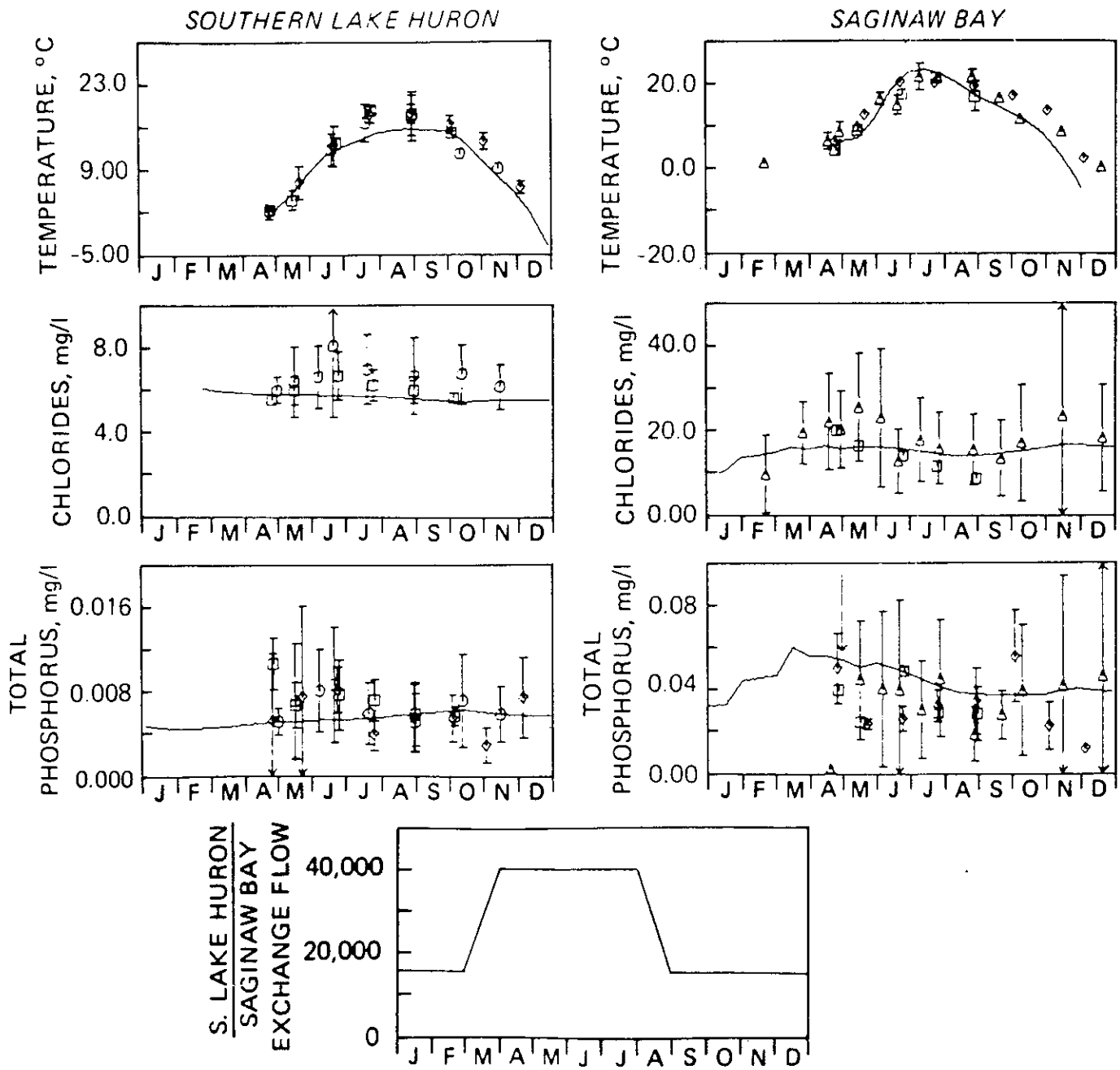


Figure 8. Calibration of Saginaw Bay - Southern Lake Huron exchange flow. Symbols are means ± standard deviation of observed temperatures, chloride, and total phosphorus concentrations. Lines are the calculated results using the indicated exchanging flow (in ft^3/sec) (Di Toro and Matystik 1979).

It is important to realize that even if the horizontal and vertical transport are calculated using hydrodynamic models, it is necessary to calibrate and verify the computed circulation against observations of velocity, and to demonstrate that the computed transport regime can reproduce the observed behavior of tracers. There is very little reason to expect that computed transport regimes have any *a priori* validity, primarily because of the uncertainty of subgrid turbulence, forcing functions, and numerical approximations.

EFFECTS OF HORIZONTAL TRANSPORT

The interactions between horizontal advective and dispersive transport and population growth can be approached using the analytical approach presented previously. However the tractable analyses are restricted to rather idealized settings. Hence the principal effects will be illustrated using computational examples.

Advective Flushing

The most readily observed advective transport effect is the effect of hydraulic detention time on the population growth or decay. Consider a simple one-segment system with only advective flow as the transport mechanism. The conservation of mass equation is:

$$\frac{dP}{dt} = (G - D)P + \frac{Q}{V}(P_{in} - P) \qquad (9)$$

where P_{in} is the inflowing boundary concentration.

It is easy to see that growth is possible if $G > D + 1/t_o$ where $t_o = V/Q$, the hydraulic detention time. If growth does not exceed death plus export, then the population decreases in time. This effect,

which can be termed washout as it is in chemostat studies, has been observed in a river setting and a reservoir.

The San Joaquin River drains the southerly portion of the delta to the east of San Francisco Bay. A two-year series of observations of phytoplankton, zooplankton, and inorganic nitrogen has been analyzed (Di Toro et al. 1971) and the results are shown in Figure 9. The seasonal variation of temperature, freshwater flow, and incident solar radiation is shown. In 1966, the first year shown, as the temperature and incident light increase and the flow decreases, the growth rate exceeds the death plus export loss rate and the phytoplankton population starts to increase. It continues until nitrogen limitation reduces the growth rate. For 1967, the situation is markedly different. Although the temperature and solar radiation distribution are essentially identical, the advective flow is quite different. Advective flow exceeding 10,000 cfs persisted until mid-summer and the washout effectively prevented any significant phytoplankton growth until the flow decreased to a point where the growth rate exceeded the loss rate. At this point the population began to grow as in the previous year.

A similar effect occurred in the upstream portion of Lake Livingston Reservoir which is located on the Trinity River in southeast Texas approximately 150 mi. south of Dallas. A eutrophication analysis of this reservoir (Di Toro et al. 1976) for the Texas Water Quality Board employed the segmentation illustrated in Figure 10. The advective flow for 1975 entering the upstream portion of the reservoir is also shown. Flows exceeding 10,000 cfs persisted until July of that year. The computed and observed chlorophyll and total inorganic nitrogen in three segments are shown in Figure 11. For segment 1 adjacent to the dam, the start of population growth is controlled by light and temperature and begins in April. For the

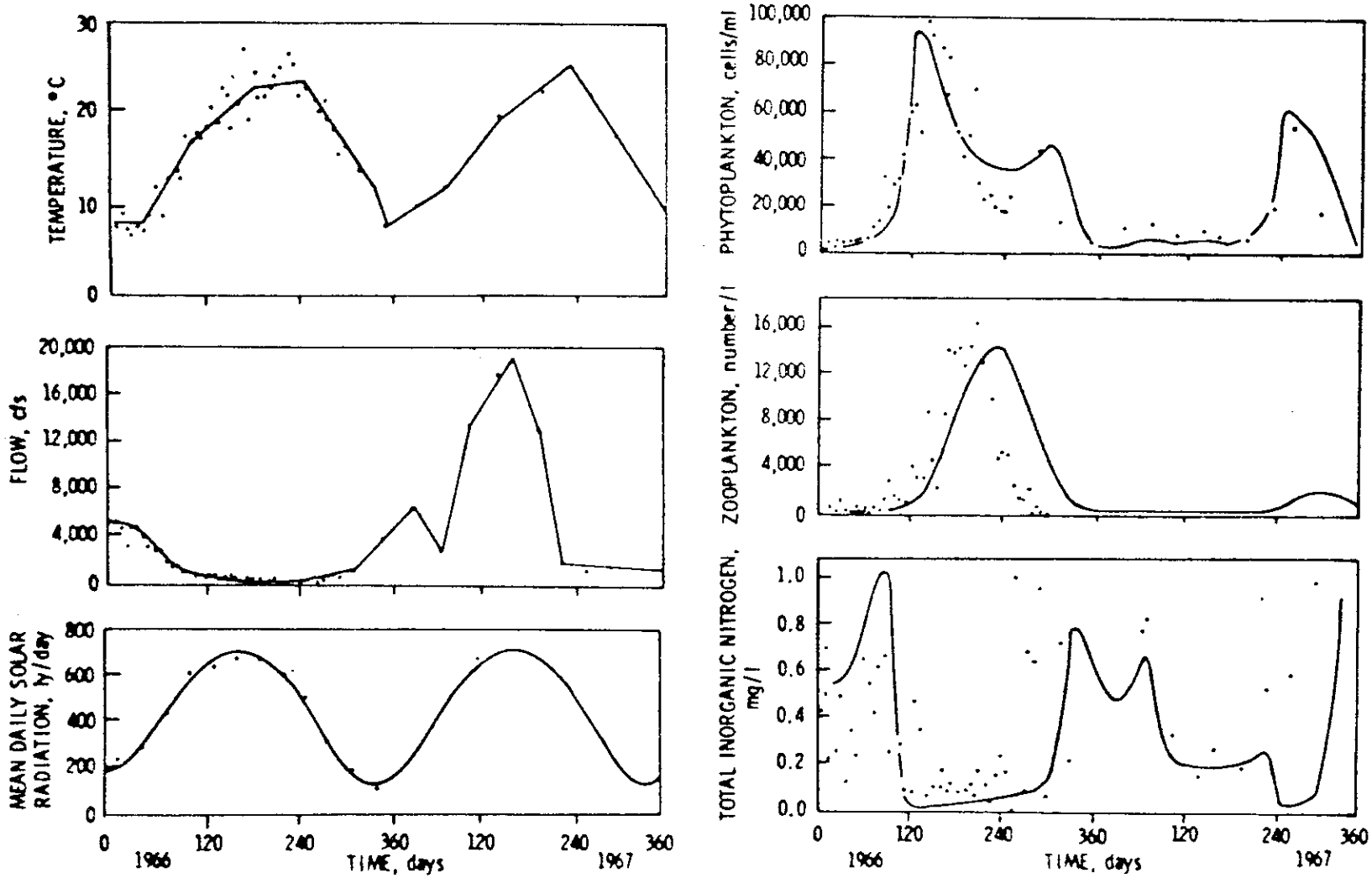
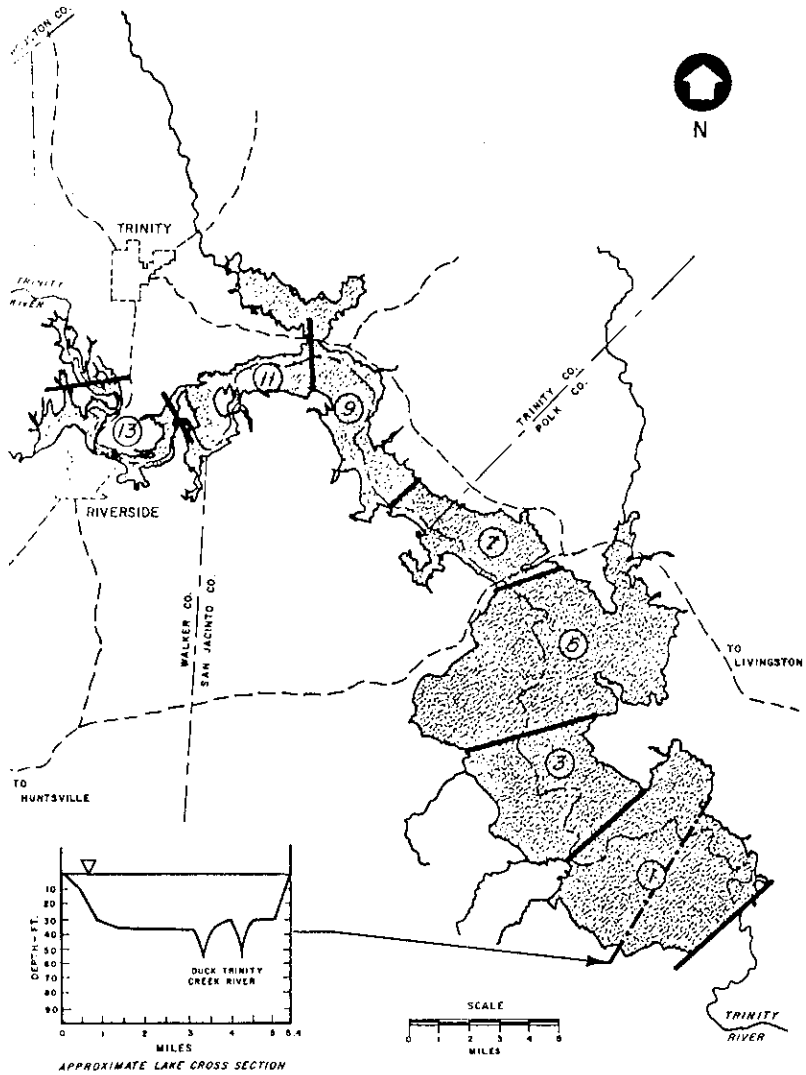


FIGURE 9. Seasonal variation of temperature, advective flow, and incident solar radiation: observations and interpolating lines (left). Comparison of computed and observed phytoplankton cell counts, zooplankton counts, and total inorganic nitrogen for the San Joaquin River, near Mossdale (right), 1966-1967 (Di Toro et al. 1971). Redrawn from Di Toro et al. (1971).



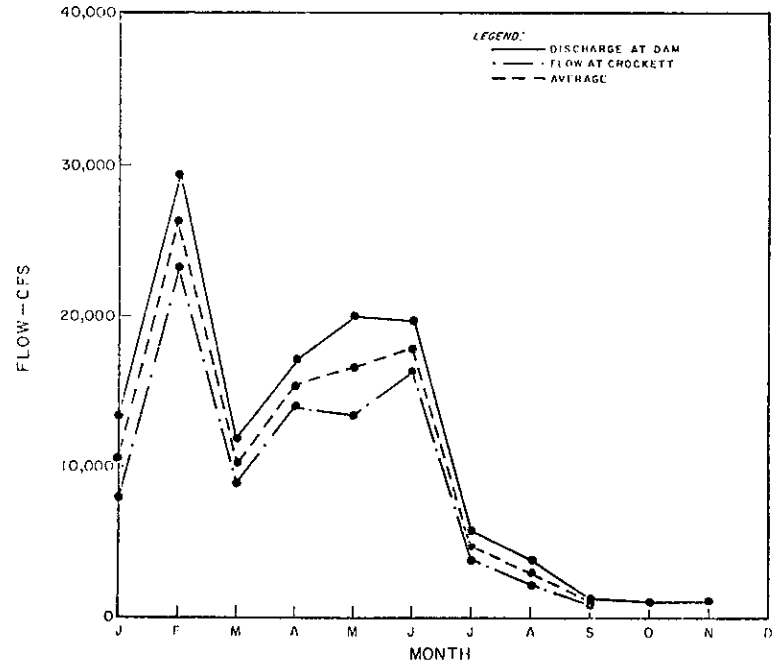


FIGURE 10. Segmentation and advective flow for Lake Livingston, 1975 (Di Toro et al. 1976). Redrawn from Di Toro et al. (1976).

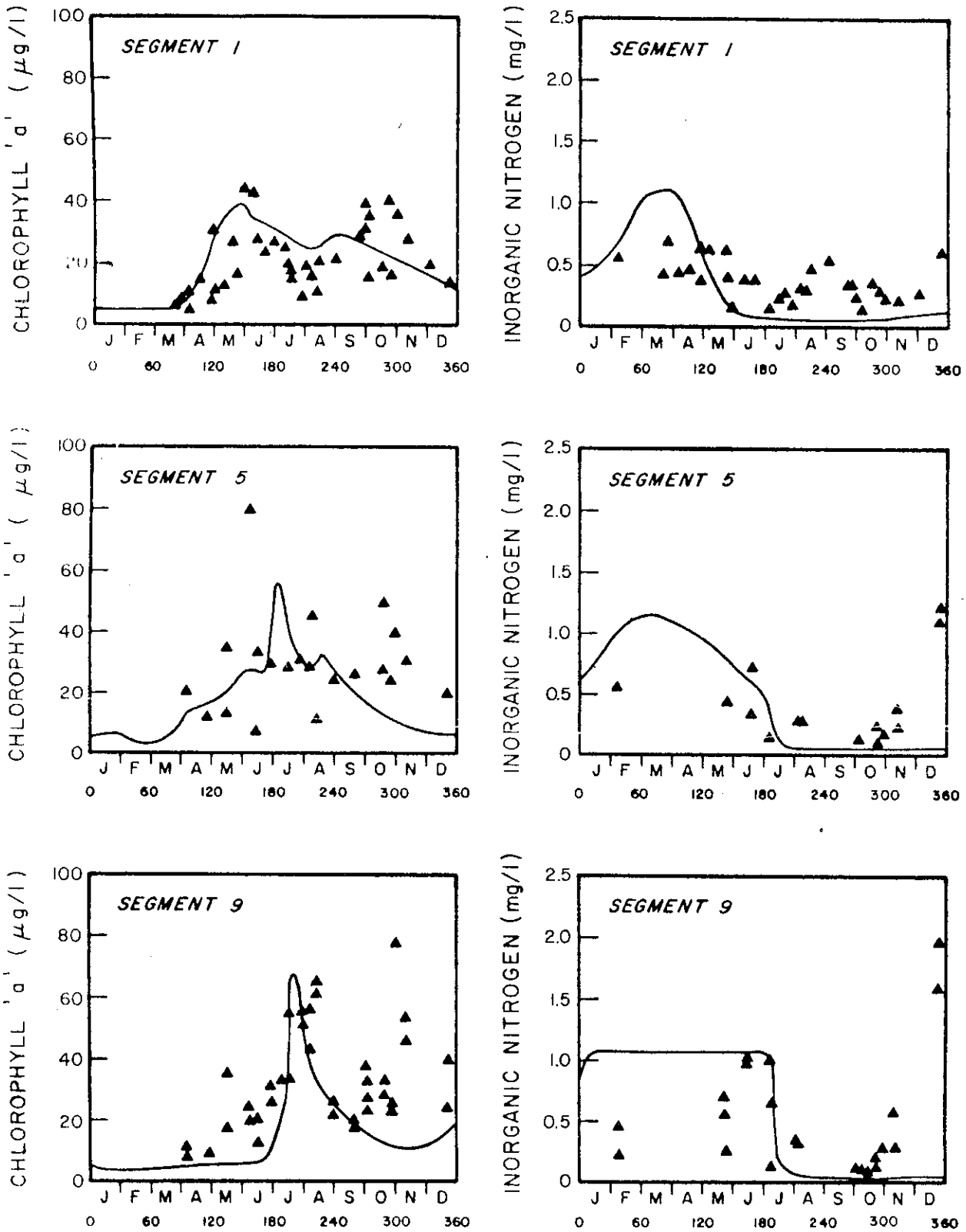


FIGURE 11. Observed and computed chlorophyll and inorganic nitrogen concentrations for Lake Livingston. Segment numbers refer to Figure 10 (Di Toro et al. 1976). Redrawn from Di Toro et al. (1976).

upstream segment 9, however, growth is not observed to begin until late May or early June and is not computed to occur until early July. The mid-reservoir segment 5 exhibits behavior that is a composite of the two extremes. This analysis also considered phosphorus which was in excess supply throughout the year.

The effect of advective transport on the phytoplankton population of Lake Livingston, therefore, is more complex than simply a washout phenomenon. The effect of washout is seen in the upstream regions of the reservoir but its effect is lessened in the lower portions of the reservoirs because of the larger volumes and detention times. The upstream segments have a combined detention time of approximately eight days at the high flow, whereas the lower reservoir segments have a combined detention time of approximately 70 days at the same flow. Hence a simple analysis which treats the entire reservoir as one completely mixed epilimnion and hypolimnion would not be able to predict any advective flow effect when in fact in the upper reservoir where the observed phytoplankton populations are largest there is a marked washout flow effect.

Dispersive Flushing

Similar flushing effects are computed to occur for exchange flows between embayments and the adjacent open-water segments. Saginaw Bay provides an example of this phenomenon. Figure 12 illustrates the computed effects for chlorophyll and total phosphorus (Di Toro and Matystik 1979). The figures on the left are the calibration calculations. The center figure illustrates the results of lowering the phosphorus recycle rate to a value consistent with the open lake waters (the total phosphorus concentration is not appreciably different). In an attempt to assess the effect of the magnitude of the flushing flow

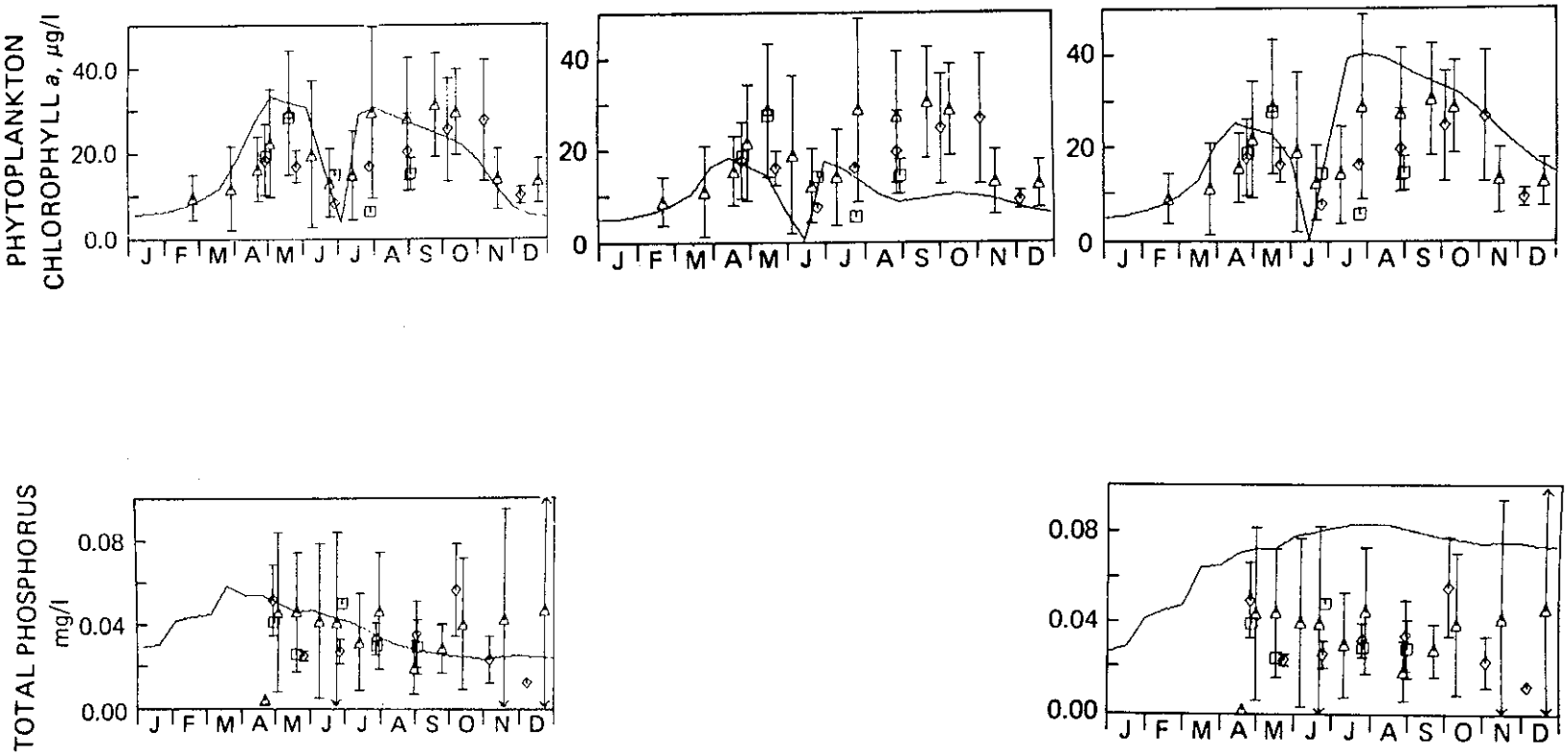


FIGURE 12. Saginaw Bay sensitivity calculations: the effect of phosphorus recycle rate and Southern Lake Huron flushing. Calibration: comparison of observed means ± standard deviation versus calculated lines (left). The effect of lowered recycle rate (center). With the lowered recycle rate, the effect of reducing the flushing flow to zero (right) (Di Toro and Matystik 1979).

estimated using tracers as described previously, a computation with the flushing flow set to zero is illustrated in the figures on the right. Only the advective flow of the Saginaw River is retained in this calculation. The result is a marked increase in computed chlorophyll and total phosphorus. The difference between the computed chlorophyll in the center and the total phosphorus on the left and the no flushing case on the right represents the effect of the flushing flow. It is interesting to note that the effect is more complex than just a change in the detention time of the segment. Both phosphorus concentration and chlorophyll concentrations are affected so that the change in flushing flow has an exaggerated effect: lowering the exchange flow increases the phosphorus available for growth and increases the detention time so that the population can respond to the increased nutrient concentration.

Shallow Embayment Flushing and Enhanced Production

The effect of dispersive exchange between productive shallow embayments and deeper less productive segments in the main channel of an estuary provides another example of the effect of transport. If the main portion of the estuary has higher nutrient concentrations than the shallow embayments, the dispersive exchange enhances the production of the entire system. Figure 13 illustrates this effect for the Potomac Estuary (Thomann *et al.* 1974; Di Toro *et al.* 1977). The segmentation includes both the tidal embayments and main channel. The calculated and observed chlorophyll concentration of August 1968 is shown in the upper right of Figure 13. The figure on the lower right shows the result of the computation with the tidal embayments removed from the computation. A nearly twofold reduction of the computed phytoplankton chlorophyll results. Whereas the effect of Saginaw Bay flushing on the computed seasonal distribution in Southern Lake Huron is only via the input of nutrients, for the Potomac

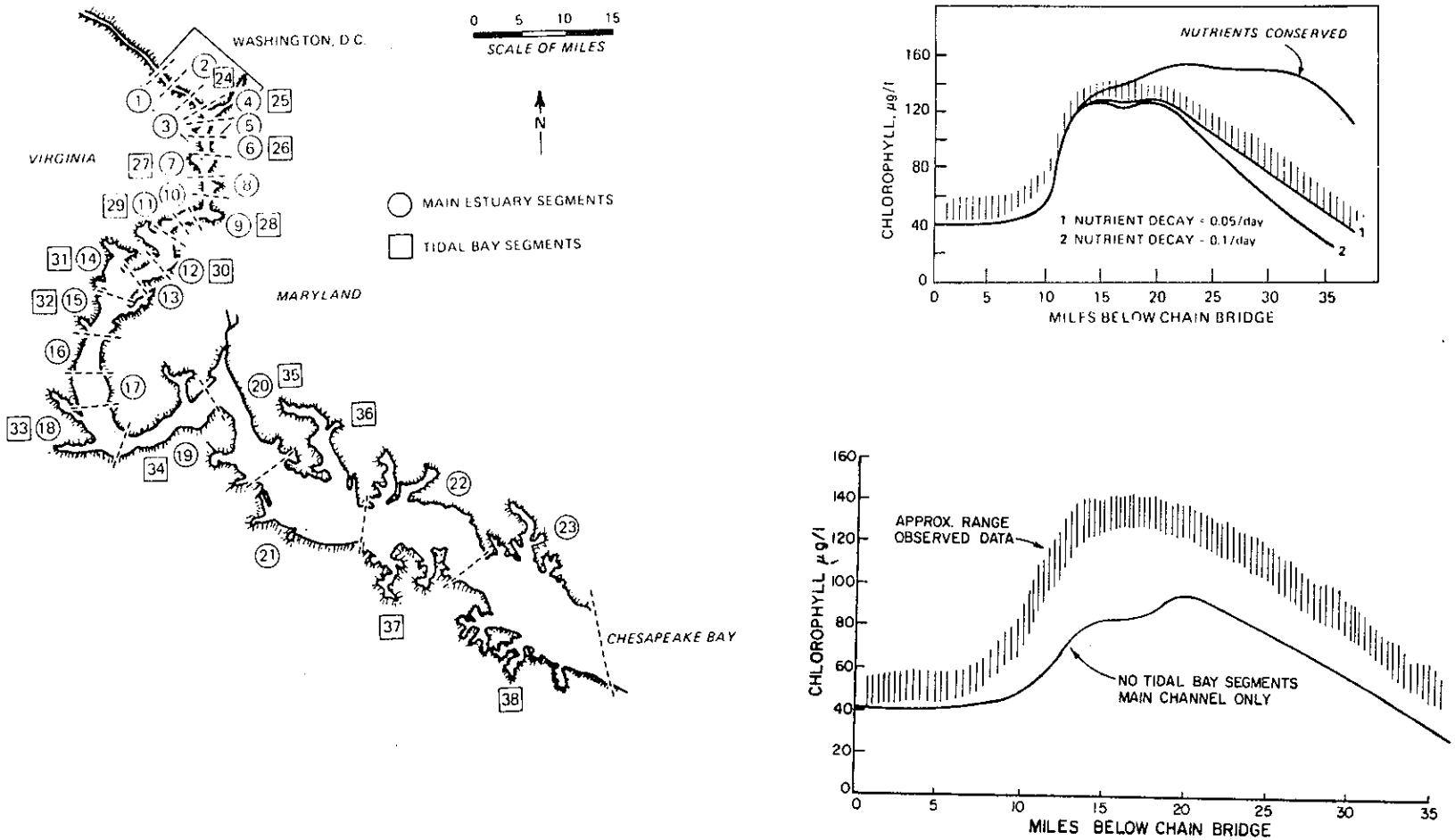


FIGURE 13. Potomac Estuary segmentation indicating tidal embayments and main channel segments (left). The calibration for nutrients as a conservative quantity and with settling (upper right). The effect of removing the tidal embayments from the calculation (lower right), August 1968 (Thomann et al. 1974; Di Toro et al. 1977). Redrawn from Thomann et al. (1974); Di Toro et al. (1977).

Estuary the tidal embayments provide regions of growth in which the phytoplankton population gross growth rate is substantially higher and the residence time is long enough so that the overall production of the system increases. This is analogous to the effect of vertical dispersion as shown in Figure 4. For small dispersive exchange the nutrients entering the embayments would be small and the production would be nutrient limited. For very large flushing exchanges the detention time would decrease to a point when residence time in the embayments would be too low for production to occur. However, there exists a range of exchanges that enhances the overall production.

Horizontal Circulation

A convenient simplification for the analysis of phytoplankton populations in lakes and reservoirs is horizontal uniformity with the analysis concentrating on the behavior of the vertical and temporal gradients. Horizontal circulation can have an effect on computed chlorophyll concentrations, however. Consider the sensitivity calculations performed for a three-dimensional Lake Ontario model (Thomann *et al*. 1978). Figure 14a illustrates the computed average May-June chlorophyll concentrations in the top four meter deep layer. The lower two figures are contours of the difference between the calibration, Figure 14a, calculation and the computed results for (b) the direction of the flow reversed but with the same magnitude and (c) the magnitude of the flow at one-tenth of the calibrated values used for the calibration. Average changes are on the order of 1-2 μg Chl-*a*/ℓ with certain regions exhibiting larger changes. For the flow reversal case, the larger changes are in the shoreline regions whereas for the reduced flow magnitude case, the larger changes are near the nutrient sources which are not being flushed by the reduced horizontal circulation. These computed changes amount to 20-40% differences when compared to the calibration case. These are

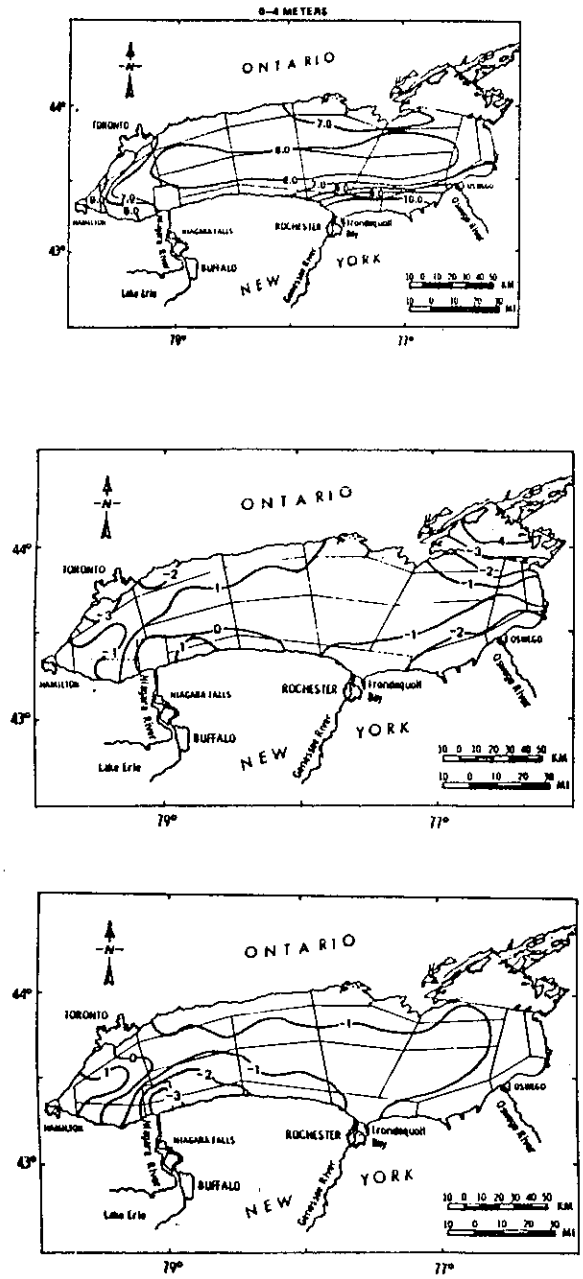


FIGURE 14. Lake Ontario three-dimensional sensitivity calculation. The computed June 1972 average chlorophyll in the 0- to 4-m layer (a). The effect of reversing the direction of all flows in the calculation (b); the effect of reducing all flow to 10% of their magnitude (c). These contours are differences in the sensitivity and the calibration computations, in μg Chl a/ℓ, for the top layer (0-4 m) average June 1972 (Thomann et al. 1978).

not excessive differences considering the violent velocity field changes imposed upon the calculation. For Lake Ontario, at least, the sensitivity of the calculation to the details of the three-dimensional circulation is not severe.

CONCLUSIONS

The effects of vertical and horizontal transport on the growth and distribution of phytoplankton populations are substantial and significant. If the vertical dispersion or algal settling velocity are too large relative to the depth of the euphotic zone, no population growth is possible. For the case of a shallow euphotic zone and a substantial settling velocity, increased dispersion can actually enhance the population growth rate by returning a substantial quantity of the population into the euphotic zone.

The washout effects of large advective flows are clearly discernible since these flows can reduce the hydraulic detention time to the point where growth is impossible. The effects of horizontal flushing and circulation are more difficult to detect in observations; however, computations designed to determine the sensitivity of the calculations to these dispersive exchanges exhibit substantial variations. Depending upon the circumstances, increasing the exchanging flow can reduce the population within the embayment or increase both it and the main open-water regions. It is uncertain as yet whether full three-dimensional hydrodynamic calculations are ever warranted (or fruitful) but in one case at least the sensitivity of the computation to radical changes in the circulation was not large.

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MECHANISMS AND MODELS FOR THE TRANSMISSION OF LIGHT, RATES OF PHOTOSYNTHESIS, AND THE REGULATION OF PHYTOPLANKTON POPULATIONS

by

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INTRODUCTION

Light is important in reservoirs and other natural waters because it is photosynthetically active. Much of the light transmitted through water may be intercepted by planktonic algae and used during photosynthesis to produce organic material. The organic material is important, not only because it is a potential source of food for aquatic animals, but also because the production and consumption of organic materials have profound effects on the chemistry of the water. For example, planktonic algae are the most abundant organisms in most reservoirs and lakes, and they produce and consume large quantities of oxygen during photosynthesis and respiration. Light and photosynthesis are therefore intimately related to problems of water quality. Indeed rates of photosynthesis and concentrations of algae are typically high in reservoirs and natural lakes with poor water quality.

TRANSMISSION OF LIGHT THROUGH NATURAL WATERS

Solar radiation in the band of wavelengths between 400 and 700 nm is photosynthetically active. This is also the range of wavelengths that we perceive as light, so we may refer to this radiation as light. Photosynthetically active radiation that enters water changes its direction of transmission because it is refracted as it crosses the surface, it changes its intensity because it is absorbed and scattered, and it changes its color or spectral composition because some wavelengths are attenuated more than others. The color changes are important for photosynthesis because the plant pigments involved in photosynthesis are more likely to absorb some wavelengths than others. Kirk (1977) has recently prepared a very readable summary of these phenomena.

A fundamental property of light is its intensity, the radiant flux per unit area, often referred to as irradiance. Irradiance may be expressed in energy units, such as $ergs \cdot m^{-2} \cdot s^{-1}$, but the most appropriate measure for photosynthesis is the flux of quanta, because photosynthesis is a photochemical reaction in which one mole of quanta is required to react with one mole of electrons to complete a reaction. One mole of quanta is defined as one einstein, and quantum meters that measure irradiance in terms of $einsteins \cdot m^{-2} \cdot s^{-1}$ are now in general use for measuring underwater irradiance.

When photosynthetically active radiation (PAR) is measured with a quantum sensor or other broad-band sensor at intervals of depth in water, the decrease of irradiance as depth increases is very nearly exponential, as would be expected from the Lambert-Bouguer Law for the transmission of light through an absorbing medium. This is somewhat surprising, however, because the light is scattered by suspended materials and it is multichromatic, including many wavelengths with different attenuation coefficients. It is not a parallel beam of monochromatic light, and the water is not perfectly homogeneous. According to the Lambert-Bouguer Law, irradiance I_z at any depth z depends upon irradiance I_0 at the surface and a vertical attenuation coefficient ε according to

$$I_z = I_0 \exp(-\varepsilon z) \qquad (1)$$

It should be emphasized that the distance travelled by a beam of light under water is greater than the distance between the surface and the depth z unless the beam enters the water vertically. If the decrease with depth conforms to the Lambert-Bouguer Law, then there should be a linear relationship between the logarithm of irradiance and depth according to

$$\ln I_z = \ln I_0 - \varepsilon z \qquad (2)$$

As may be discerned from data obtained by Kirk (1977) in Australian waters (Figure 1), the rate of attenuation is very nearly linear when

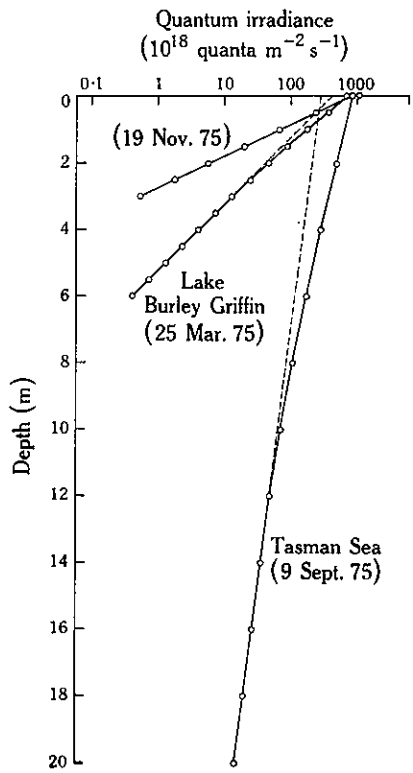

FIGURE 1. Relationship between log PAR and depth in Lake Burley Griffin (Australia) and the Tasman Sea (from Kirk 1977). Redrawn from Kirk 1977.

the water is most turbid in Lake Burley Griffin. However, the slope changes as depth increases in the more transparent water of the Tasman Sea. The water is a differential filter; strongly absorbed wavelengths are removed near the surface and weakly absorbed wavelengths are transmitted to greater depths. The attenuation coefficient for PAR decreases and the light changes color as depth increases. The inherent tendency for the attenuation coefficient for PAR to

decrease by differential absorption of wavelengths is opposed by an increase due to scattering in the more turbid water of Lake Burley Griffin; the decrease of ln (PAR) with depth in inland lakes often may be described with a single attenuation coefficient, as in Lake Burley Griffin, but this is somewhat spurious.

The color changes that occur as light is transmitted also may be illustrated with data obtained by Kirk, who has computed the spectral distribution of light transmitted through two meters of water containing different concentrations of dissolved organic materials (Figure 2). Clear coastal water from Batemens Bay transmits mostly blue and green light, wavelengths between 475 and 575 nm.

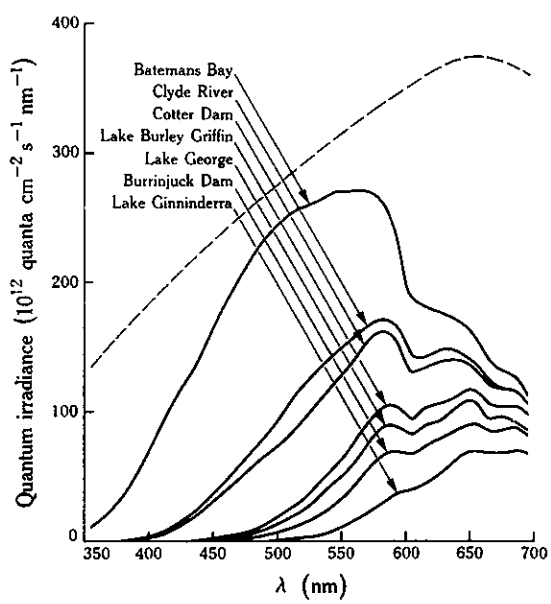

FIGURE 2. Effects of different concentrations of dissolved organic materials on the spectral composition of underwater PAR (from Kirk 1977). Redrawn from Kirk 1977.

However, the dissolved organic materials that are often present at high concentrations in inland waters absorb blue light, so that mostly yellow and red light are transmitted more than 2 m in Lake Ginninderra, where concentrations of organics are highest. In filtered water from this lake, 81% of the light is absorbed by yellowish organic substances, and only 19% is absorbed by the water itself. The dissolved organic materials are important because they compete with algae for photosynthetically active radiation.

The data from Lake Burley Griffin indicate that the vertical attenuation coefficient is subject to large seasonal changes. These changes are often caused by changes in the abundance of planktonic algae, as first described by Talling (1960), who measured underwater light during a period of time when population densities of algae were changing in Windermere, the largest lake in England. Changes in the abundance of algae may be detected easily by measuring concentrations of chlorophyll in the water. In Lake Minnetonka and in the Mississippi River near Minneapolis and St. Paul, Minnesota, the attenuation coefficient increases linearly as concentrations of chlorophyll increase (Figure 3). Many others have observed similar linear relationships between the total attenuation coefficient, ε, and concentrations of chlorophyll (Bindloss 1974; Ganf 1974; Scott 1978). Thus, the total coefficient may be partitioned into two components: one component is a chlorophyll attenuation coefficient, ε_c, and the other is a background coefficient, ε_w, due to the water itself and substances other than chlorophyll in the water. The components may be related to each other by the equation

$$\varepsilon = \varepsilon_w + \varepsilon_c c \qquad (3)$$

where c is the concentration of chlorophyll. The partial coefficients ε_w and ε_c may be evaluated from the intercept and the slope

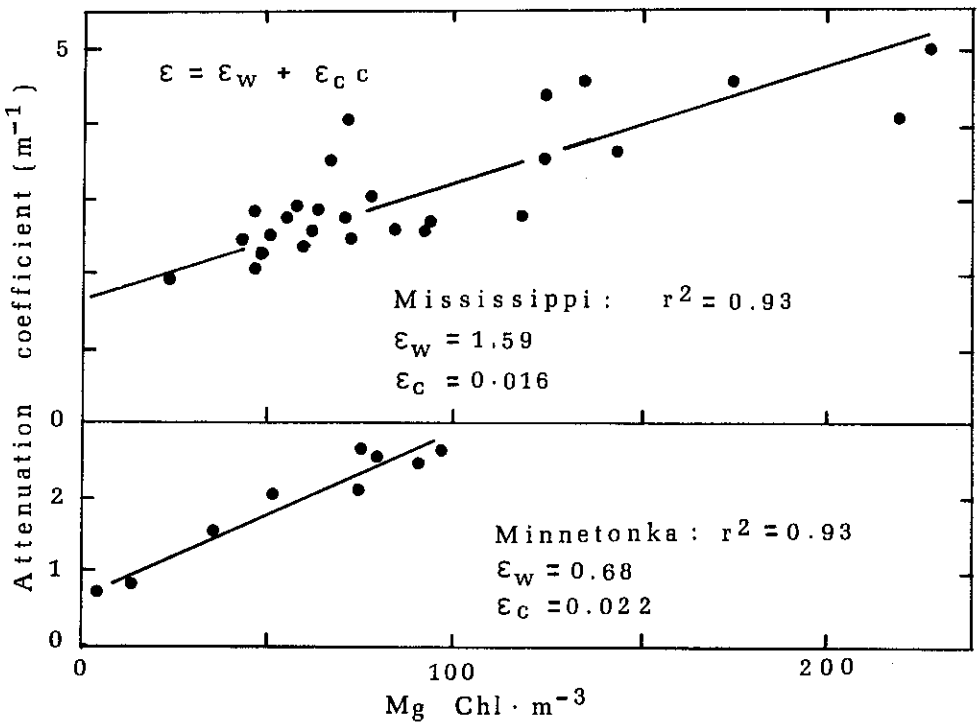

FIGURE 3. Regression of the vertical attenuation coefficient for PAR on concentrations of chlorophyll a in Lake Minnetonka and in the section of the Mississippi River that flows through Minneapolis and St. Paul, Minnesota.

for the linear regression of ε on chlorophyll concentration. The intercepts for the regressions from the Mississippi River and Lake Minnetonka are different from each other, but the slopes are similar. The background coefficient, ε_w, is high in the river because concentrations of dissolved organic materials are higher than in the lake. The background coefficient may vary extensively from lake to lake, because it includes attenuation by both the water and dissolved organic materials. However, regressions such as these usually have very similar slopes, because the chlorophyll attenuation coefficient, ε_c, is relatively constant, usually between 0.015 and 0.022 $m^2 \cdot mg\ Chl^{-1}$. This suggests that attenuation of light by the algae depends more upon the optical properties of chlorophyll and other pigments associated with chlorophyll than upon the morphology of the cells and colonies.

The optical changes caused by algae also may be detected by measuring the transparency of water with a Secchi disc, a white disc 20 cm in diameter that is lowered on a calibrated line into the water until it disappears from sight. The depth at which the disc disappears is a distance that light travels until it is reduced to a standard intensity. The Secchi disc transparency in Lake Minnetonka increases from 1 m to 3 m during late May (Figure 4, top) as concentrations of chlorophyll decrease from 29 to 2 $mg \cdot m^{-3}$ (Figure 4, bottom). Transparency then decreases to 0.5 m as chlorophyll increases to 60 $mg \cdot m^{-3}$ in mid-July. Temporal variations of the reciprocal Secchi Depth are also shown in Figure 4 (middle), and it is notable that reciprocal Secchi depth is proportional to chlorophyll concentration. The reason is that the Secchi Disc is a simple reflecting photometer that depends upon the same optical principles as the quantum sensor. The intensity of light, I_S, at the Secchi depth, S, depends upon the intensity at the surface,

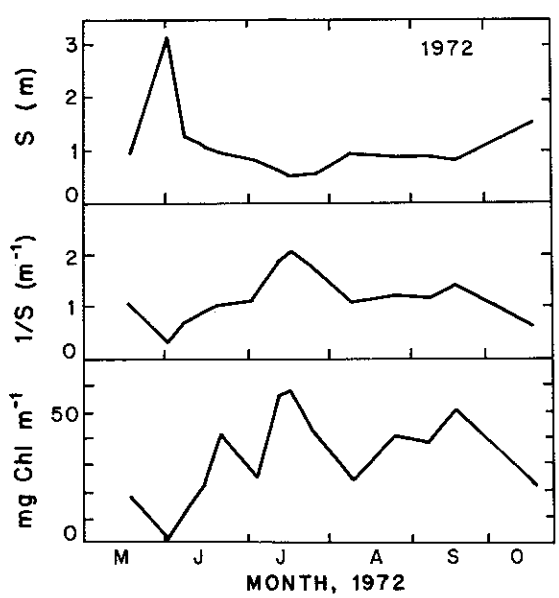

FIGURE 4. Temporal relationships between the Secchi depth, S (top), reciprocal Secchi depth (middle), and concentrations of chlorophyll a in Halsted Bay of Lake Minnetonka during 1972.

I_o, the concentration of chlorophyll, and attenuation coefficients according to

$$I_s = I_o \exp - S\,(\varepsilon_w + \varepsilon_c c) \tag{4}$$

From this, the reciprocal Secchi depth is

$$1/S = \left[\frac{\varepsilon_w}{\ln\,(I_o/I_s)}\right] + \left[\frac{\varepsilon_c}{\ln(I_o/I_s}\right] c \tag{5}$$

Thus, there is a linear relationship between reciprocal Secchi depth and concentrations of chlorophyll where ε_w and ε_c are relatively constant, as in Lake Minnetonka (Figure 5).

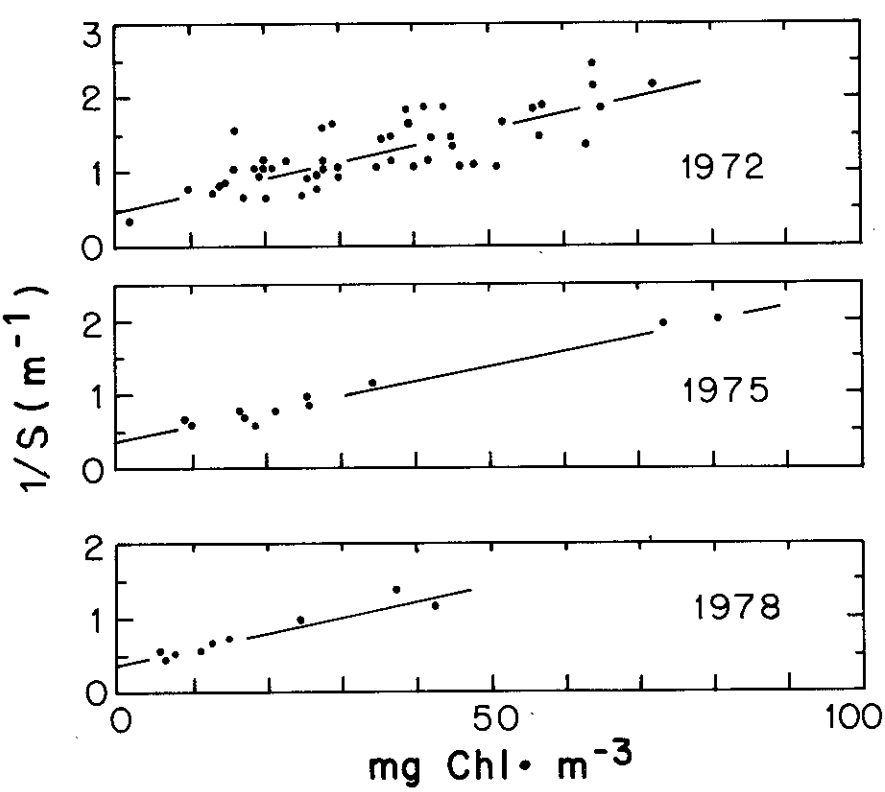

FIGURE 5. Linear regressions of reciprocal Secchi depth on concentrations of chlorophyll in Halsted Bay, Lake Minnetonka (from Megard, Settles, Boyer, and Combs 1979). Redrawn from Megard, Settles, Boyer, and Combs (1979).

I have emphasized the effects of chlorophyll and dissolved organic materials on optical properties because they are closely related to algal photosynthesis and they have been intensively studied recently. However, suspended inorganic materials are often important components of optical environments in rivers, reservoirs, and estuaries. It is evident that the equation for the attenuation coefficient would have to be expanded to include another term for suspended inorganic materials if they contribute significantly to the optical environment. Smith and Baker (1978) partitioned the total coefficient into four components for an analysis of light transmission in the sea, where organic detritus often contributes significantly to the total attenuation coefficient.

LIGHT AND PHOTOSYNTHESIS

Most photosynthesis in inland waters is accomplished by planktonic algae dispersed in the mixed layer. Each cell or colony in the mixed layer has approximately equal access to light, because the algae are transported by water movements. The average thickness of the mixed layer cannot exceed the mean depth of the basin, but it may be less than the mean depth if a thermocline is present. The rate of production of new organic material by the algae in the mixed layer depends upon the daily total of all rates of photosynthesis beneath the surface in the mixed layer. The daily total beneath a unit of surface is the daily integral rate of photosynthesis. The daily integral rate is highly variable, but the controlling mechanisms are now rather well understood.

Rates of photosynthesis by planktonic algae may be computed from the changes of oxygen concentrations that occur during the day in bottles of lake water suspended in a lake at depth intervals. Such measurements typically yield depth profiles of photosynthesis

that resemble the curves observed by Talling in different parts of Lake Victoria in central Africa (Figure 6). Light intensities and temperatures were similar during these measurements, but notice that the shapes of the profiles change in response to changes in chlorophyll concentration.

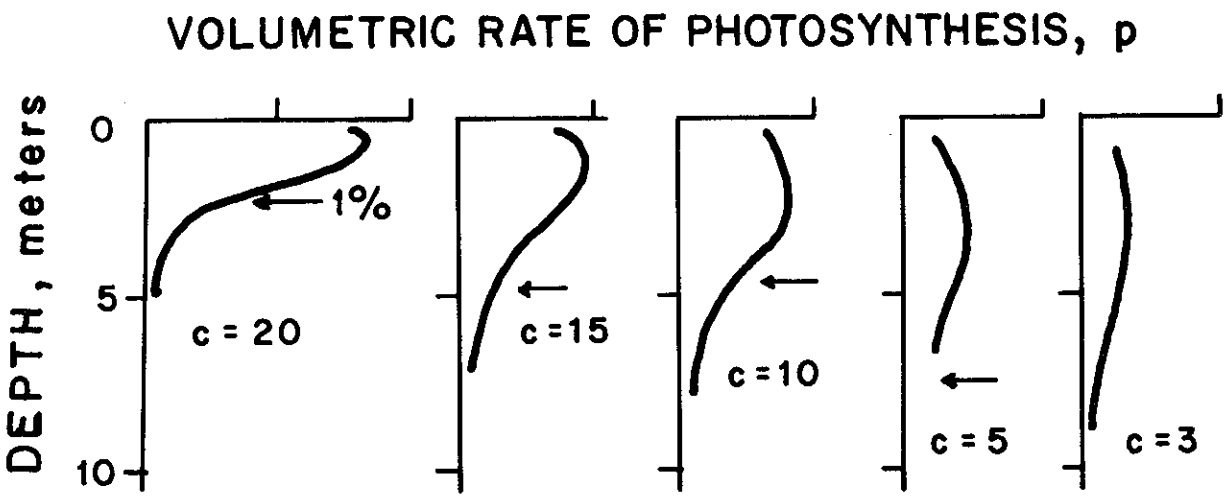

FIGURE 6. Relationships between rates of photosynthesis and depth at nearshore sites of Lake Victoria, central Africa, at concentrations, c, of chlorophyll a between 3 mg m^{-3} and 20 mg m^{-3} (from Talling 1965) Redrawn from Talling 1965.

The depth at which light is reduced to 1% of the intensity at the surface increases from 2.5 m to 6.5 m as concentrations of chlorophyll decrease from 20 mg m^{-3} to 5 mg m^{-3}. The area enclosed by these curves is the integral rate of photosynthesis, π. It is notable that the maximum rate of photosynthesis per unit volume of water, p_{max}, usually occurs somewhat beneath the surface, because intense irradiance at the surface inhibits photosynthesis. Also, p_{max} decreases as concentrations of chlorophyll decrease.

The oxygen produced by planktonic algae during photosynthesis may be a significant component of the oxygen balance of the mixed layer, as may be illustrated with data from the Mississippi River, in and near impoundments behind Lock and Dam #1 and Lock and Dam #2 (Figure 7). The mean concentration for a period of two weeks decreases from 8.2 mg liter^{-1} at Lock and Dam #1 to 1.7 mg liter^{-1} at Inver Grove, which is six miles (9.6 km) downstream from the Minneapolis-St. Paul Metropolitan Waste Treatment Plant. It then increases to 11.3 mg liter^{-1} at Nininger, near Lock and Dam #2. Concentrations of oxygen oscillate at all localities, increasing during the day and decreasing at night. The amplitude of the oscillations is greatest at Nininger, where algae are most abundant. These daily oscillations could be caused only by photosynthesis and respiration.

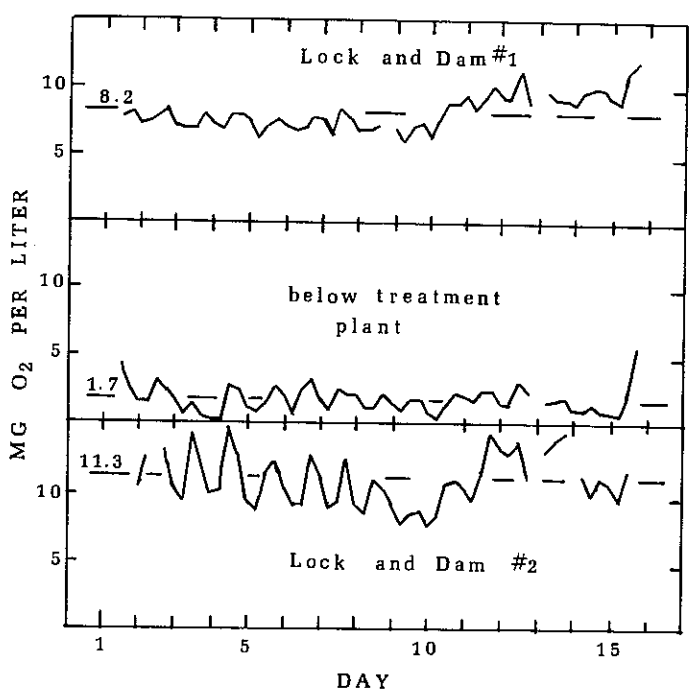

FIGURE 7. Daily oscillations of oxygen concentrations in the Mississippi River during August and September 1976 (from data obtained by the Minneapolis-St. Paul Metropolitan Waste Control Commission).

We have shown (Megard, Combs, Smith, and Knoll 1979) that the daily integral rate of photosynthesis conforms to the equation

$$\pi = \left[\frac{\ln (I_o/I_{z'})\, P_{max}}{\varepsilon_c} \right] \left[\frac{c}{(\varepsilon_w/\varepsilon_c) + c} \right] \tag{6}$$

In this equation I_o is the irradiance at the surface, $I_{z'}$ is the irradiance at a depth z', and P_{max} is the daily maximum specific rate of photosynthesis per unit concentration of chlorophyll. The expression with the first set of brackets is an upper limit, Ψ, that would be attained by very dense populations of algae, so the equation may be simplified to yield an equation proposed by Bannister (1974a):

$$\pi = \Psi \frac{c}{(\varepsilon_w/\varepsilon_c) + c} \tag{7}$$

The quotient $\varepsilon_w/\varepsilon_c$ corresponds to a concentration of chlorophyll at which the algae attenuate 50% of the underwater PAR. This equation is relevant to the regulation of algal populations because integral photosynthesis is expressed as a function of chlorophyll concentration, a measure of algal population density.

To show how photosynthesis affects the abundance of algae in the mixed layer, another equation is needed for the total quantity of algae beneath a unit of surface, M, as a function of chlorophyll. If the amount of algal organic material per unit of chlorophyll concentration is θ and the thickness of the mixed layer is z_m, then

$$M = c\theta z_m \tag{8}$$

If the fraction of the algal population lost each day from the mixed layer is Λ day^{-1}, then the daily rate of change of algal population density is

$$dM/dt = \pi - \Lambda c \theta z_m \tag{9}$$

From this, it is easy to show that the concentration of chlorophyll at the steady-state would be

$$c^* = \left[\frac{\Psi}{\Lambda\ \theta}\right]\left[\frac{1}{z_m}\right] - \left[\frac{\varepsilon_w}{\varepsilon_c}\right] \tag{10}$$

This equation is similar to equations proposed by Bannister (1974, Eq. 11) and Lorenzen and Mitchell (1973, Eq. 11). It is relevent to the design and operation of reservoirs, because it predicts that the steady-state concentration of chlorophyll, c*, depends fundamentally on the thickness of the mixed layer, z_m. The steady-state concentration is a linear function of $1/z_m$. A large reservoir with a thick mixed layer is likely to have fewer algae than a reservoir with a thin mixed layer. The equation also suggests that nuisance blooms of algae are more likely to occur during periods of drawdown, particularly as a reservoir fills with sediment and its mean depth decreases. It also suggests that algae are likely to increase if the background attenuation coefficient ε_w decreases.

The effect of changing the thickness of the mixed layer is indicated by the changes of chlorophyll concentration that occurred during August and September 1976 in the Mississippi River as it entered the impoundment behind Lock and Dam #2. The mean concentration of chlorophyll a during a two-week interval increased by a factor of 5, from about 50 mg m^{-3} upstream to 250 mg m^{-3} in the

impoundment (Figure 8). We assumed initially that chlorophyll increased because photosynthesis was stimulated by nutrients added to the river by the Minneapolis-St. Paul Metropolitan Waste Treatment Plant.

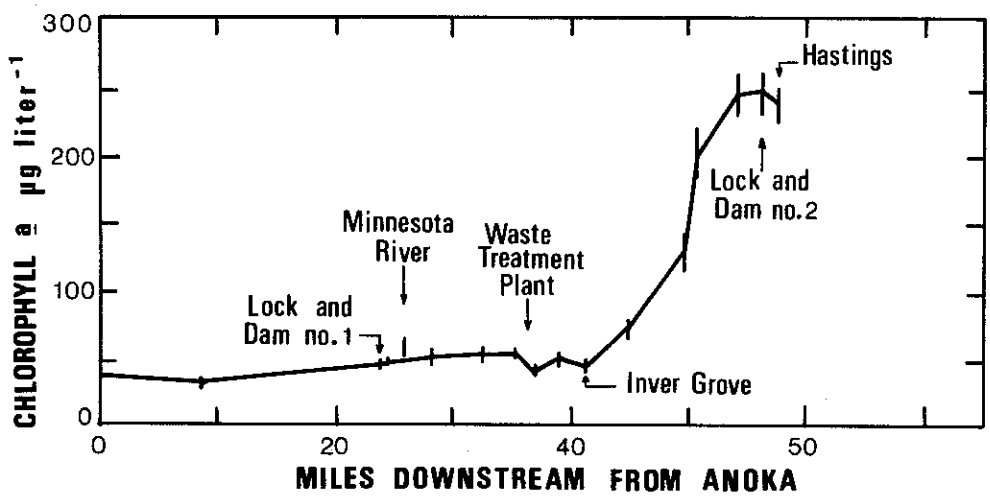

FIGURE 8. Mean concentrations of chlorophyll a during August and September 1976 in the Mississippi River near Minneapolis and St. Paul, Minnesota. The vertical line through each point indicates the 95% confidence interval for the mean (from data obtained by the Minneapolis-St. Paul Metropolitan Waste Control Commission).

However, the photosynthetic activity of chlorophyll at saturating irradiance, P_{max}, at sites downstream from the treatment plant was the same as at sites upstream; planktonic algae were probably saturated with nutrients at all sites, and nutrients from the treatment plant did not stimulate photosynthesis. However, the thickness of the mixed layer decreased from about 3 m upstream to about 1 m in the impoundment. Much of the impoundment is less than 1 m deep,

and a shallow thermocline developed at a depth of about 1 m during a series of warm, sunny days. The equation for the steady-state concentration of chlorophyll predicts that a reduction in the thickness of the mixed layer from 3 m to 1 m would be sufficient to cause the chlorophyll increase observed in the impoundment (Figure 9).

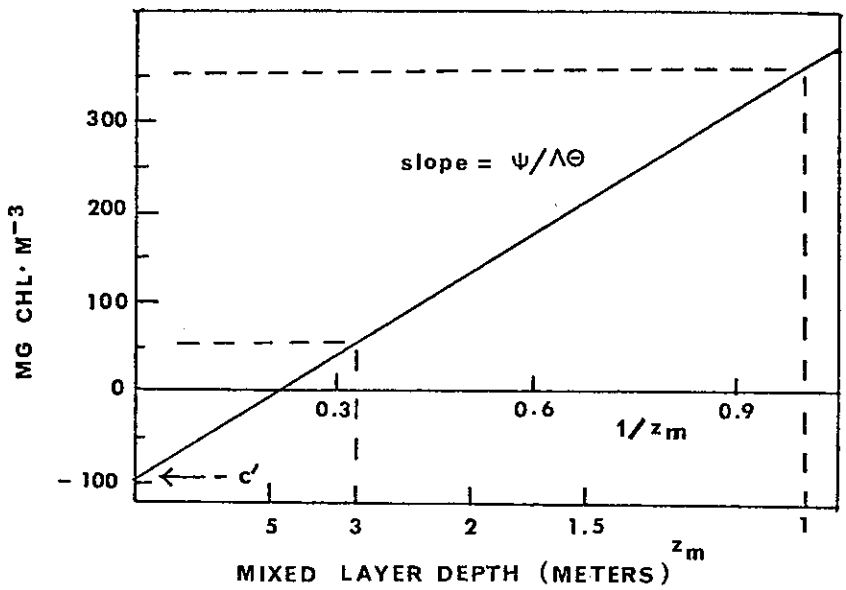

FIGURE 9. Steady-state concentrations of chlorophyll a in the Mississippi River as a function of the thickness of the mixed layer z_m. A decrease of z_m from 3 m to 1 m would increase concentrations of chlorophyll from 50 mg m^{-3} to 350 mg m^{-3}.

The thickness of the mixed layer has a very significant effect on population densities of planktonic algae that is neither intuitively obvious nor generally appreciated. Notice in Figure 9, for example, that concentrations of chlorophyll approach zero and that planktonic algae would become very scarce if the mixed layer in the

Mississippi River increased to approximately 4.5 m. The mixed-layer depth of a reservoir depends partly upon how the reservoir is designed and operated, and this analysis suggests that nuisance blooms of planktonic algae may be alleviated somewhat by retaining as much water as possible in reservoirs during periods when algae are likely to become a nuisance.

In conclusion, I should mention briefly how population densities of planktonic algae are affected by factors that will be discussed by other participants at this workshop. Nutrients and temperature affect P_{max} and therefore they cause the limit Ψ to change. Grazing or predation is a component of the total loss rate, Λ. Other components of Λ are respiration, excretion, and sinking. Much additional research will be required before we understand the mechanisms that control these processes.

I should emphasize that the parameters in dynamic equations for natural populations of algae are very dependent on physical conditions and the physiology of the algae that are present. I have discussed the fundamental importance of the background coefficient and the depth of the mixed layer, which are both obviously characteristic of particular sites. A large amount of information is therefore required about each site, even to solve equations that contain as few parameters as the equation I discussed here.

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MODELING COMBINED EFFECTS OF ENVIRONMENTAL FACTORS ON PHYTOPLANKTON

by

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INTRODUCTION

Modeling phytoplankton growth in existing and planned reservoirs requires a knowledge of both the peculiarities of reservoirs and the dynamics of phytoplankton. Because of low retention times and close coupling to hydrology, reservoirs often exhibit pronounced fluctuations in physical and chemical conditions. Therefore, accurate prediction of phytoplankton growth in any one reservoir depends on the capability of representing a variety of individual and combined responses to changing environment.

The purpose of this paper is to describe the characteristics of reservoirs that necessitate specific modeling approaches, review the combinations of process equations that are used in representative phytoplankton models, and consider the ways in which these equations are combined in light of current concepts of algal physiology, with illustrative examples.

We thank our colleagues James Albanese and Chris Connolly for their valuable exchange of ideas; the assistance of Petter Larsson, Zoological Museum, University of Oslo and Milan Straškraba, Hydrobiological Laboratory, Czechoslovakia Academy of Sciences is gratefully acknowledged. This project has been financed with federal funds from the Environmental Protection Agency under Grants No. R80504701-1 and R806299010.

RESERVOIR CHARACTERISTICS AND MODELING

Advection

Because of high inflow and withdrawal rates, reservoirs tend to be advection-dominated. Simple throughflow may account for appreciable loss of phytoplankton and flushing of nutrients. Hypolimnetic

withdrawal can affect phytoplankton more severely by accelerating their removal from the euphotic zone upstream from the dam. Therefore, throughflow must be accounted for in a reservoir model. Advective turbulence, as a consequence of short retention time and wind, can have a pervasive effect on phytoplankton by altering their physiological and ecological responses and the grazing of zooplankton, by transporting them from one zone to another, and by altering the entire physical-chemical environment of the reservoir.

Little is known about the effect of turbulence on the physiological and ecological responses of phytoplankton and zooplankton. Pasciak and Gavis (1974) showed that when algae absorb nutrients from the water they may deplete a boundary layer and become transport-limited in their uptake rates. Shearing motions generated by turbulence may reduce the extent of the nutrient-depleted region around the cells. More recently, Nixon, Oviatt, and Buckley (in press) obtained results from microcosm experiments suggesting that turbulence leads to increased phytoplankton biomass and decreased zooplankton biomass during the summer, but not during the winter and spring. This pioneering research needs to be extended in an effort to determine if phytoplankton growth is stimulated directly and what the actual effect is on zooplankton. We know of no effort to incorporate this into a model.

The effect of advective turbulence on the vertical distribution of phytoplankton can be modeled most easily by using multiple vertical segments with turbulence as a function of throughflow; it is difficult to represent in a point model. Horizontal patchiness as a result of advection can have a profound effect on both phytoplankton and zooplankton. D.G. George (personal communication) has observed a hundredfold difference in phytoplankton abundance in a Welsh reservoir. McNaught (1979), in an excellent review, characterizes phytoplankton patches as being from less than one meter to more than a kilometer in size and less than an hour to four days in duration;

zooplankton patches may range from less than five meters to more than fifty km in size and less than an hour to forty days in duration. We agree with McNaught that this should be considered in model development and in obtaining data for calibration. Kamykowski (1978) has modeled patchiness in lakes, and there is appreciable literature on modeling patchiness associated with coastal upwelling (cf. Wroblewski and O'Brien 1976; O'Brien and Wroblewski 1976).

Sinking

The sudden, rapid sedimentation of phytoplankton has been observed in a number of reservoirs. Prediction of this phenomenon would improve our representation of ecosystem dynamics and would be particularly helpful in management of reservoirs used for drinking water. Likewise, the formation of blue-green algal scums, which are common in many reservoirs, is of interest. It would be quite useful to be able to model scum formation.

Sinking is a function of the shape, specific gravity, surface area to volume ratio (size), and surface chemistry of the alga and the viscosity and turbulence of the surrounding water. [In vacuolated blue-green algae buoyancy is controlled quite differently; the reader is referred to Fogg et al. (1973) for a thorough discussion.] The effects of shape and, to a certain extent, size are essentially species-specified. However, the other algal characteristics are related to physiological state, which implies an interaction with the various growth factors. Even size can be a function of suboptimal conditions which permit growth but not cell division. Cells in the stationary phase sink two to four times as fast as cells in the exponential phase of growth (Eppley, Holmes, and Strickland 1967; Smayda 1970). Titman and Kilham (1976) have demonstrated that increased sinking is not due to a lack of viability and have shown that it can be a function of nutrient depletion (see also Boleyn 1972, Smayda 1974). Light can also be a controlling factor (Steele and Yentsch 1960; Eppley, Holmes,

and Strickland 1967). The tendency to sink can be partially negated by the viscosity of the water, which in fresh water is a function of temperature. Turbulence may negate or enhance sinking (Stefan, Skoglund, and Megard 1976; Titman and Kilham 1976).

Many models treat sinking as a constant, which is an oversimplification. Several employ Stoke's Law, which accounts for viscosity. Stoke's Law can implicity account for reduction in sinking due to turbulence if the Reynold's number is treated as a site variable, dependent on size of the water body (we know of no model that does this). The model of Scavia, Eadie, and Robertson (1976) is apparently the only one at present that considers physiological state as a factor in sinking. We know of no model that considers the environmental control of buoyancy of blue-green algae explicitly.

Temperature

The thermal regime of a reservoir can vary greatly from a dry year to a wet year (Figure 1). During a dry, sunny summer a reservoir will have a long retention time, low advective turbulence, marked stratification, and relatively high insolation to surface water. A wet, cloudy summer will result in a short retention time, high advective turbulence, poor stratification, and lower surface temperature (Straškraba 1973).

Algae can compensate partially for the variable temperature regime of a reservoir. For example, the concentration of photosynthetic enzymes increases with decreasing temperature as an adaptive response (Jorgensen and Nielsen 1965). The optimum temperature for photosynthesis varies seasonally with ambient temperature (Aruga 1965), although there may not be adaptation to winter temperatures (Boylen and Brock 1973, 1974). The temperature response of plankton should be modeled realistically or large discrepancies can arise

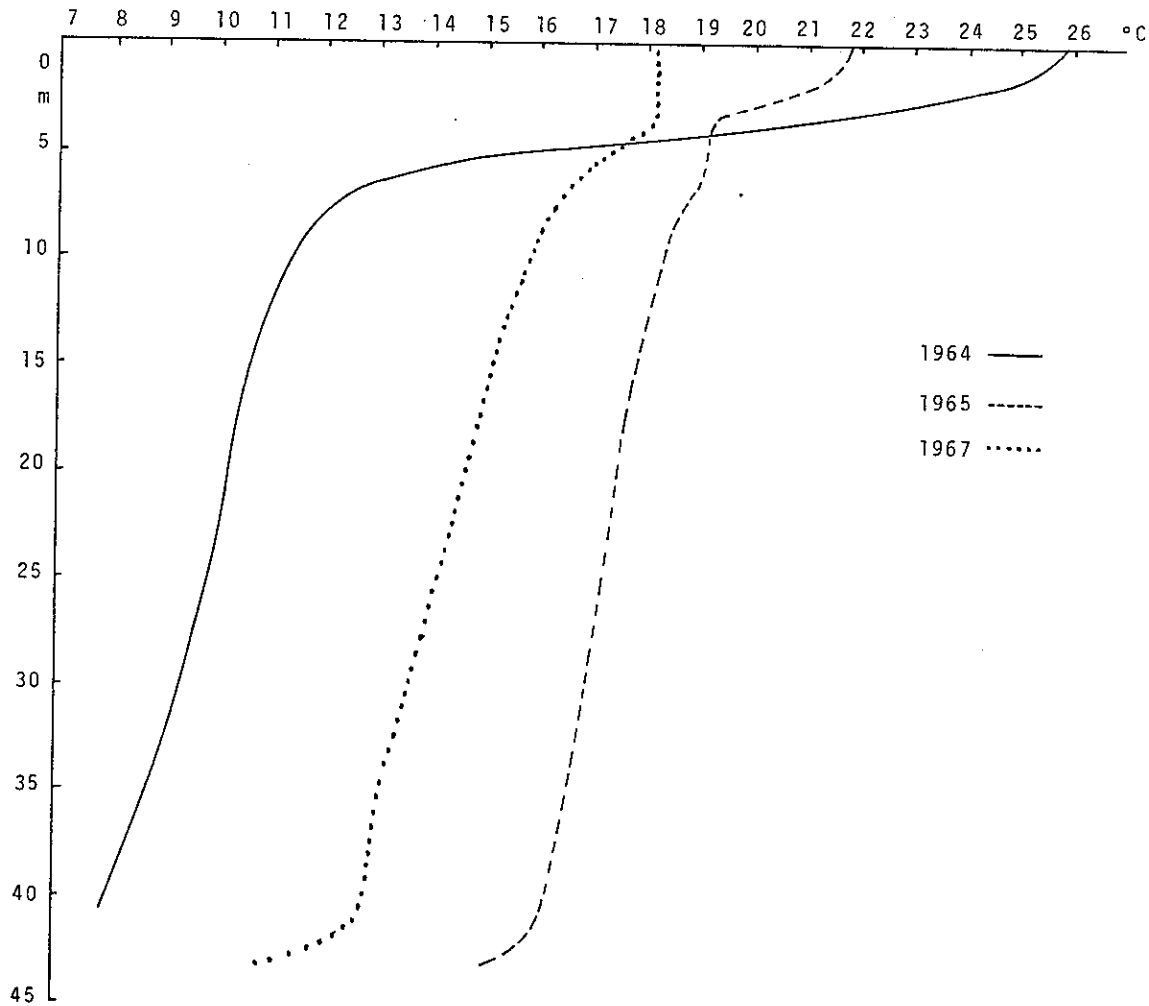


FIGURE 1. Plots of summer temperature against depth in Slapy Reservoir; — 1964 (dry year), ... 1967 (medium year), and --- 1965 (wet year). After Straškraba (1973). Redrawn from Straškraba (1973).

between dry and wet years. Nonlinear temperature response with adaptation is considered in the model of Straškraba (1976) and in the MS•CLEANER model described below.

Nutrients

Nutrient, organic matter, and suspended-sediment loadings may be sporadic, varying directly with inflow. Of specific interest, phosphate loading is often highly correlated with inflow; however, phytoplankton production may not respond immediately because of high turbidity.

The effect of luxury consumption and storage of intracellular nutrients in natural environments is poorly understood. There is now strong experimental evidence that intracellular nutrients are important in regulating pure cultures (Fuhs 1969; Caperon and Meyer 1972; Droop 1974; Rhee 1978). However, it has been argued that algae may not be able to store sufficient nutrients to make a significant difference under field conditions (Scavia 1979). We feel that in reservoirs subject to sporadic loading of nutrients concomitant with light-limiting turbidity during high inflow, intracellular storage is important. Serruya and Berman (1975) have demonstrated that it is important in Lake Kinneret, Israel. In eutrophic Danish lakes the time lag between high nutrient loading and maximum phytoplankton peak may be as long as six weeks (S.E. Jorgensen and N. Nyholm, personal communication). Intracellular storage is simulated in a number of models (Koonce 1972; Grenney *et al*. 1973; Bierman 1974; Nyholm 1975, 1977, 1978; Lehman, Botkin, and Likens 1975; Cloern 1978; Jorgensen, Mejer, and Friis 1978; Desormeau 1978). However, some of these are inadequate in light of current knowledge of algal physiology (Park *et al*. 1979).

Light

Allochthonous sources of turbidity and high density of phytoplankton can combine to make phytoplankton light-limited in many

reservoirs. Ecosystem feedback in the form of autochthonous production of particulate and dissolved organic matter, including the so-called "self-shading" by algae, should be represented in reservoir models, otherwise under eutrophic conditions the algae will not be properly constrained. Fortunately, many models treat light extinction as a function of phytoplankton and detritus. Patten et al. (1975) assume that light extinction at low to moderate turbidity is due to algae whereas at high turbidity it is a function of suspended inorganic sediment, with a corresponding shift in absorption of photosynthetically available energy; therefore different correction factors are used. Straškraba (1976) describes in detail the rationale behind modeling light extinction as a function of both particulate and dissolved organic matter and suspended inorganic sediment.

The varying light climate to which algae are subjected due to turbid inflow, advective turbulence, and self-shading places a premium on adaptation. Tilzer (1972) has shown that algae can undergo a twofold change in their light saturation response during a single day; Nielsen et al. (1962) have observed a threefold change in light saturation within two days. Straškraba (personal communication) believes that light adaptation of algae caught up in advective turbulence plays an important role in the algal dynamics of Slapy Reservoir, Czechoslovakia. To our knowledge only the models of Kremer and Nixon (1978) and Nyholm (1978) and the MS•CLEANER model described below account for light adaption.

Predatory Mortality

Zooplankton grazing plays an important role in reservoirs, limiting phytoplankton blooms and regulating the composition of phytoplankton assemblages. It is not our intention to discuss zooplankton dynamics, so we will restrict ourselves to pointing out that two aspects of grazing are particularly important: dependency on prey density and size selectivity. Cladocerans filter at a more or less constant rate, rejecting excess food in the form of pseudofeces. Other zooplankton

exhibit saturation-kinetic feeding, with an asymptote at the maximum consumption rate (Burns and Rigler 1967; Chisholm, Stross, and Nobbs 1975), and with a minimum threshold, below which feeding ceases (McAllister 1970) or occurs at a minimal level (Frost 1975). Some or all of these density-dependent characteristics are included in several models (Bloomfield et al. 1973; Park et al. 1974; Canale et al. 1976; Scavia, Eadie and Robertson 1976; Steele and Mullin 1977; Leung 1978).

Cladocerans are relatively unselective in their filtering, whereas copepods selectively graze smaller phytoplankton (Bogdan and McNaught 1975). Neither group is able to graze filamentous blue-green algae effectively. As a result, there can be significant shifts in algal composition, including promotion of blue-green algal blooms. A number of models consider differential grazing of zooplankton (Bloomfield et al. 1973; Park et al. 1974; Canale et al. 1976; Scavia, Eadie, and Robertson 1976; Youngberg 1977; Park et al. in press).

Nonpredatory Mortality

Blue-green algae, and other algae to a lesser extent, exhibit high nonpredatory mortality under adverse conditions, reducing the dissolved oxygen in the reservoir as a consequence of their sudden decomposition. The physiological state of an alga is important in determining the point at which growth ceases and cell death begins. When growth conditions become unfavorable and expecially as cells become nutrient-deficient, they become susceptible to colonization by decomposers, and lysis may eventually occur (Daft and Stewart 1973; Jones 1976). The role of the decomposers in colonization of algae is still unclear. Some feel unhealthy cells are more likely to be attacked, whereas others feel bacteria may colonize healthy cells as well. DePinto (1979) presents a comprehensive discussion of colonication and nonpredatory mortality.

Because the process is not well understood, several different approaches have been taken by modelers. In the model of Lehman, Botkins and Likens (1975) the death rate is a function of the number of days of algal growth at suboptimal conditions. Bierman (1976) uses a second-order algal death rate, thereby modeling bacteria implicitly. Others have treated nonpredatory mortality as a function of temperature (Thomann et al. 1975; Canale et al. 1976). Both high temperature and the physiological state of the cells are used in determining death rate in the model of Scavia, Eadie, and Robertson (1976) and in the MS•CLEANER model. Inhibition by blue-greens is included by Cloern (1978).

Other Environmental Responses

There are also subtle interactions of environmental responses involving respiration and excretion in phytoplankton. Although these are not unique to reservoirs, they are important in correctly predicting phytoplankton dynamics.

Respiration is a significant contribution to the loss rate of the phytoplankton. The actual rate of respiration increases with increasing temperatures and is dependent on the rates of endogenous respiration and photorespiration. Endogenous respiration represents the amount of energy expended to maintain a certain level of biomass and increases exponentially with increasing temperatures (Aruga 1965). Photorespiration is a light-stimulated oxidation of organic compounds which can occur simultaneously with photosynthesis.

Respiration has been modeled as a linear function of temperature, including both photorespiration and endogenous respiration (Scavia, Eadie, and Robertson 1976; Straškraba 1976). Youngberg (1977) models respiration as a function of the temperature dependence term. MS•CLEANER (1978) models endogenous respiration as an exponentially increasing function of increasing temperature based on data of Aruga

(1965), with respiratory products going to the CO_2 compartment. Photorespiration is included with excretion, with products going to the organic matter compartments.

Excretion is essential to keep cell division in phase with photosynthesis (Strickland 1966). In general any environmental or physical condition, which inhibits cell multiplication but permits photoassimulation, results in the release of a high proportion of photoassimulate. Under light intensities so high as to inhibit photosynthesis and under low light intensities and darkness, large proportions of photosynthate are produced (Watt 1966; Fogg et al. 1965). The proportion of photoassimilated carbon released is relatively unaffected by light intensities over an intermediate range where little or no inhibition of photosynthesis occurs (Nalewajko 1966). Glycolate production by photorespiration is largely dependent on the partial pressure of carbon dioxide and oxygen concentrations. When CO_2 limits photosynthesis and oxygen is available there is an increase in glycolate release (Chapman and Rae 1969). Under nutrient deficiency, a stationary population of phytoplankton will excrete a large proportion of its photoassimilated carbon; however, the absolute rate of excretion by such a population may not be any higher than that of a rapidly growing population with a smaller relative excretion rate (Hellebust 1967). Excretion may also be a function of temperature. Few models consider excretion by phytoplankton. The model of Lehman et al. (1975) assumes excretion is proportional to cell carbon quota so that the production of extracellular material is related to the different growth regimes. MS·CLEANER, described below, models extracellular release including photorespiratory products as a linear function of the light dependence term and as a proportion of the photosynthetic rate.

Toxic Chemicals

Largely ignored until now, significant pesticide and other toxic-substance loadings may affect many reservoirs. Anecdotal evidence suggests that massive zooplankton and fish kills may result from

contamination. (Although not documented in the literature, the complete absence of zooplankton has been noted in some systems.) Insecticides may selectively remove cladocerans (Gasith, Sneh, and Perry 1978), thereby favoring copepods that graze on nannophytoplankton. Toxic substances can also impact phytoplankton directly. Mechanistic models capable of predicting the fate of toxic chemicals in aquatic systems are still in the development stage (Park et al. 1977; Smith et al. 1977; Leung 1978; Thomann 1979). There is no general model of toxic-chemical impact on aquatic ecosystems at this time.

REPRESENTATIVE MODELS

Although superficially there are many similarities among photoplankton models, there are also many dissimilarities in the individual process equations and in the ways in which they are combined. Certainly over the past nine years there has been an evolution toward more complex models that are more representative of what is presently known about algal physiology.

Eight models were chosen to demonstrate the different approaches that have been taken. Several have not been applied to reservoirs and one is a marine model, but the underlying principles are the same. Because the models share some process equations, but differ in others, it is almost impossible to compare them systematically. (Also, it is difficult to determine specific model details without access to the computer code; we apologize in advance for any misinterpretations that we might make.)

The model of Chen et al. (1975) is perhaps the simplest at the process level (Figure 2). Light and nutrients are represented by saturation kinetics, and temperature by the exponential Van't Hoff equation. Nutrient limitation is taken as the minimum of nitrogen, phosphorus, and silica limitations. Combination of the light, nutrient,

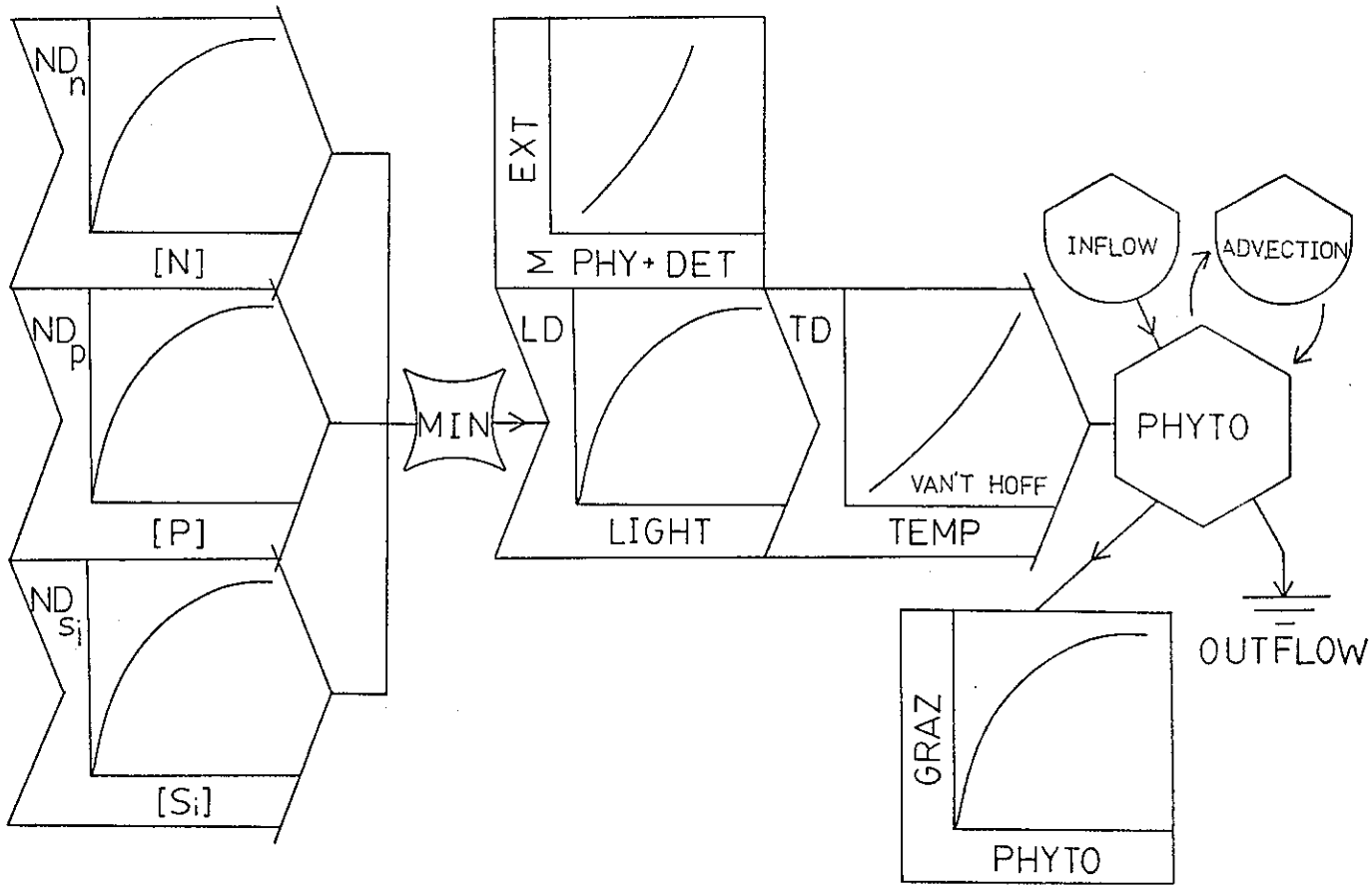


FIGURE 2. Flow chart of the phytoplankton model of Chen *et al*. (1975). See Legend on page 187.

and temperature limitations is multiplicative. Saturation-kinetic grazing, inflow, outflow, and advection are also represented. Light extinction is a function of detritus and phytoplankton biomass.

The model of DiToro et al. (1977) is of approximately the same complexity (Figure 3). Steele's (1962) equation is used for light and temperature limitations. Grazing and mortality are linear with temperature. Inflow, outflow, and advection are also represented.

The phytoplankton model of Kremer and Nixon (1978) is only slightly more complex (Figure 4). Limitations for nutrients, light, and temperature are multiplied; the functions are the same as in the model of DiToro et al. (1977). However, diurnal variations in light are taken into account, and a three-day running average is used to represent adaptation to varying light levels. Inflow, outflow, and a constant sinking rate are included; advection is treated implicitly. A saturation-kinetic equation is used to represent grazing. The model was developed for a marine system, but is almost directly applicable to freshwater systems as well.

The following models are more complex at the process level. The one proposed by Straškraba (1976) (Figure 5) represents temperature response as a normal curve with an adaptive optimum temperature; light limitation is based on Steel's (1972) equation, which Straškraba feels gives the best fit to available data. The light, nutrient, and temperature factors are multiplicative. Sinking utilizes Stoke's law; grazing accounts for prey saturation; and respiration (not included in the above models) is linear with respect to temperature. Advection is a function of throughflow. Light extinction is dependent on particulate organic matter, dissolved organic matter, and suspended sediment, as well as phytoplankton biomass.

The model of Lehman, Botkin, and Likens (1975) provides for intracellular storage of nutrients, with growth dependent on the cell quotas

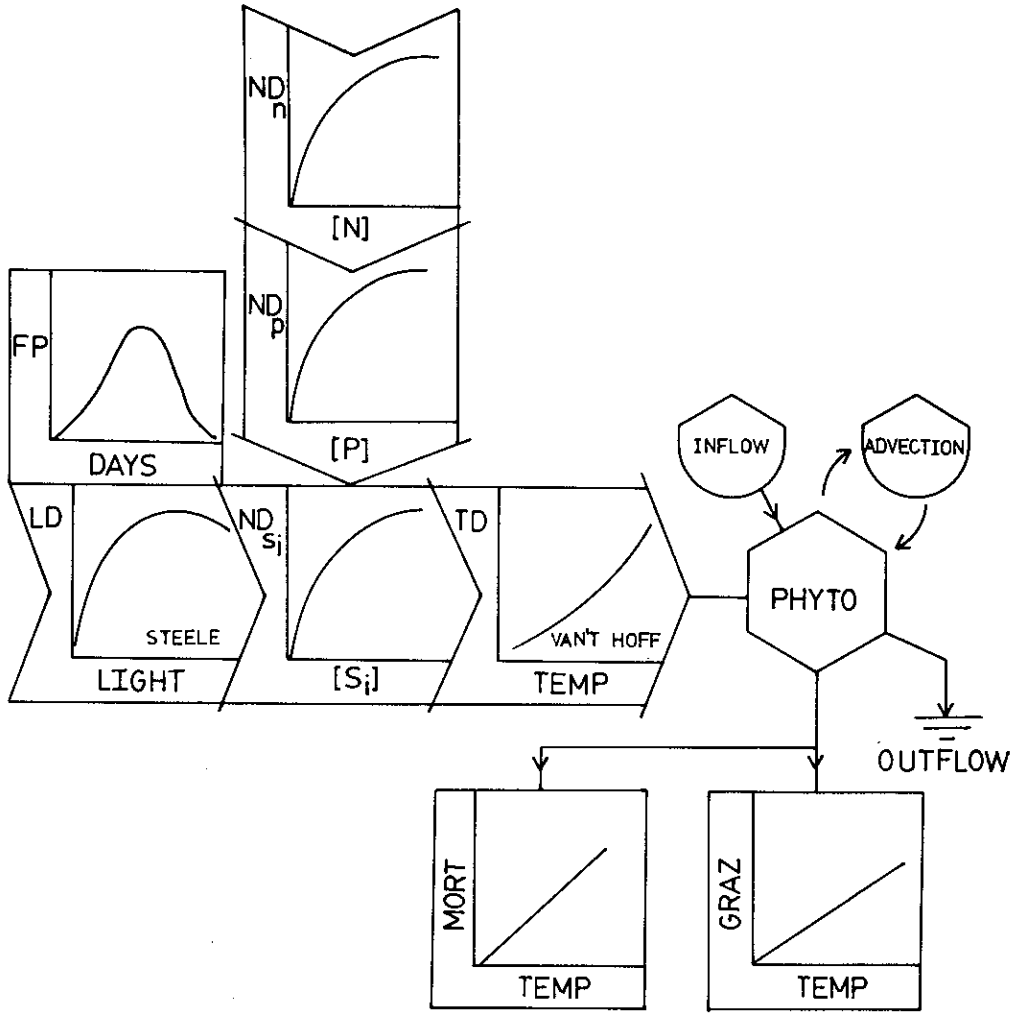


FIGURE 3. Flow chart of the phytoplankton model of DiToro *et al*. (1977). Redrawn from DiToro *et al*. (1977).

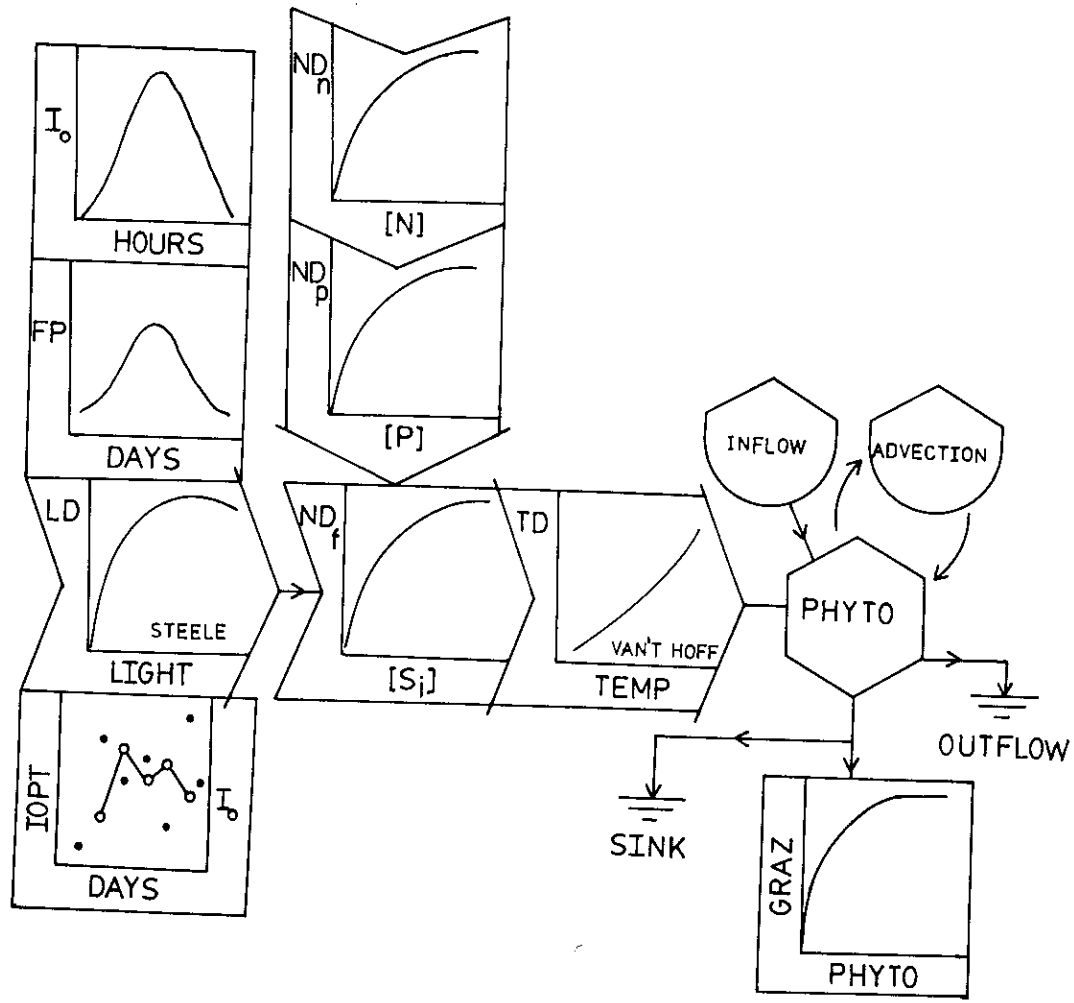


FIGURE 4. Flow chart of the phytoplankton model of Kremer and Nixon (1976). Redrawn from Nixon (1976).

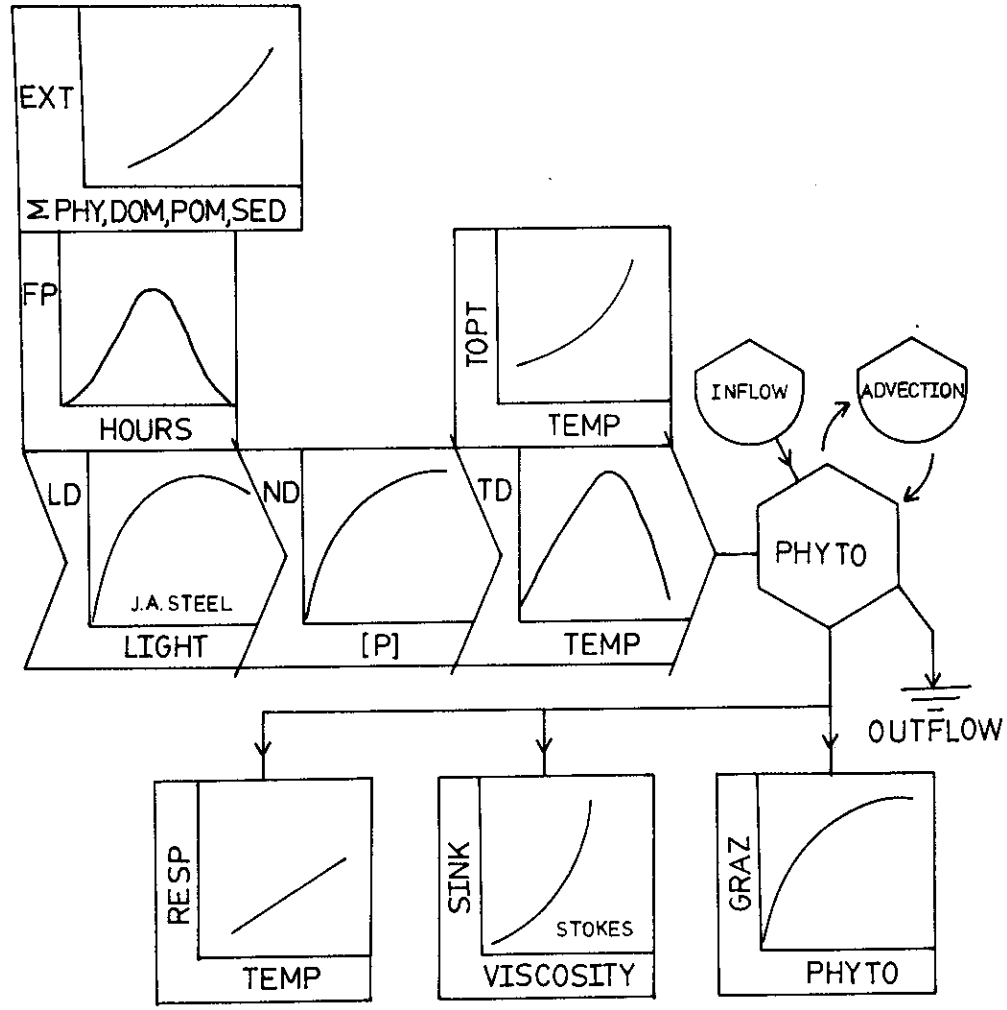


FIGURE 5. Flow chart of the phytoplankton model of Straškraba (1976). Redrawn from Straškraba (1976).

(Figure 6). Because the model simulates numbers instead of biomass, carbon dependency is introduced as well. Combination of the saturation-kinetic limitations is multiplicative. Sinking is constant; throughflow and advection are not considered, perhaps because the model was developed to represent a pond during the summer months. Mortality is a function of the number of days that growth is suboptimal.

Nyholm (1978) accounts for intracellular nutrients in a completely different manner (Figure 7). Rate of uptake is dependent on whether or not the cell quota has been achieved. Growth limitation is linear for nitrogen and nonlinear, with an inhibitory factor, for phosphorus; the nutrient limitation terms are combined using the harmonic mean, the so-called "resistors in series" construct of Bloomfield et al. (1973). A set of equations provides a piecewise response curve for light, with a linear subsaturation slope, a plateau at light saturation, and a rapid decline above the inhibitory level. Light adaptation is incorporated by using light-saturation parameter values observed during the year. The Van't Hoff equation is used for temperature limitation. The limitation factors are multiplicative. Sinking is constant, and grazing is simulated by saturation kinetics.

The model of Scavia et al. (1976) uses saturation-kinetic functions for light and nutrient limitations and takes the minimum as being the limiting factor value (Figure 8). That is then multiplied by the nonlinear temperature factor of Bloomfield et al. (1973). Inflow, outflow, and advection are included. Loss due to grazing is a nonlinear function of phytoplankton biomass, with a minimum grazing level, and is modified by temperature and prey preference using a modification of the formulation of Park et al. (1974). Sinking is based on an innovative variation of Stoke's Law, with provision for shape differences and effects of nutrient limitation. Respiration is linear with respect to temperature. Mortality is a function of temperature (Scavia and Park 1976) and nutrient limitation.

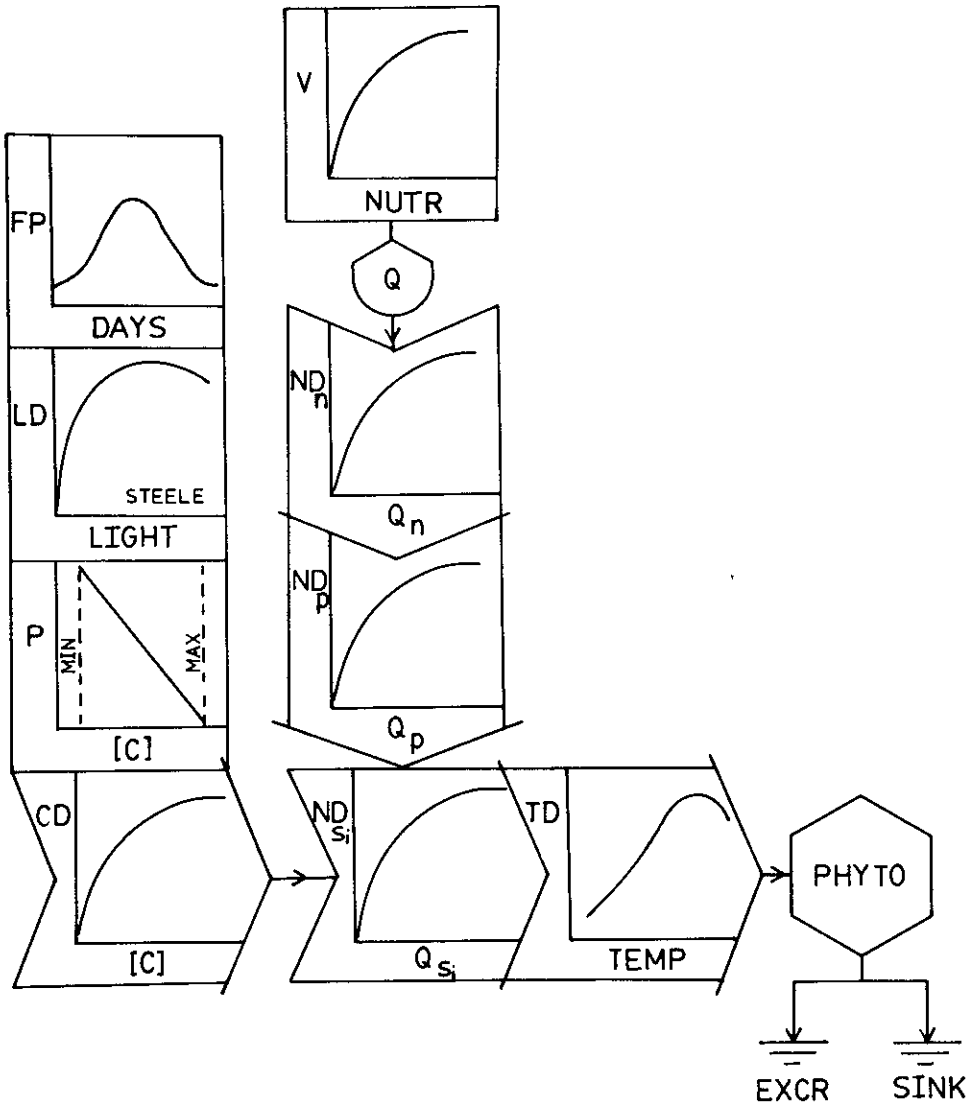


FIGURE 6. Flow chart of the phytoplankton model of Lehman, Botkin, and Likens (1975). Redrawn from Lehman, Botkin, and Likens (1975).

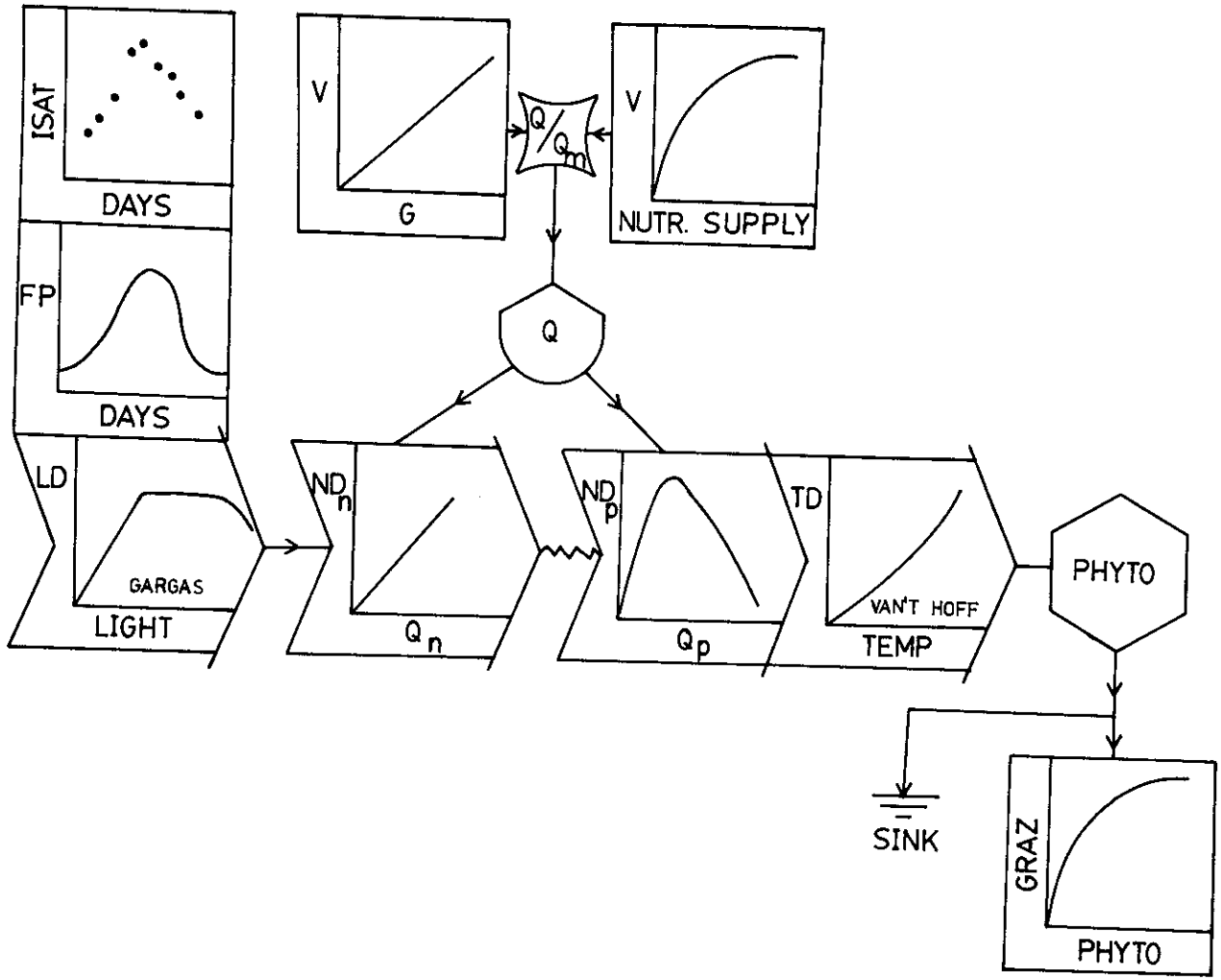


FIGURE 7. Flow chart of the phytoplankton model of Nyholm (1978). Redrawn from Nyholm 1978.

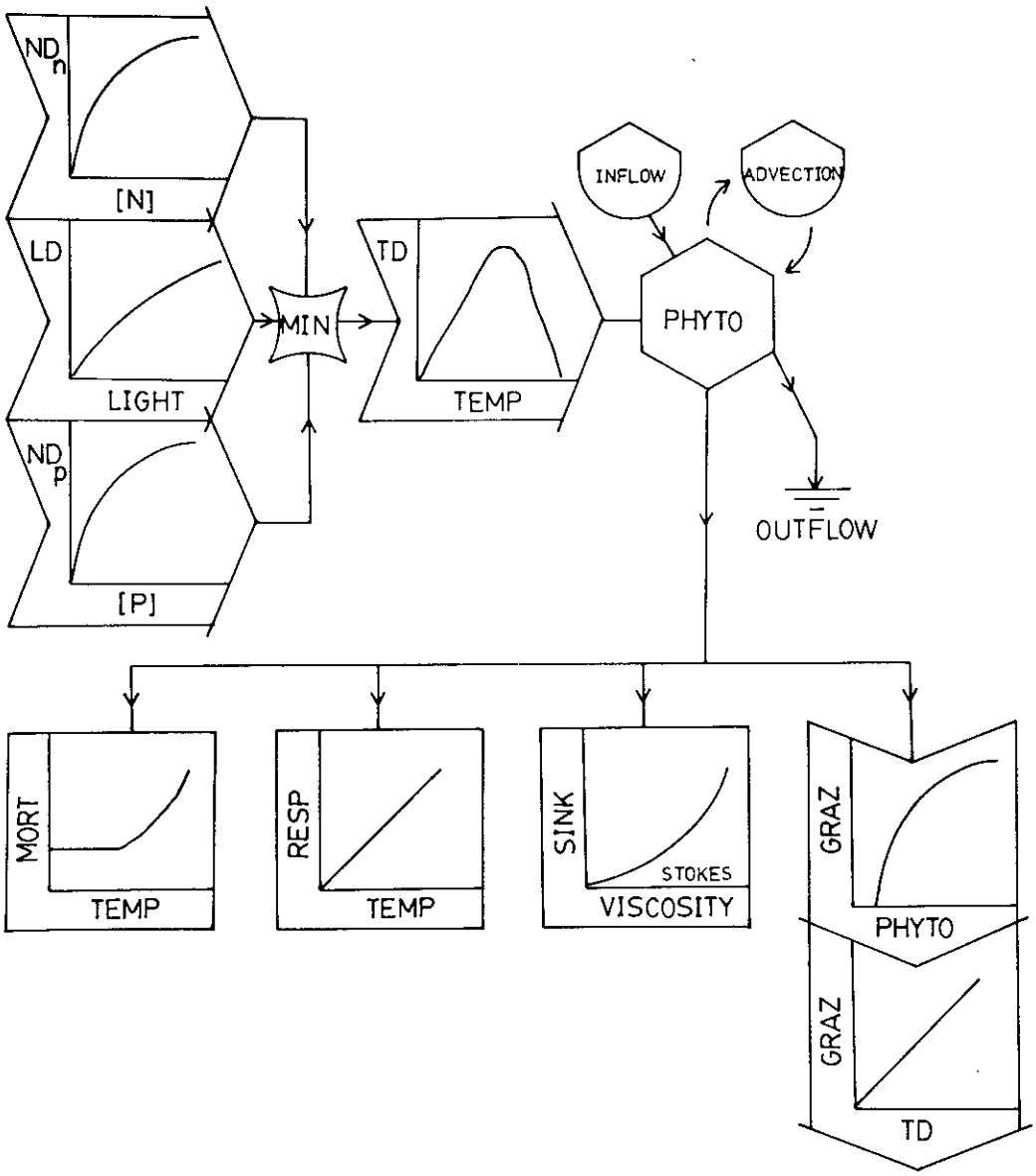


FIGURE 8. Flow chart of the phytoplankton model of Scavia *et al*. (1976).

The CLEANER model of Youngberg (1977) (Figure 9) is of interest because it shows the evolution from the original CLEAN model of Park et al. (1974) to the MS•CLEANER model described later in this paper. It was the first version of CLEANER to account for stratification, advective turbulence, and throughflow, and was developed specifically for Slapy Reservoir, Czechoslovakia. It uses Steele's (1962) equation for light limitation, and uses the harmonic mean construct of Bloomfield et al. (1973) to combine Michaelis-Menten functions for nutrient limitations for nitrogen, phosphorus, and silica (in diatoms). The nonlinear temperature function of Bloomfield et al. (1973) is used. Grazing is represented by the saturation-kinetic formulation of Park et al. (1974), including the nonlinear temperature construct and prey preference; grazing by cladocerans is differentiated from that of copepods by the absence of a threshold level. Sinking is a function of temperature and is represented by an exponential curve, which is an empirical fit to Smayda's (1974) data. Respiration is a nonlinear function of temperature. Mortality is a function of temperature (Scavia and Park 1976) and nutrient limitation (similar to Scavia et al. 1976).

In summary, out of eight representative models, some present environmental responses as exponential, some use saturation kinetics, and some use nonlinear equations to account for optimal responses. Most combine some or all of the responses in a multiplicative fashion, but some use only the minimum limitation among some combination of factors, and two use the harmonic mean. Storage of intracellular nutrients is provided for in three. Adaptive constructs for light or temperature are included in two models. Loss terms, self-shading, and advection are treated in various ways or are ignored.

COMBINATION OF FACTORS LIMITING PHOTOSYNTHESIS

Adequate justification for the combinations of effects of light intensity, temperature, and nutrient concentration used by various

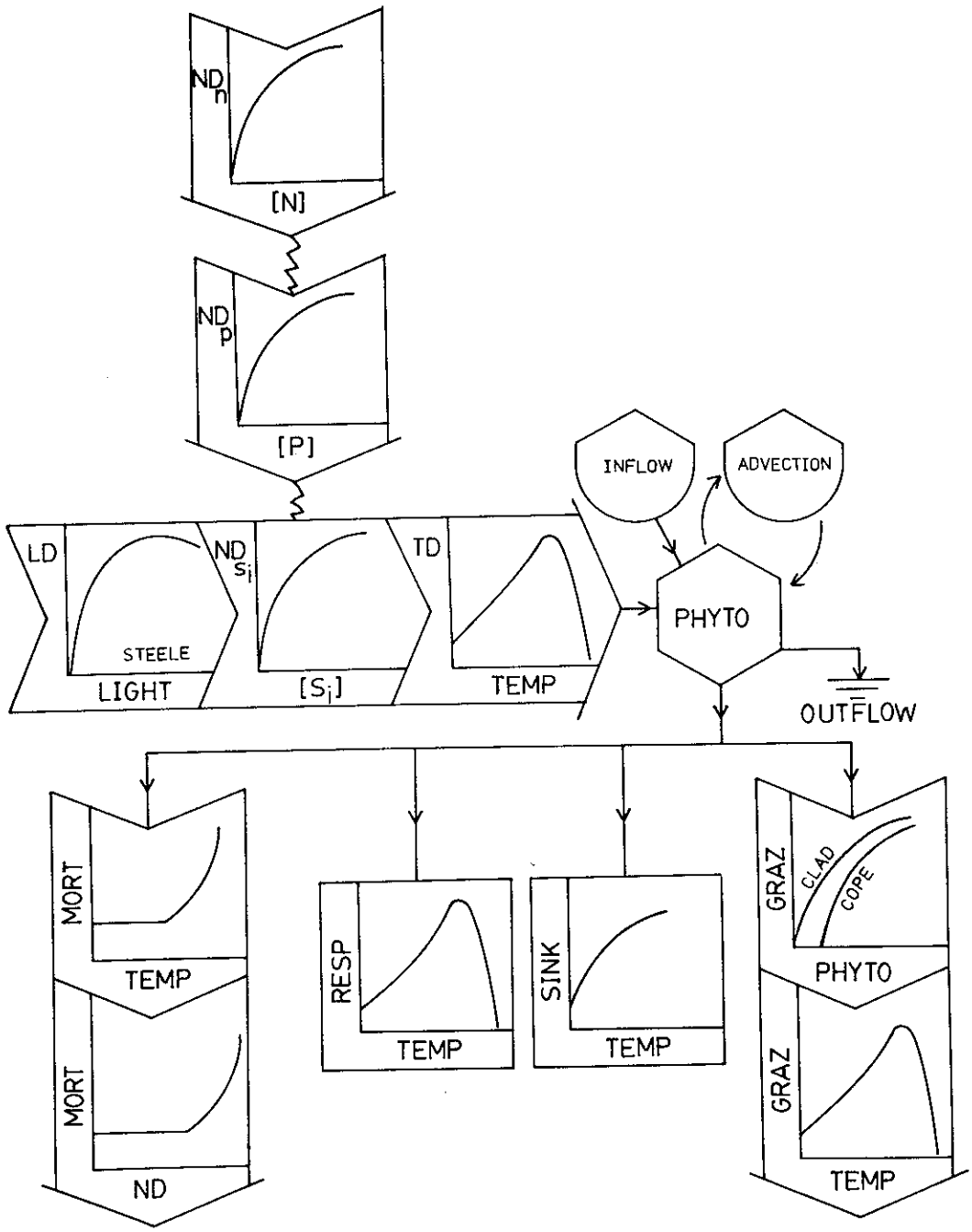


FIGURE 9. Flow chart of the CLEANER model of Youngberg (1977). Redrawn from Youngberg 1977.

mathematical models is difficult to obtain. The interactions of these factors has made experimental evaluation very complex.

The way in which photosynthetic rate is measured is an important consideration in evaluating the combined effects on photosynthesis, and it can be used to distinguish the effect of each factor. Ultimately, this information can be used to mathematically describe the combined effects, by knowing the dependence of the factors on one another. One method of determining the rate of the photochemical reaction of photosynthesis is to measure in terms of carbon fixed. Because the photochemical reaction is largely independent of temperature and nutrient levels, one can determine the contribution of light intensity to photosynthesis by measuring the O_2 evolved. Simultaneous measurement of carbon fixed may indicate the effect of temperature and nutrients under various combinations of limiting and nonlimiting conditions.

The photosynthesis-light intensity curve consists of three regions: the region of light limitation, where the photosynthetic rate increases linearly with respect to light intensity; the saturation region, where the maximum rate of photosynthesis is limited by the rate of the dark reaction; and the region of photoinhibition, where the rate of photosynthesis decreases markedly due to photolytic destruction of the pigments. The slope of the initial part of the curve is primarily a function of the photochemical part of photosynthesis and is indicative of the primary quantum efficiency of photosynthesis. When measuring O_2 evolved, the curve in this region would be essentially the same and therefore is independent of temperature. The light-saturated rate of photosynthesis represents the maximum rate of the enzymatic processes (Yentsch and Lee 1966). Because enzymatic processes are dependent on temperature, photosynthetic rate at high light intensities appears to be temperature-dependent; this is seen when carbon fixation is used as a measurement of photosynthetic rate (Figure 10). Photoinhibition appears to be reversible and is temperature-independent (Kok 1956; Nielsen 1962).

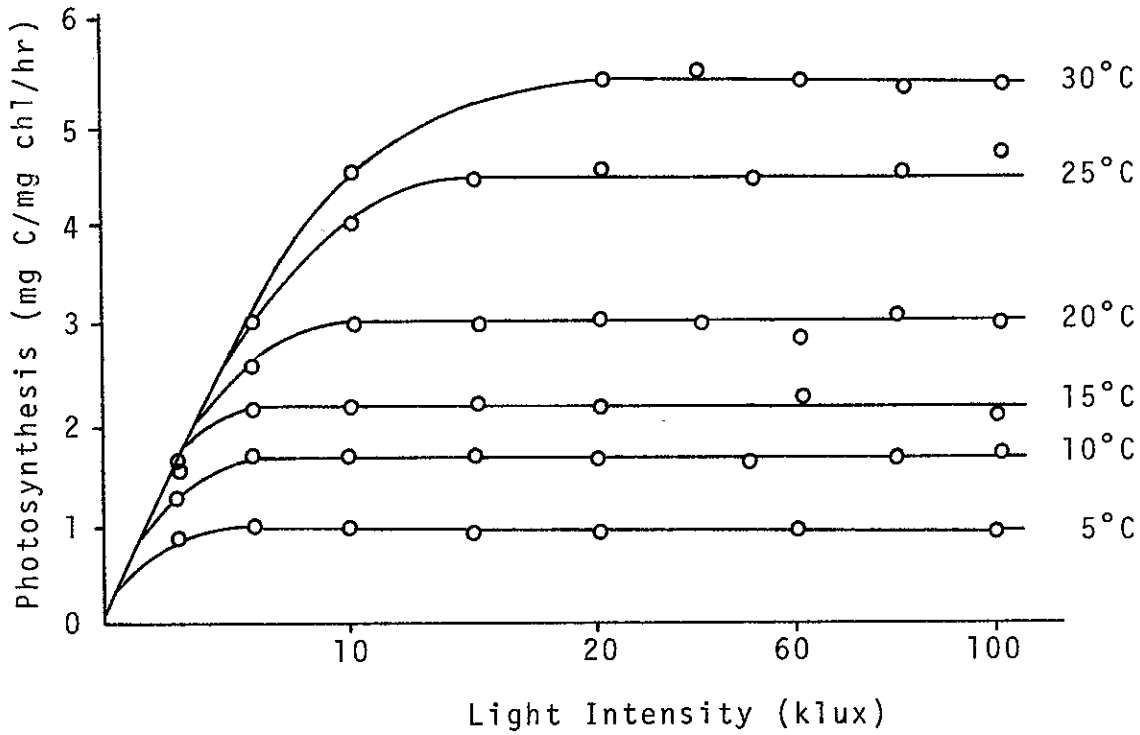


FIGURE 10. Increase in the light-saturated rate of photosynthesis with increasing temperature (from Aruga 1965). Redrawn from Aruga 1965.

Because the rate-limiting step of photosynthesis is determined by the rate of dark reaction (Blackman 1905), it seems reasonable that any factors affecting the dark reaction, such as temperature or nutrient concentration, may become rate-limiting factors. A simplifying assumption can be made that if nutrients were limiting under conditions of light saturation, the availability of nutrients would act as the ultimate rate-limiting step. However, the relationship of simultaneous nutrient limitation and light limitation on photosynthetic rate is uncertain and is confounded by the light-intensity dependence of nutrient uptake (MacIssac and Dugdale 1969; Davis 1976). Photosynthesis may be independent of temperature under low light conditions; however, nutrient uptake remains temperature-dependent at all light levels (Cloern 1977).

Existing mathematical models combine the effects of light intensity, temperature, and nutrient concentration in a variety of ways. Methods of combining the effects include the following:

- multiplication of all three together (Lehman, Botkin, and Likens 1975; Patten et al. 1975; Kremer and Nixon 1978; Youngberg 1977; and many other models); this implies that the factors are independent of each other and are of equal importance;

- light and nutrient limitations combined using the harmonic mean and then multiplied by the temperature limitation (Bloomfield et al. 1973; Park et al. 1974); this assumes interaction between nutrients and light and results in partial compensation for one by the others; temperature is treated as if it were independent;

- the minimum of light and nutrient limitations multiplied by temperature (Scavia, Eadie, and Robertson 1976); this implies that light and nutrients cannot be limiting at the same time and that temperature is independent;

- multiplication of nutrient limitation by the light limitation, with factors in the light and nutrient-uptake equations being temperature-dependent; this implies independence of the nutrient and light limitations, and a complex interaction with temperature and is in line with the conceptualization of photosynthesis described above; this method of combination is used in MS•CLEANER (Desormeau 1978; Park et al. in press; Collins 1979) and is described below; it is also used by Cloern (1978).

THE MS•CLEANER MODEL

In consideration of the special demands that reservoir dynamics place on ecosystem models and the current state of knowledge of algal physiology, the MS•CLEANER model has been developed by our group (Groden 1977; Desormeau 1978; Park et al. in press). It is not the definitive answer to modeling phytoplankton dynamics, but we feel that it does exemplify approaches that can be taken toward incorporating realistic process equations and combinations of equations in a reservoir model.

The model is much more complex than the models previously discussed (Figure 11). However, the complexity is supported by laboratory and field evidence. Because the parameters have physical (or biologic) meaning (Desormeau 1978; Park et al. in press; Collins 1979), extensive recalibration is not necessary in order to apply MS•CLEANER to a new site. In fact, data requirements are probably equal to those of many simpler models.

Intracellular storage of nutrients is modeled based on the work of Droop (1974) and Rhee (1973, 1974, 1978). Uptake of phosphorus and nitrogen is represented by a saturation-kinetic formation, with inhibition by a fraction of the nutrient being stored. Uptake is a function of light intensity, as shown by many investigators, and temperature, as shown by Fuhs et al. (1972) and Cloern (1977). At present assimilation of internally stored nutrients for growth is light-dependent. Single-nutrient limitation is determined by comparing the N:P atomic ratio to the threshold (Droop 1974; Rhee 1978) for the particular group of phytoplankton being simulated. Actual nutrient limitation is a function of the subsistence quota (the concentration of the nutrient per unit algal biomass) of the limiting nutrient and is independent of the nutrient uptake and assimilation terms.

Light limitation is treated in an equally complex manner, primarily because of representing adaptation to varying light intensities (Groden

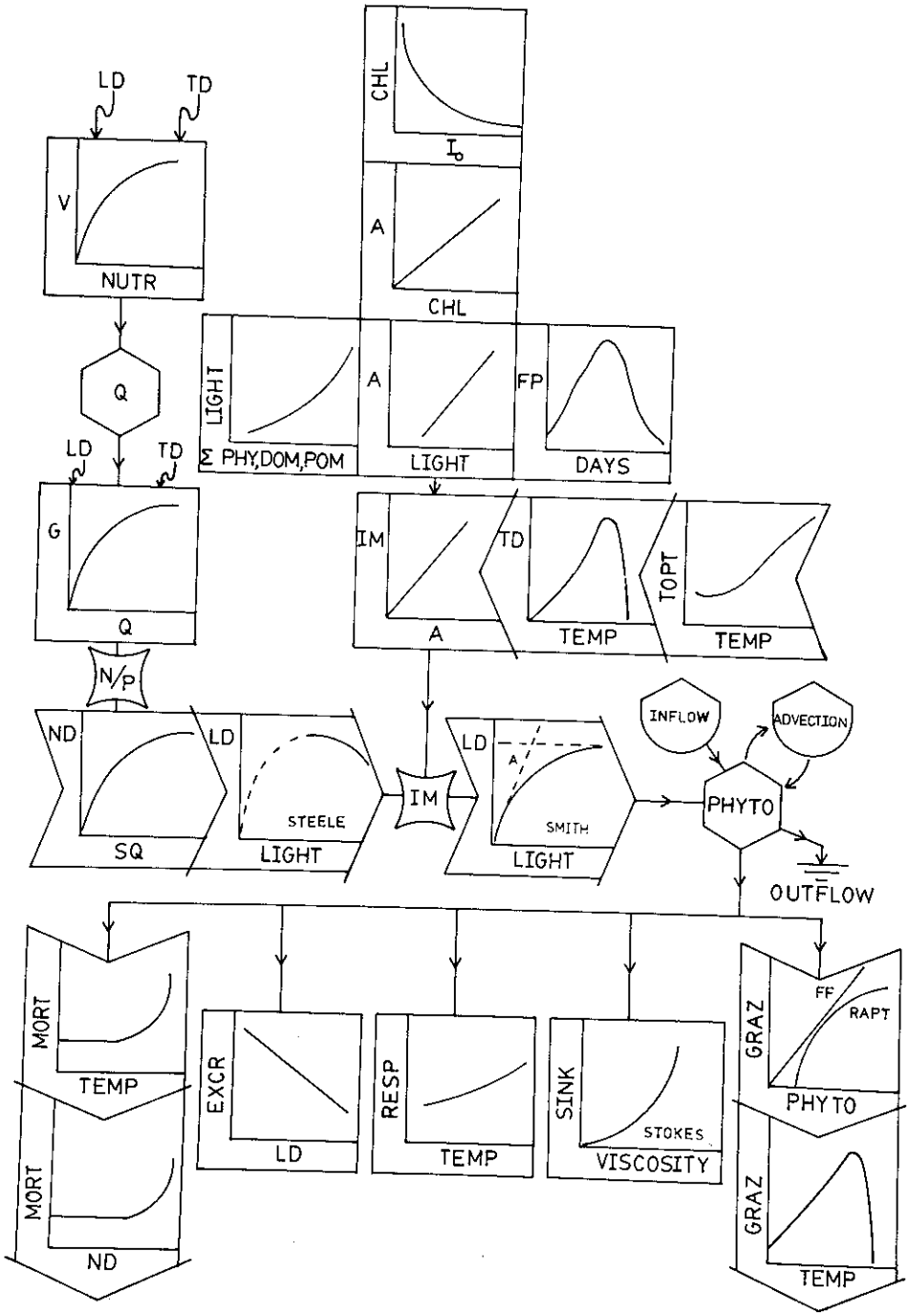


FIGURE 11. Flow chart of the phytoplankton submodel of MS•CLEANER.

1977). The slope of photosynthesis to light in the light-limited range is a linear function of chlorophyll concentration and the chlorophyll concentration is an exponential function of light in phytoplankton other than diatoms. The light saturation value for photosynthesis is a function of the slope. Light limitation at inhibitory levels is represented by Steele's (1962) equation; below inhibitory levels, Smith's (1936) equation is used, following the recommendation of Jassby and Platt (1976). Light extinction is a function of dissolved organic matter, particulate organic matter, and phytoplankton concentrations. Photoperiod is taken into account.

Temperature limitation does not enter into the photosynthesis equation directly, but rather is used to determine the light-saturation value and the rate of nutrient uptake. A nonlinear curve developed by Groden (1977) is used to calculate temperature dependency. Optimum temperature is a nonlinear function of ambient temperature, using a generalization (Groden 1977) of Straškraba's (1976) empirical function.

Inflow, outflow, and advective transport among vertical and horizontal segments are modeled explicitly by means of linking subroutines that can simulate up to ten segments simultaneously.

Grazing differentiates between saturation-kinetic feeding, exhibited by copepods and fish, and uniform-rate feeding, exhibited by cladocerans that filter at a constant rate. Grazing is a function of temperature and is modified by prey preference using a generalization of the construct of Park et al. (1974).

CASE STUDIES

Because of the complexity and multiple interactions of the environmental responses of phytoplankton, it is difficult to know intuitively what will happen under a particular set of circumstances.

Simulation models are useful because they can formalize our concepts of these responses and can keep track of the combined interactions. Two examples will be given to demonstrate this.

Slapy Reservoir, Czechoslovakia

The reservoir has a surface area of 13.1 km^2; length is 44.5 km; maximum depth is 53 m; mean depth is 20 m; mean retention time is 38.5 days; and withdrawal is hypolimnetic (Hrbáček and Straškraba 1966).

The two-layer version of the model CLEANER developed by Youngberg (1977) was used to simulate the reservoir ecosystem. The frequent oscillations in the three phytoplankton groups (Figure 12) do not seem to be borne out by the observed levels. This suggests that the model is too sensitive to changing nutrient levels, and that intracellular storage of nutrients is needed to stabilize the dynamics (Park 1978).

The model was perturbed by increasing the nitrogen loadings by a factor of 3.6 and the phosphorus loading by a factor of 2, corresponding to conversion of the drainage basin to 100 percent cultivation (based on data from Straškraba and Straškrabova 1976). The simulation of phytoplankton (Figure 13) is very similar to the normal simulation. This suggests that the phytoplankton are light-limited rather than nutrient-limited because of the high allochthonous turbidity and self-shading due to their already high biomass. A reduction in nutrients (not shown) resulted in a significant decrease in biomass, especially in diatoms.

Øvre Heimdalsvatn, Norway

The lake has a surface area of 0.775 km^2; length is 3 km; maximum depth is 13 m; and mean depth is 4.7 m. It is subalpine and is ultra-lingotrophic (Larsson *et al.* in press).

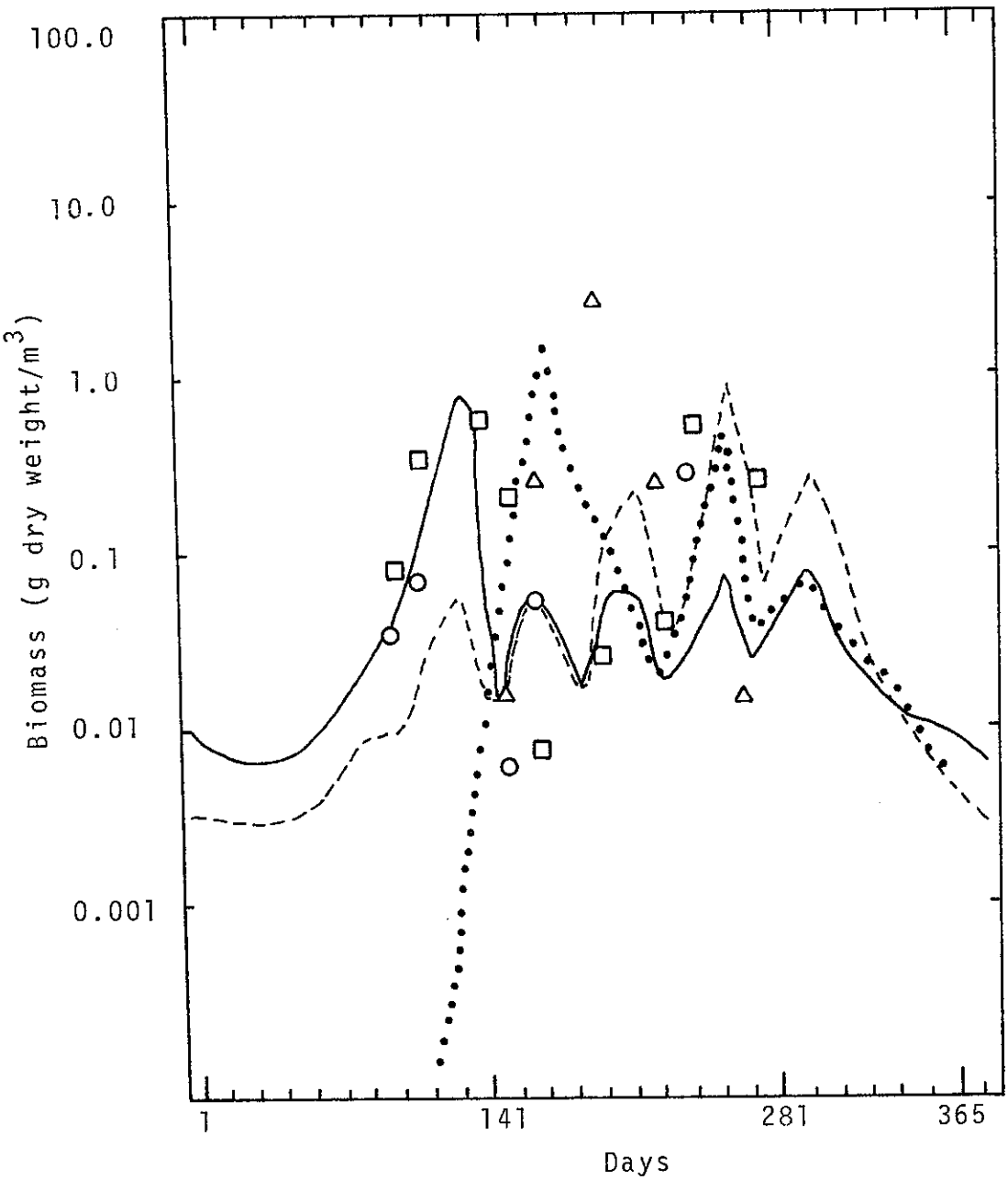


FIGURE 12. Simulation of phytoplankton biomass in epilimnion of Slapy Reservoir, Czechoslovakia, 1960.
—— = predicted, □ = observed diatoms;
--- = predicted, ○ = observed nannophytoplankton;
... = predicted, △ = observed blue-green algae.
Unpublished data courtesy of M. Straškraba. After Youngberg (1977). Redrawn from Youngberg 1977.

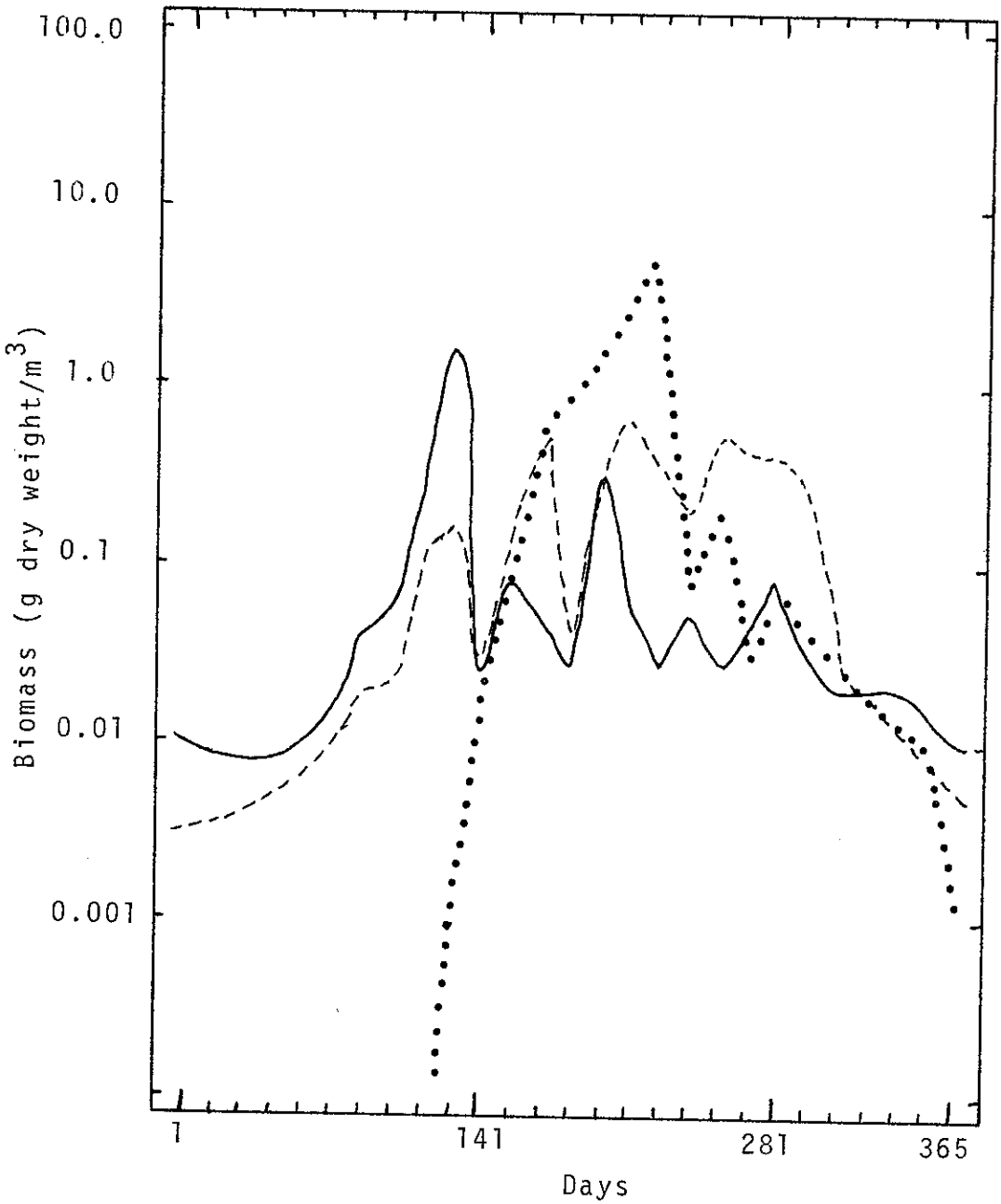


FIGURE 13. Simulation of phytoplankton biomass in Slapy Reservoir, Czechoslovakia, with nitrogen loading 3.6 times normal and phosphate loading 2 times normal. Legend same as Figure 12.

Although it is a natural lake, it is illustrative of the problems of simulating throughflow because the mean retention time is two months and during spring runoff the retention time may be two to three days. Furthermore, nutrient loading is highly variable. We found that a version of CLEANER without intracellular storage of nutrients consistently predicted a phytoplankton peak that corresponded to the peak phosphate loading, instead of the observed phytoplankton peak three weeks later.

The MS•CLEANER model, with an intracellular nutrient submodel developed by Collins (1979), yielded an excellent fit to the data (Figure 14). A plot of the process rates (Figure 15) demonstrates that the simple biomass curve is actually a function of several complex biological responses, reflecting the combined effects of the environmental factors. Loss due to outflow, even during the spring spate, was negligible and was not plotted.

Both light and nutrients limited growth (Figure 16), with nutrient limitation being by far the most severe--even with intracellular storage. Light limitation was important during times of heavy ice cover and in the summer when photoinhibition occurred. Temperature had little effect because of the adaptive capability of the algae, which was simulated well with the adaptive temperature formation (Figure 17).

When the flow rate was increased a hundredfold, the phytoplankton biomass decreased to approximately one half normal and zooplankton, with a slower turnover rate, decreased to 13 percent of normal (Figure 18).

Because of its realistic process equations, MS•CLEANER is capable of modeling the highly variable, combined effects of light, temperature, nutrients, and flow rate as in this example. Although its antecedent, CLEANER, is not as powerful (lacking adaptive constructs and state variables for intracellular nutrient), it is still capable of simulating

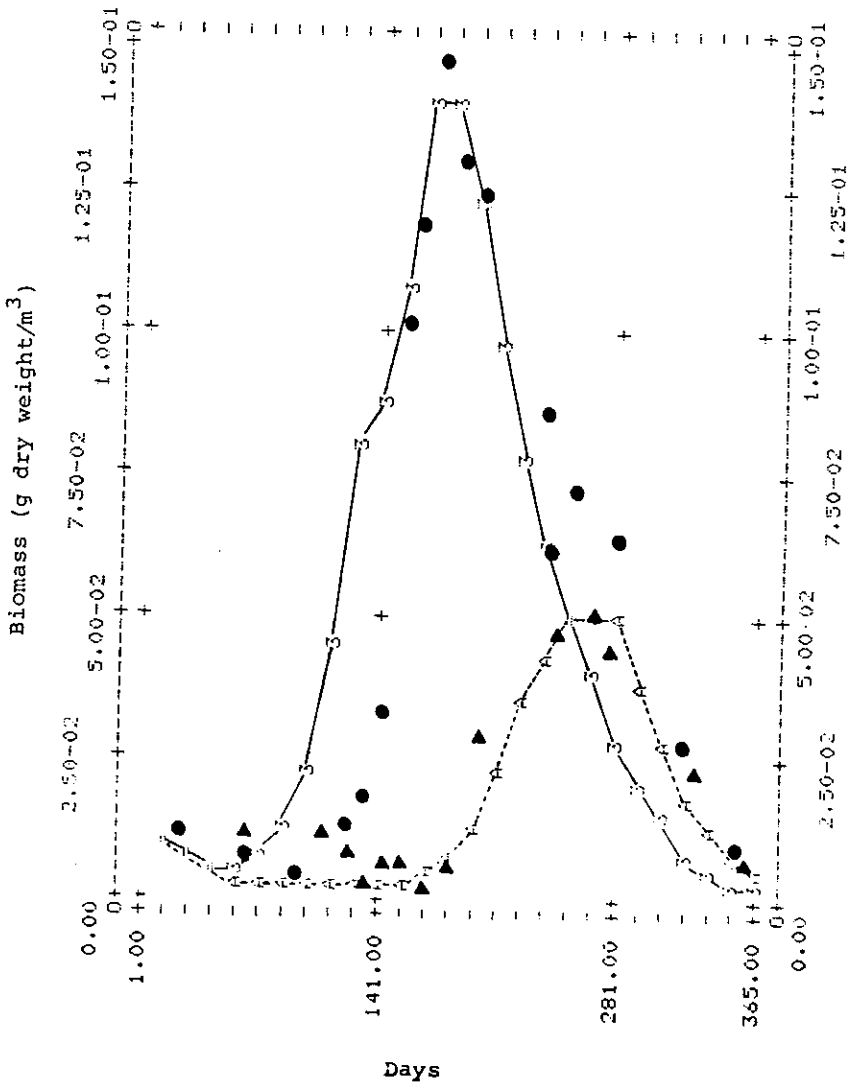


FIGURE 14. Simulation of biomass in Øvre Heimdalsvatn, Norway, 1972. -3- = predicted, ● = observed phytoplankton; --A-- = predicted, ▲ = observed zooplankton. Unpublished data courtesy of P. Larsson. From Collins (1979). Redrawn from Collins 1979.

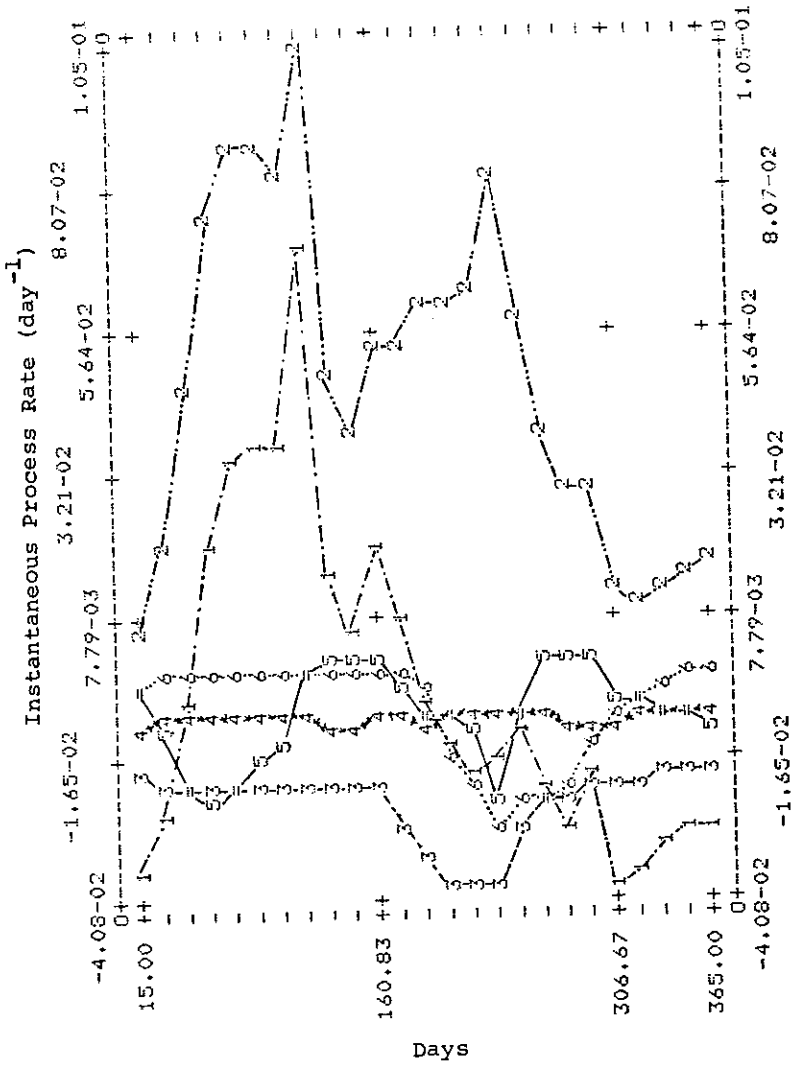


FIGURE 15. Process rates of phytoplankton for Øvre Heimdalsvatn, Norway, 1972. 1 = db/dt, 2 = net primary production, 3 = respiration, 4 = nonpredatory mortality, 5 = excretion, 6 = grazing. From Collins (1979). Redrawn from Collins 1979.

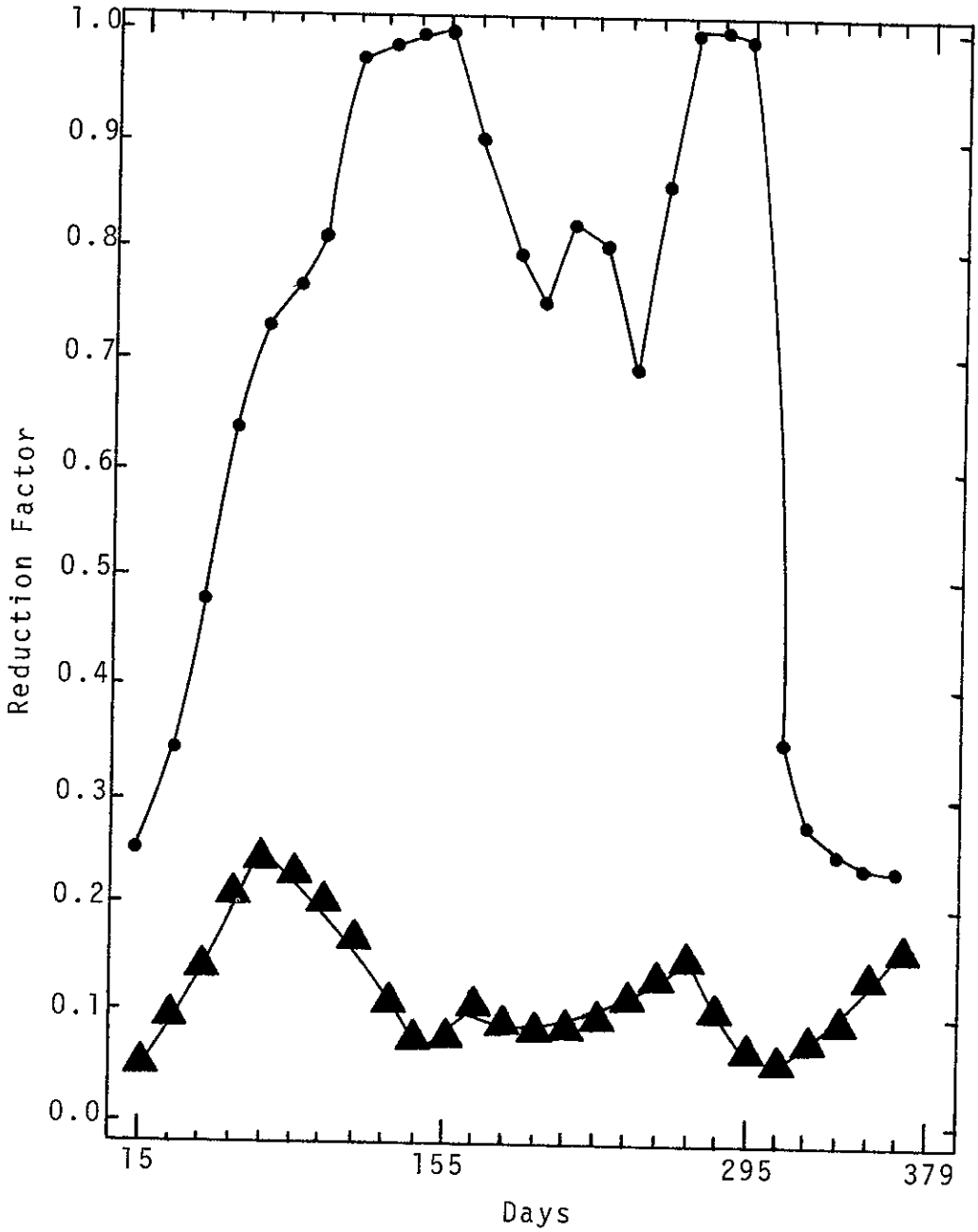


FIGURE 16. Seasonal plots of the simulated light reduction factor (●) and the nutrient reduction factor (▲) for phytoplankton growth in Øvre Heimdalsvatn, Norway. After Desormeau (1978). Redrawn from Desormeau 1978.

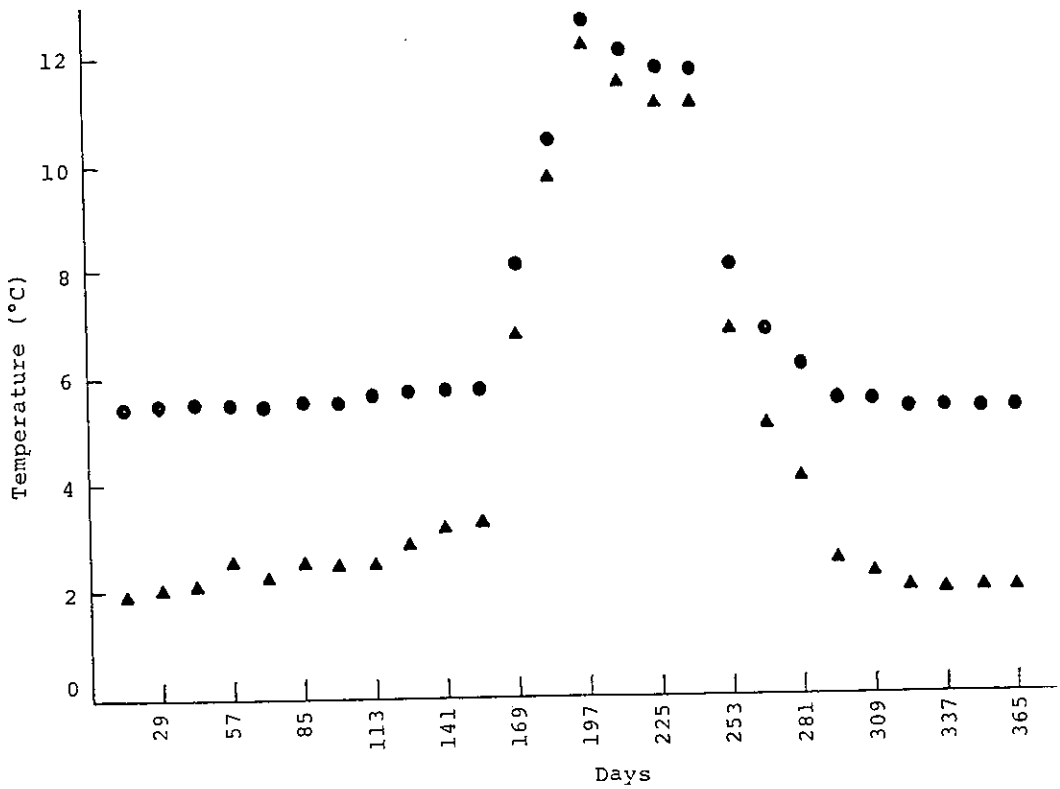


FIGURE 17. Comparison of simulated optimum temperature for photosynthesis (●) with ambient water temperature (▲); Øvre Heimdalsvatn, Norway, 1972. Unpublished data courtesy of P. Larsson. From Desormeau (1978). Redrawn from Desormeau 1978.

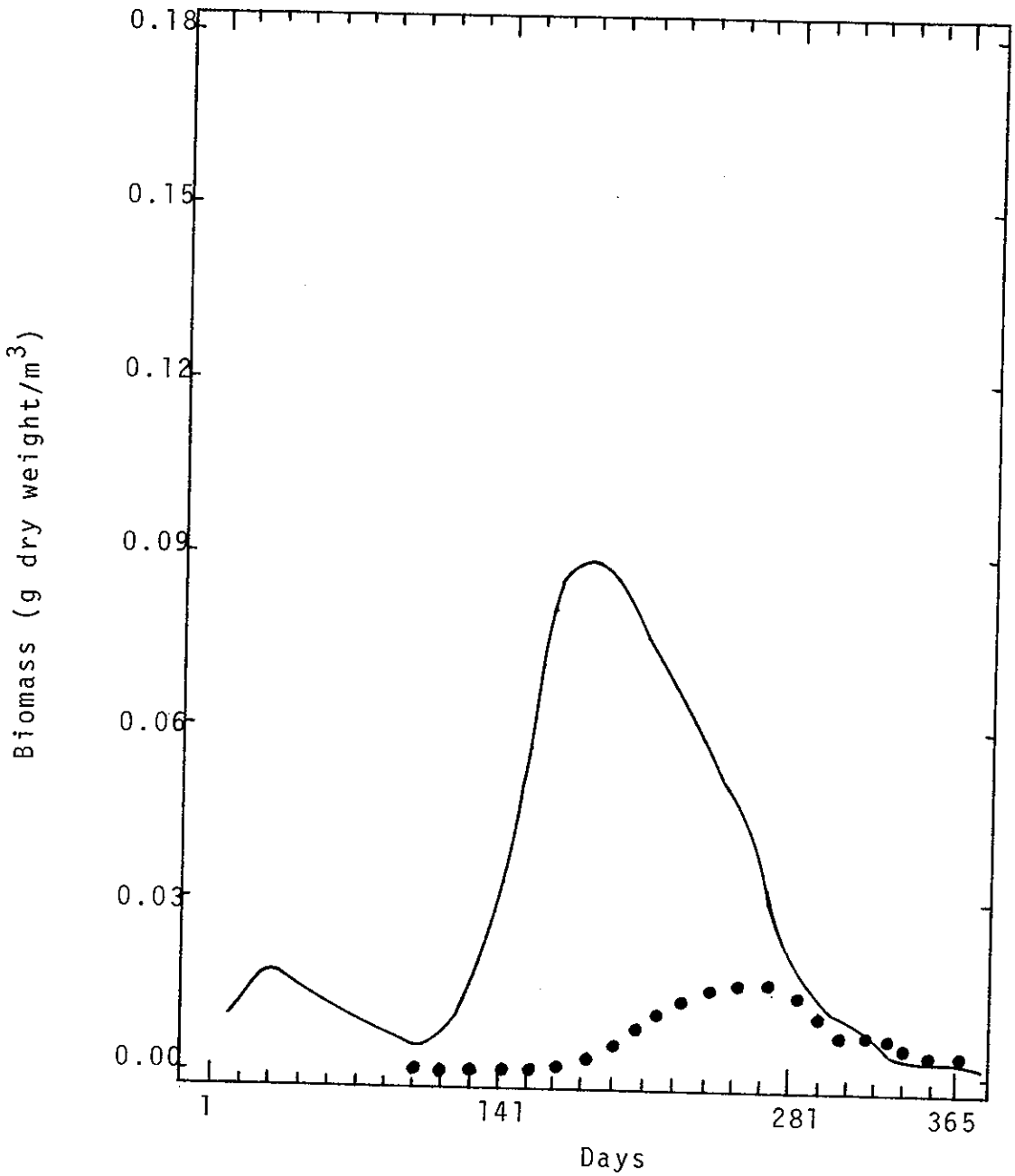
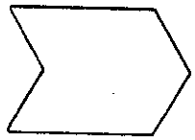


FIGURE 18. Perturbation of flow rate (hundredfold increase) for Øvre Heimdalsvatn, Norway; —— phytoplankton, ●●● zooplankton.

interactions such as the negative feedback of light limitation on phytoplankton in a hypereutrophic reservoir. We feel that the dynamics of reservoirs can be best understood and predicted through the use of realistic models such as these.

LEGEND



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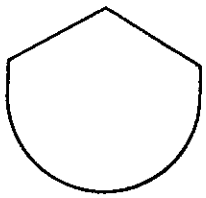

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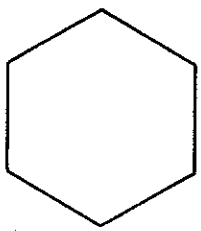
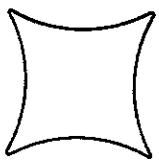
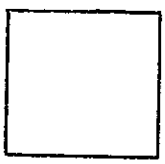


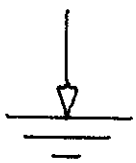
State Variable



Switch



Function



Sink

Harmonic Mean

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USE AND INTERPRETATION OF DETAILED, MECHANISTIC MODELS OF PHYTOPLANKTON DYNAMICS[1]

by

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[1]GLERL Contribution No. 188

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INTRODUCTION

Aquatic ecosystems comprise complex interactions of many biological, chemical, and physical processes. Effects of our impact on these systems are manifest also in complicated ways and at several levels of detail. For example, symptoms of eutrophication include increases in total algal biomass (a gross symptom) and shifts in algal dominance from diatoms to blue-greens (a detailed symptom). Complicated mechanistic models of the aquatic ecosystem are often suggested as a method of predicting such detailed symptoms because several of these models have been successful in simulating observed conditions in certain lakes. It is my opinion, however, based on experience with such models, that their use for long-term predictions is at best dubious. The main reason for this is that coefficient values (e.g., half-saturation constants, sinking rates, selective feeding constants for zooplankton) necessary to discern functional groups of phytoplankton (e.g., diatoms, greens, blue-greens) are not available; that is, overlap in measured coefficients for the individual functional groups precludes use of significantly different values.

This situation presents water resource managers with a difficulty. The problems, on the one hand, often require analysis at the level of detailed symptoms (i.e., filter clogging and taste and odor problems are species-specific or at least functional-group dependent). The technology, on the other hand, is generally only capable of estimating responses at the level of gross symptoms (e.g., annual average total phosphorus, total algal biomass dynamics).

Given this situation, the manager must still make important decisions. I suggest the following guide as an aid to making those decisions. The procedure involves use of simple engineering tools, traditional limnological analyses, and detailed, mechanistic models and is as follows: (1) Use simple mass balance models to estimate future nutrient conditions on the basis of proposed alterations to the water body (e.g., load alterations). (2) Estimate important gross parameters, such as N:P:Si ratios, on the basis of changes in nutrient levels and the geochemical settings of the water body. (3) Use total phytoplankton biomass models to estimate dynamics and magnitude of future algal biomass. (4) Use both traditional analysis of field and experimental data and analysis of simulations with a detailed, mechanistic model to determine controls of plankton and nutrient cycle dynamics under present conditions. (5) Combine results from the above analyses with expert limnological judgment to estimate detailed future conditions.

A very simple example of the above approach would be as follows: (1) Based on mass balance models, annual average total phosphorus is expected to decrease by 10 percent. (2) Based on present load calculations and basin geochemistry, future silica concentrations are expected to remain constant; the P:Si ratio will therefore decrease. (3) Gross phytoplankton models estimate only a 2-5 percent decrease in total algal biomass. (4) Analysis of present reservoir conditions indicates that the algal composition is controlled initially by the rate of thermocline setup and later by the relative supplies of phosphorus and silica. (5) By combining the above information, one might expect that the reduction in phosphorus load would not significantly reduce total algal

biomass but rather produce an important shift of algal dominance from green algae to diatoms based on the suspected control mechanisms and the expected reduction in the P:Si ratio.

I feel that this approach of combining data analysis, limnological judgment, and a spectrum of models will serve the decisionmaker and water resource manager well. It is in this context that I will discuss the use of detailed, mechanistic models in reservoir management, specifically as an aid to understanding present system controls.

UNDERSTANDING PRESENT ECOSYSTEM DYNAMICS

Examination of isolated biological, chemical, or physical processes provides insight into that process and perhaps some qualitative estimate of its importance relative to other processes. The best way to estimate quantitatively the relative influence of various processes on the control of phytoplankton dynamics is to examine several of the processes simultaneously. This is both difficult and expensive, especially for large systems. Thus, we are often left with "snap-shots in time" of state variable concentrations. I will demonstrate below how the use of a detailed, mechanistic model to synthesize isolated process information and to interpolate between snap-shots of state variables can provide additional insight into control of phytoplankton dynamics.

This particular application is for Lake Ontario and comprises three phases. The primary phase was collection of data on both state variables and some processes. The second phase was development and testing of a detailed, mechanistic model to simulate these measurements and to

become a functionally based data interpolator. The third phase was analysis of simulation output, measured system variables, and *in situ* and *in vivo* process measurements to determine system controls. In the following sections of the present paper, I briefly describe the model, show the dynamics of the measured variables, report the results of testing the adequacy of the model as an interpolator of those data (Scavia 1979a), and summarize model tests at the level of process dynamics and use of the model to examine control of phytoplankton production and phosphorus cycling in Lake Ontario (Scavia 1979b).

Model and Data

Scavia *et al*. (1976a) developed an ecological model of Lake Ontario that simulates the seasonal dynamics of several biological and chemical properties in the epilimnion, the metalimnion, the hypolimnion, and the lake sediment. The main objective of this work was to investigate the basic limnological and ecological properties of Lake Ontario on a lake-wide averaged basis. That model has been tested by application to the other Great Lakes (Scavia *et al*. 1976b) and by comparison (Scavia and Chapra 1977) to output from models of the phosphorus loading concept (Dillon and Rigler 1974a,b); a modified version has been used to examine specific aspects of the ecology of Lake Ontario (Robertson and Scavia 1979; Scavia 1979b). The model used herein is an extension of that work.

The model (Figure 1) includes phytoplankton; zooplankton; cycles of phosphorus, nitrogen, silicon, and carbon; an oxygen balance; and

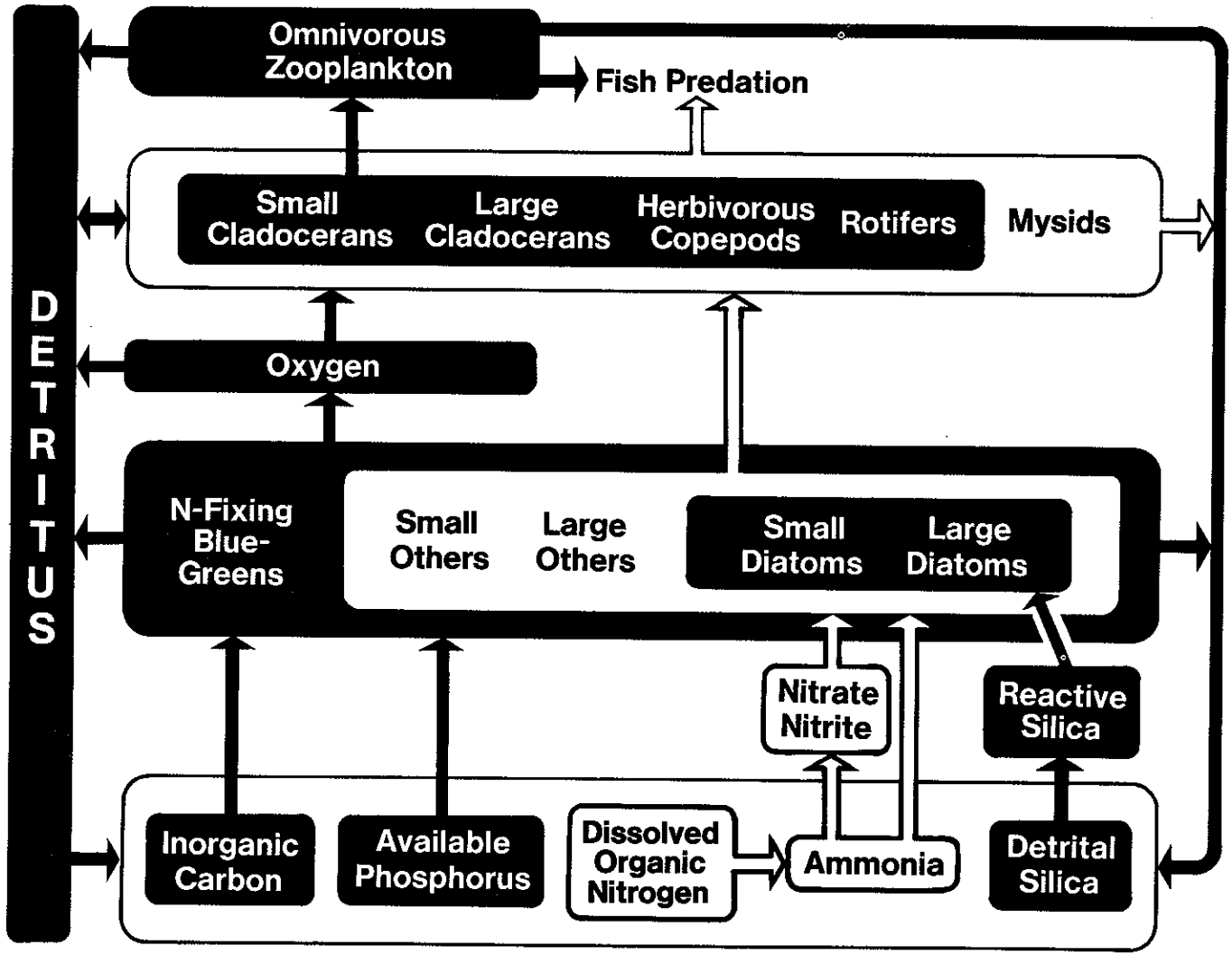

FIGURE 1. Conceptualization of Lake Ontario ecological model (from Scavia 1979a). Redrawn from Scavia 1979a.

calculations of the carbonate equilibrium system. A sediment compartment includes benthic invertebrates as well as cycles of carbon, phosphorus, nitrogen, and silicon. The reason for segregating phytoplankton and zooplankton each into several groups is to allow for differences in functional requirements (e.g., diatoms versus nondiatoms) and processes (e.g., size-selective filter feeders versus nonselective feeders).

Each model compartment is represented by a differential equation composed of important biological, chemical, and physical processes. For example, the phytoplankton equation includes terms for gross primary production, respiration, excretion, grazing, sinking, and vertical mixing; the zooplankton equation includes terms for grazing, assimilation, respiration, excretion, defecation, and predation. Justification and rationales for the process equations used, as well as detailed documentation of the overall model, are presented in Scavia (1979a). What follows is a general description of the processes included in the model.

Gross phytoplankton production is considered to be a single-step process that assumes, for the time scale of the model (several days), that rates of uptake and growth are in equilibrium. The process is modeled with a temperature-dependent, maximum growth rate times a reduction factor for light- and nutrient-limitation. Potential light-limitation is modeled after Vollenweider (1965) and Steele (1965) and potential nutrient-limitation is expressed as a Michaelis-Menten term for each nutrient. The threshold formulation is used to determine overall limitation. Phytoplankton respiration is considered to be the

sum of a low maintenance rate plus a term proportional to production, as well as a function of temperature. For the purpose of maintaining constant nutrient stoichiometry within the plankton, nutrient excretion is assumed to be proportional to respired carbon.

Zooplankton grazing is handled as a temperature-dependent saturating expression based on total food supply. The expression includes a minimum threshold for feeding as well as resource partitioning based on size selection. Feeding and assimilation efficiencies are regarded as food-specific constants. Food ingested but not assimilated is egested as detritus. Respiration is a temperature-dependent process that is the sum of a low maintenance rate and a term proportional to the feeding rate. Nutrient excretion is proportional to respiration.

Transformation rates between detritus, dissolved organic nitrogen, ammonia, nitrite plus nitrate, available phosphorus, and available silicon pools all are temperature-dependent and first order. Sinking rates of phytoplankton and detritus are size- and density-dependent. Vertical mixing is modeled as an exchange coefficient times the concentration gradient.

The model considers the lake to be horizontally homogeneous and vertically segmented into two layers representing the epilimnion and hypolimnion. A one-dimensional, 18-layer diffusion model calibrated to temperature profiles measured in Lake Ontario is used to calculate depth of the thermocline and average epilimnion and hypolimnion temperatures. Values of the diffusion (or exchange) coefficient between the two layers

are then calculated from temperature changes in the two layers and from the velocity of thermocline displacement (Figure 2).

The ecological model was calibrated with data collected during the International Field Year for the Great Lakes (IFYGL) in 1972-73. Documentation of the seasonal cycles of the IFYGL data and the model output, as well as discussions of the model equations, coefficients, and sensitivity analyses, are presented in detail elsewhere (Scavia 1979a). Although the model includes detailed process equations describing the food web and nutrient cycles in Lake Ontario, it is still a crude representation of reality. Therefore, before this model was used in examination of lake-scale phytoplankton production and phosphorus cycling, it was tested, in this context, as to its adequacy as a representation of the seasonal changes in relevant lakewide averaged properties in Lake Ontario. This was done by comparing measured and simulated properties (Scavia 1979a). The comparisons are best for those properties measured with most certainty (i.e., chemical properties) and worst for those properties difficult to measure (i.e., photoplankton and zooplankton carbon densities); however, these comparisons resulted in general agreement between measured and simulated properties (Figures 3-6). These results demonstrate the model's ability to simulate the seasonal dynamics of photoplankton, zooplankton, and the major nutrients; however, model output should also be compared to measurements of process rates to see how well the model simulates the internal dynamics of the system. Throughout the discussions that follow and in Scavia (1979b), simulated process rates are compared to process rates that were measured in Lake Ontario during IFYGL or during other years. Also, where certain processes

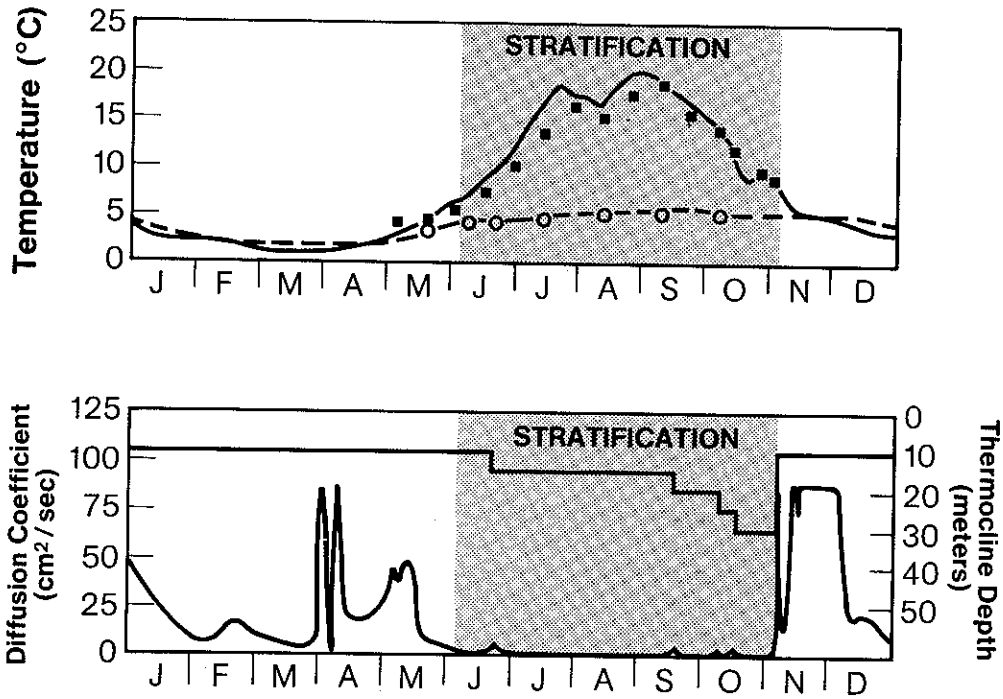

FIGURE 2. Simulated and observed (Pickett 1976) lakewide averaged temperatures (top): ■ - epilimnion, o - hypolimnion. Simulated thermocline depth and diffusion coefficients (bottom) (from Scavia 1979a). Redrawn from Scavia (1979a).

have not been observed in Lake Ontario, information from other field and laboratory studies are used for general comparisons. The simulated and measured rates are also in general agreement, which allows one to use the model to speculate about the relative importance of these processes.

Control of Phytoplankton Dynamics

The simulated processes controlling the seasonal dynamics of one of the phytoplankton groups in the epilimnion are shown in Figure 7. The stippled area indicates the net rate of change of the population biomass. In winter and early spring, the phytoplankton is controlled primarily by the balance between gross primary production and two physical processes, sinking and vertical mixing. During these times, phytoplankton gross production is limited mainly by the availability of light, which is controlled both by the amount of incoming solar radiation and the depth to which the phytoplankters are mixed. Mixing between the two model layers becomes quite intense in early spring (Figure 2), indicating that the mixing depth is the depth of the entire water column. This loss to the dark, deeper layers prevents substantial increases in algal biomass, which occur only after mid-spring when the surface waters in Lake Ontario begin to warm and the lake begins to stratify vertically. At this time (early June), phytoplankton populations increase rapidly and the concentrations of the nutrients they assimilate begin to decrease. The concentrations of nutrients decrease because they also become relatively isolated from the nutrient-rich lower strata. Phytoplankton production is limited by nutrients (silicon and phosphorus) from this time until the end of September, which has

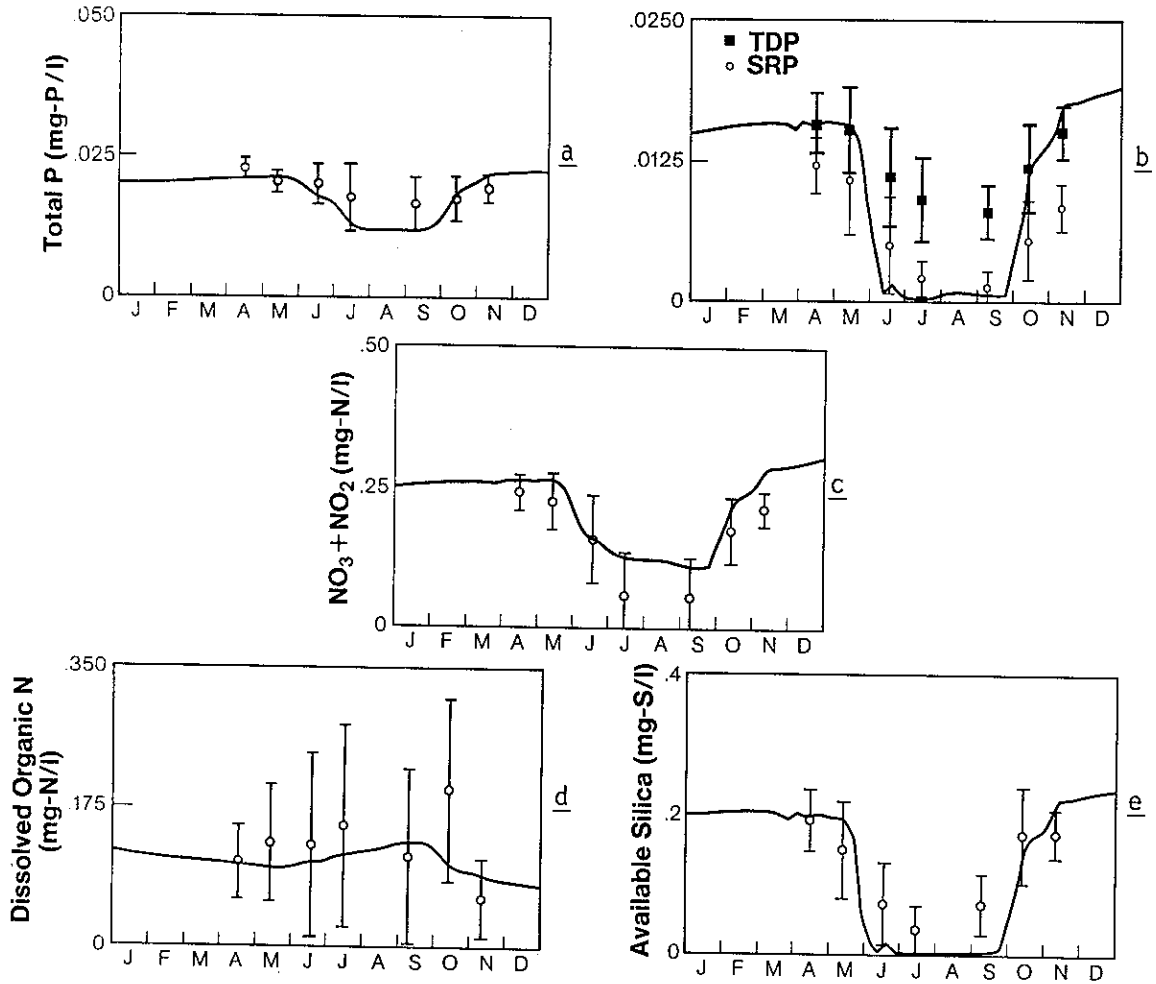

FIGURE 3. Seasonal dynamics of data and model output for epilimnion (0-20 m) of Lake Ontario during 1972; a - Total P, b - Filterable P, c - $NO_3 + NO_2$, d - Dissolved organic N, e - Soluble reactive silicon. Data are lakewide mean ± 1 S.D. (from Scavia 1979a). Redrawn from Scavia 1979a.

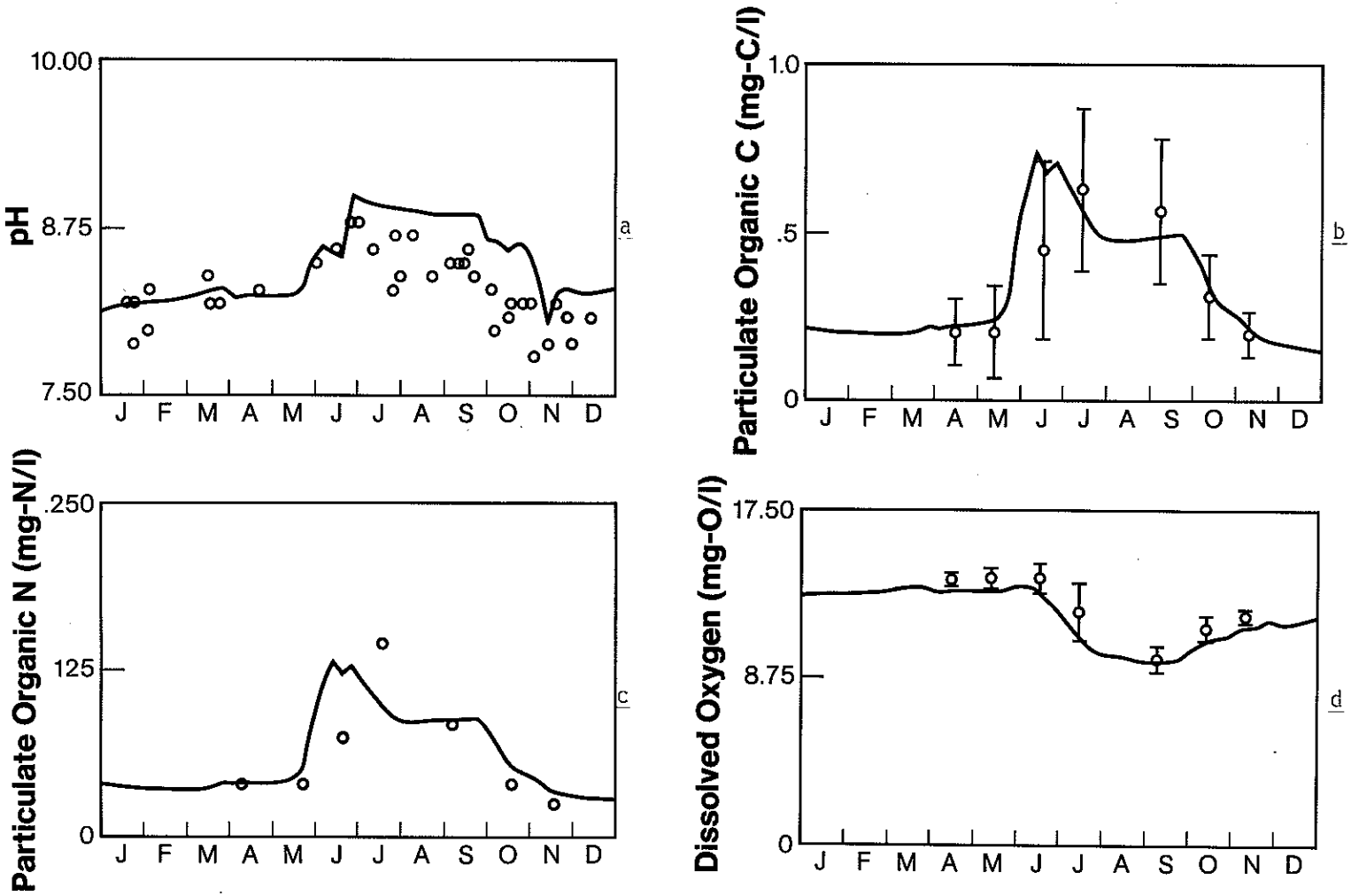

FIGURE 4. Seasonal dynamics of data and model output for epilimnion (0-20 m) of Lake Ontario during 1972; a - pH, b - Particulate organic C, c - Particulate organic N, d - DO. Data are lakewide mean ± 1 S.D. (from Scavia 1979a). Redrawn from Scavia 1979a.

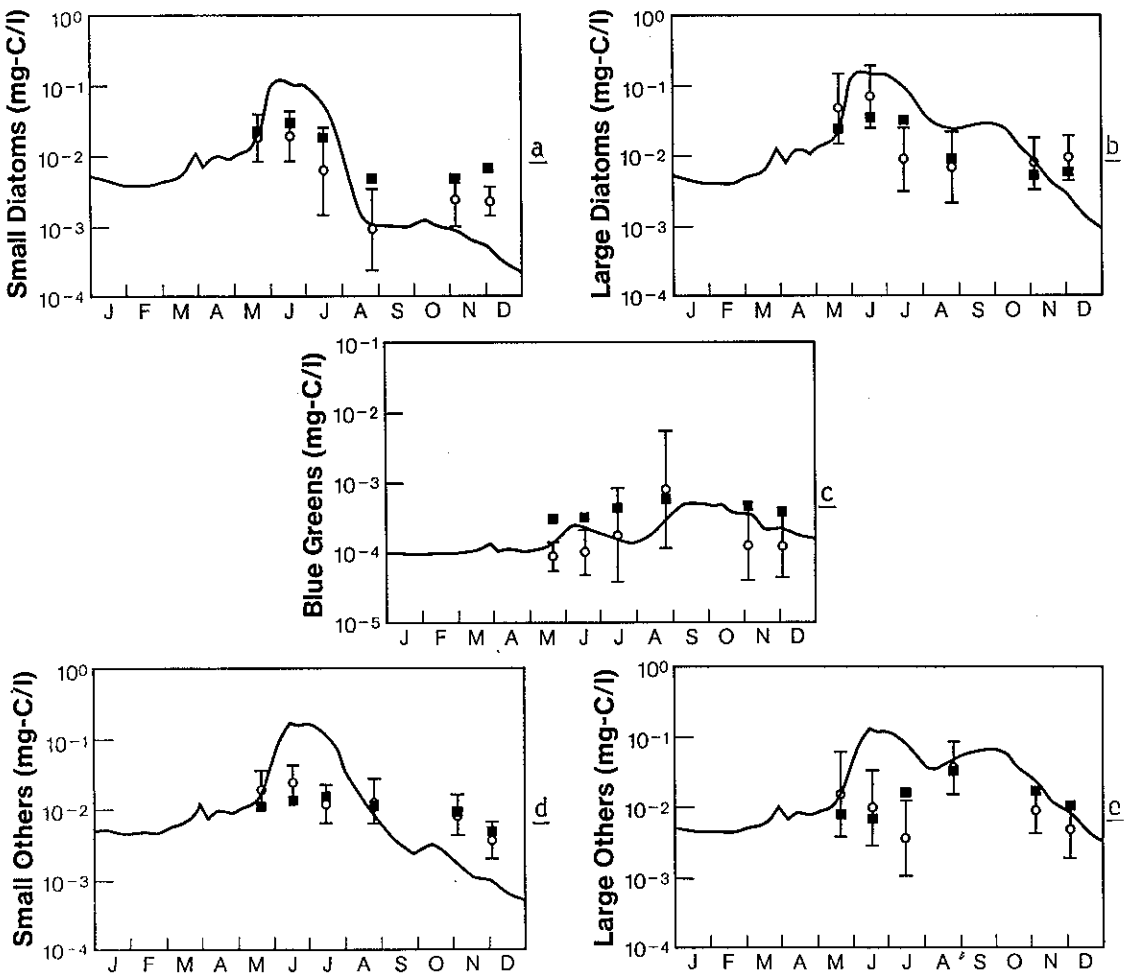

FIGURE 5. Seasonal dynamics of data and model output from epilimnion (0-20 m) of Lake Ontario during 1972; a - Small diatoms, b - Large diatoms, c - Blue-greens, d - Small others, e - Large others. ⊥○⊥ = lake-wide mean ± 1 S.D. for surface samples and ■ = lakewide mean for depth-integrated profiles (from Scavia 1979a). Redrawn from Scavia 1979a.

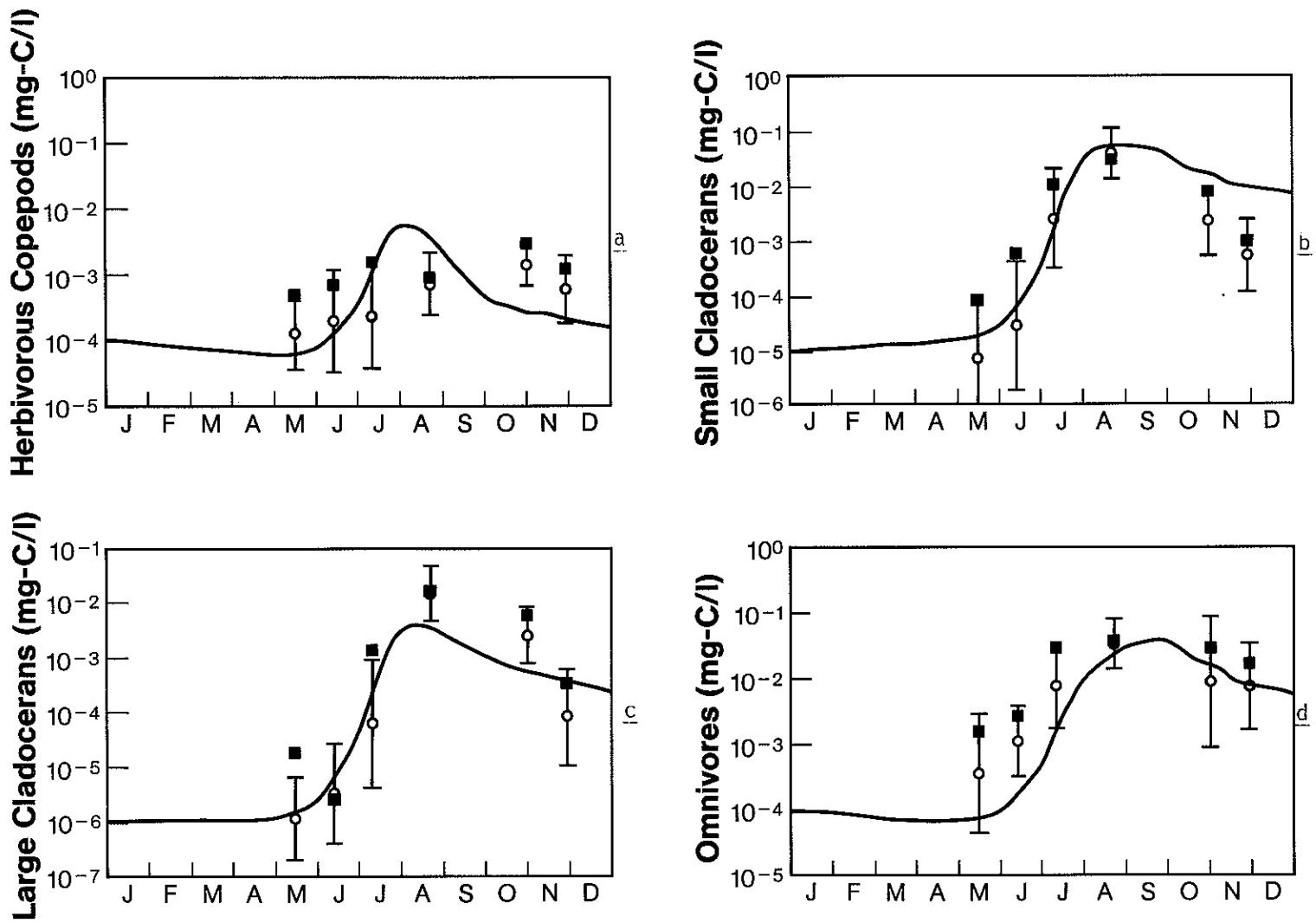

FIGURE 6. Seasonal dynamics of data and model output for epilimnion (0-20m) of Lake Ontario during 1972; a - Herbivorous copepods, b - Small cladocerans, c - Large cladocerans, d - Omnivores. Symbols as in Figure 5 (from Scavia 1979a). Redrawn from Scavia 1979a.

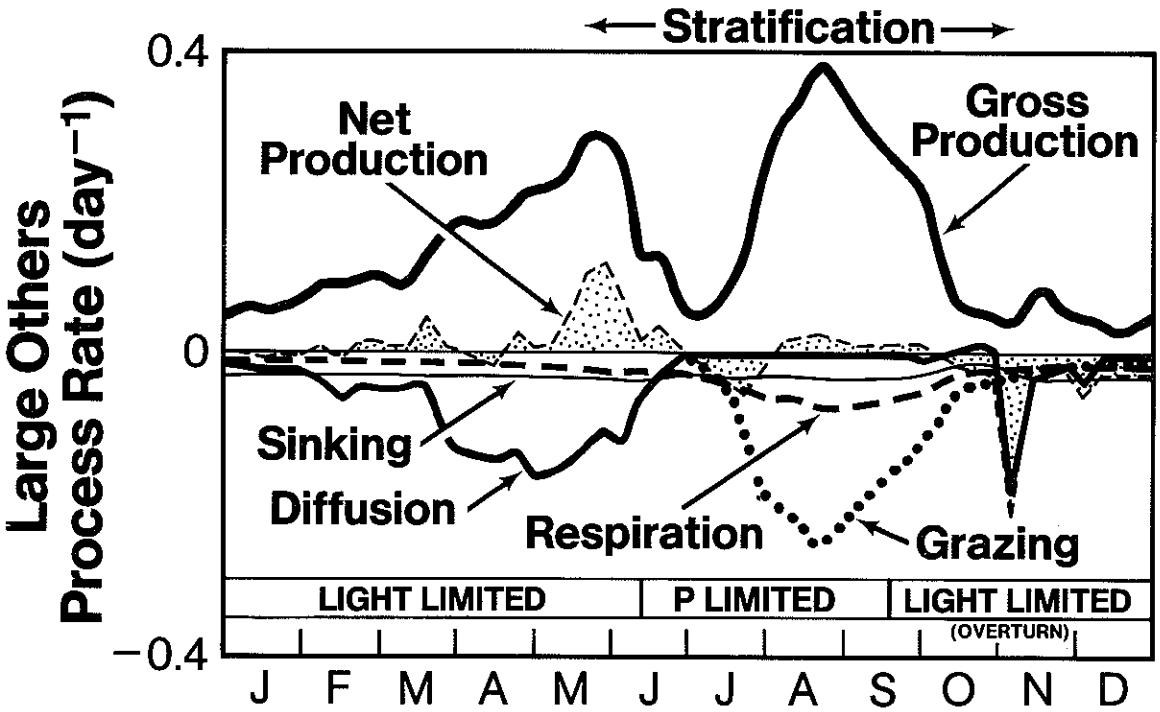

FIGURE 7. Rate plots indicating simulated controls of epilimnion photoplankton dynamics in Lake Ontario during 1972. Stippled area represents net growth rate (from Scavia 1979c).

previously been suggested based on mass balance considerations (Stadelmann and Fraser 1974) and on algal assays (Sridharan and Lee 1977).

During the same time period (late summer), grazing stress exerted by zooplankton becomes most intense (Figure 3). This time history of simulated grazing pressure reflects the general seasonal pattern of crustacean zooplankton biomass (Scavia 1979a). All of the dominant species in Lake Ontario produced major biomass peaks during July or August in 1972 (McNaught et al. 1975). Also, for a previous year in Lake Ontario, Glooschenko et al. (1972) measured and compared the relative abundances of chlorophyll a and pheo-pigments and suggested that a high correlation between average percent pheo-pigment (relative to total chlorophyll a zooplankton abundance) was probably a result of zooplankton grazing. On a lakewide average basis, they found highest values for the percent of total chlorophyll a as pheo-pigments to occur in August-October. This further substantiates the simulation results in Figure 7.

In late September, the thermocline deepens (Figure 2) and nutrient-rich, hypolimnetic water is mixed with epilimnetic water. Because of this increase in nutrient concentrations and the simultaneous increase in mixing depth, the algae again become limited by light. In early November, the lake overturns and becomes vertically homogeneous and phytoplankton concentrations begin to approach winter values. Of course, this is a simplification of the actual three-dimensional effects; however, in a one-dimensional model, all advective and dispersive processes are parameterized as vertical mixing.

Control of Phosphorus Dynamics

Although it is clear that nutrient limitation does not solely control phytoplankton dynamics, the role of nutrients, especially phosphorus, is certainly crucial during the period of stratification. Therefore, to better understand the control of phytoplankton dynamics in Lake Ontario, one must investigate the processes influencing the cycling of phosphorus. To accomplish this, I constructed a phosphorus flow diagram (Figure 8) from model output averaged over the period of July-September and compared the results with available information (Scavia 1979b). The sizes of the five phosphorus compartments are representative of Lake Ontario for this time period (see Figures 3-6 of Scavia 1979a). The rate of conversion of available phosphorus to particulate phosphorus (Stadelmann and Fraser 1974) and the fluxes of phosphorus across the thermocline (Stadelmann and Fraser 1974; Burns and Pashley 1974) are also representative. Zooplankton grazing rates represent 50 percent and 53 percent of the animals' body phosphorus per day for omnivores and herbivores, respectively. This is consistent with general dry weight ratios for small crustacean zooplankton (Parsons and Takahaski 1973). Zooplankton excretion rates represent 14 percent and 11 percent of body phosphorus per day for omnivores and herbivores, respectively. These rates agree with excretion rates summarized by Ganf and Blazka (1974) if one assumes for these animals a nitrogen to phosphorus body weight ratio of approximately 11 (cf. Parsons and Takahaski 1973). Quantitative information about other processes is not available and, therefore, in those cases, model information alone will be used.

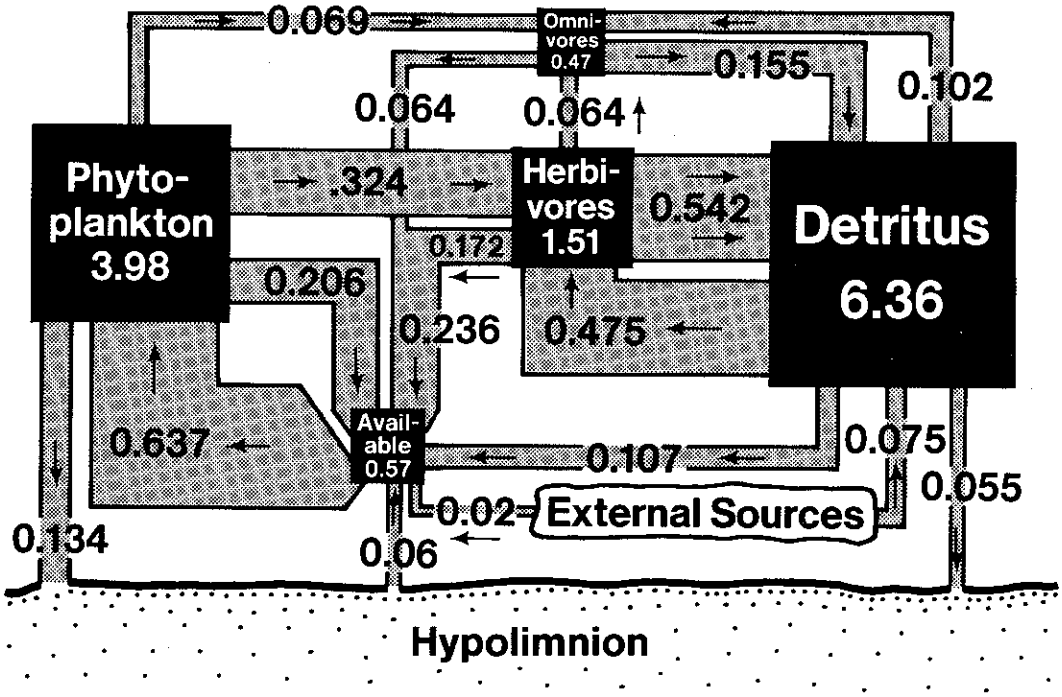

FIGURE 8. Phosphorus flow diagram. Concentration in boxes are in μg-P/l and in pipes in μg-P/l/day. These values are averaged over the period of July-September for the top 15 m. Phytoplankton, zooplankton, and detritus are evaluated in the model in terms of carbon and are converted to phosphorus for this figure by assuming a $C_{106}P_1$ atomic ratio (from Scavia 1979c).

It can be seen (Figure 8) that it would take less than one day for the phytoplankton to deplete the available phosphorus pool in the summer epilimnion if there were no recycling, and that external sources and hypolimnetic sources alone could not meet this algal phosphorus demand. In fact, this analysis indicates that 87 percent of the assimilated phosphorus is recycled within the epilimnion. Stadelmann and Fraser (1974) estimate this recycling to be 87-93 percent for the upper 20 m at a single station during the same time period.

Rigler (1973) suggested three possible sources for biological recycling of soluble PO_4-P: (1) direct release by ultraplankton (bacteria plus phytoplankton <30 μm), (2) excretion by zooplankton, and (3) enzymatic hydrolysis of organic compounds. He also suggested that excretion by zooplankton and direct release from ultraplankton were equally important. The results from Scavia (1979b) (Figure 8, Table 1) suggest that, for this five-compartment conceptualization, zooplankton excretion and direct release by phytoplankton are approximately equal and are the most important processes supplying phosphorus to the available pool. The rate of remineralization of detrital phosphorus is somewhat slower. This rate represents regeneration of approximately 1.7 percent of the detrital phosphorus per day, which is within the range measured by DePinto and Verhoff (1977) in laboratory experiments.

The role of zooplankton in the phosphorus cycle must be emphasized. While zooplankton has an obvious role in applying pressure to reduce algal concentrations (Figure 7), it also appears to play a dual role in recycling phosphorus. Not only does the zooplankton input directly to

Table 1. Relative recycle rates of phosphorus in the epilimnion during stratification; total rate = 0.629 μg-P/l/day (from Scavia 1979c).

	Percent of Total Recycle Rate
Phytoplankton Excretion	33
Zooplankton Excretion	
Herbivores	27
Omnivores	10
Total	37
Detritus Decay	17
External Load	3
Hypolimnion Load	10

the available nutrient pools through excretion, but it also serves as a supplier of detrital material (feces), which undergoes additional degradation by the decomposers and eventually adds to the available nutrient supply. Thus, it may well be that the zooplankton is principally responsible for the high recycling rates estimated by Stadelmann and Fraser in Lake Ontario. In fact, simulations (Figure 7) indicate that during the period of intense zooplankton grazing (August-September), algal gross production increases dramatically due to recycled nutrients.

In summarizing the information generated from this analysis, the following statements can be made (Scavia 1979b):

(1) In spring and fall, phytoplankton dynamics are controlled by light. This light-limitation is a function of the amount of incoming solar radiation and the relationship of the euphotic depth to the mixing depth.

(2) In late spring and summer, phytoplankton production is limited primarily by silicon and phosphorus; however, some phytoplankton production continues throughout the period of stratification because recycling processes maintain sufficient supplies of nutrients.

(3) During stratification, available phosphorus is supplied to the epilimnion through external sources (3 percent of total), influx from the hypolimnion (10 percent), and biological recycling (87 percent). The latter process is by far the most important; influx from the hypolimnion is only important at the beginning and end of stratification, and external sources are low in comparison to the recycling supplies.

(4) The roles of zooplankton in controlling phytoplankton are complex. Grazing pressures tend to reduce algal populations in mid-summer; however, during this time period, zooplankton contributes to nutrient supplies by excretion and egestion. These nutrients are supplied most during mid-summer when the algae are under the greatest nutrient stress.

In Scavia (1979b) and the above summary, I have used an ecological model of Lake Ontario to synthesize information collected on individual

ecosystem components and on processes. By coupling this synthesis tool with traditional limnological analyses, one can synthesize a more complete description of the system's control. This tool, with the other tools mentioned above, can provide the resource manager with information required in the decisionmaking process.

CAVEAT

Suggesting this type of analysis (i.e., use of a detailed, mechanistic model at the process level to aid in understanding system control) is dangerous. Generating the type of model output displayed above is certainly not difficult. Because it is a natural "by-product" of any time-varying model, it may be tempting to generate this output without proper validation of the model. Also, what has become accepted as one method of validation (i.e., accurate simulation of state variables) may not be acceptable in this new context. I provide one example (see Scavia 1979c) to illustrate this point and to emphasize the need to validate models based both on state variables and processes.

After initial calibration of the model described above to state variables measured during IFYGL, I generated the phosphorus cycling diagram shown in Figure 9a and began to examine the cycling rates. I found that, although the model adequately represented the state variables in Lake Ontario, its estimates of several process rates were very much lower than experimentally and theoretically derived rates. By recalibrating the model while still keeping coefficient values within the broad "acceptable ranges," I was able to obtain more realistic

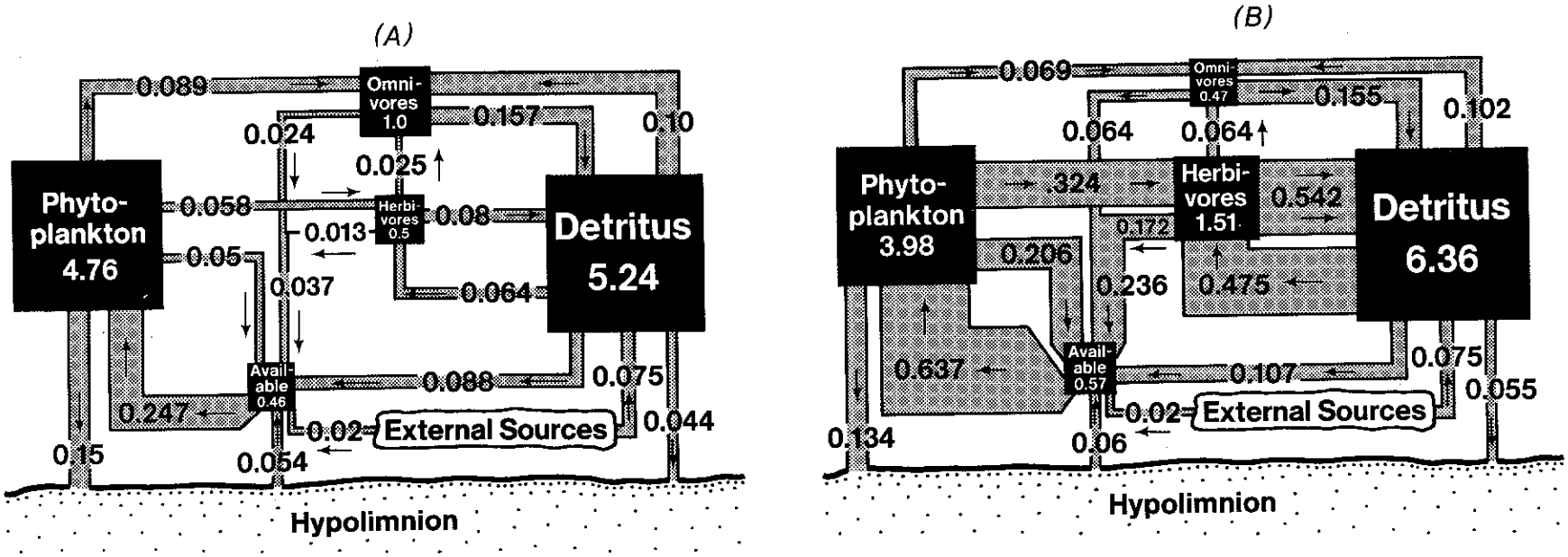

FIGURE 9. As in Figure 8. (a) after state variable calibration only; (b) after state variable and process calibration (from Scavia 1979b). Redrawn from Scavia 1979b.

process rates and at the same time maintain a good calibration to state variables (Figure 9b).

Conclusions concerning the relative importance of particular processes in the cycling of phosphorus, based on model output that was not validated on the process level (e.g., Figure 9a), would be quite different from conclusions based on the more realistic simulation (e.g., Figure 9b).

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COMBINED LIGHT AND TEMPERATURE EFFECTS ON PHYTOPLANKTON PERFORMANCE-- EFFECTS OF A VARIETY OF TIME SCALES

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INTRODUCTION

In a series of papers (Harris et al. 1979a, b; Harris and Piccinin, 1979; Haffner et al. 1979) we have recently described the limnology of Hamilton Harbour and the factors which govern the productivity and community dynamics of the phytoplankton. We have shown that, during the period of summer stratification, rapid changes in mixing depth suppress algal photosynthesis so that the observed summer algal biomass is less than that predicted by the usual relationships between phosphorus inputs and summer chlorophyll a (Vollenweider 1976; Dillon 1974; Schindler 1978).

The photosynthetic capacity (P_{max}) of the algae has, in previous years, responded to changes in the ratio of the euphotic zone depth to the mixing depth (Z_{eu}/Z_m) and has been the major factor controlling integral photosynthesis (Harris et al. 1979b). We have concluded that phosphorus utilization was reduced due to the optically deep, physically perturbed water column (Harris et al. 1979b; Haffner et al. 1979) and have stated that phosphorus was not a limiting nutrient. We have previously presented no direct evidence for this conclusion, however.

Previous observations have been carried out only during ice-free periods (1975-1977), so the observations were carried out during periods when the temperature changed relatively little but the physical structure of the Harbour stratification was highly variable. In this paper we present conclusions drawn from the entire 1978-1979 period which includes the fall-winter-spring period of more-or-less continuous deep mixing but varying temperatures. The data could not have been fully interpreted without considering both physical regimes.

There have been a number of recent papers in which versions of the phosphorus loading concent and their applications to lakes have been discussed (e.g., Schindler 1978; Shaffner and Oglesby 1978; Oglesby and Schaffner 1978). Essentially all such papers assume that phosphorus is

the major limiting nutrient in fresh waters and that the availability of such a nutrient controls such parameters as the summer concentration of chlorophyll a in surface waters. With few exceptions such data as are used for these relationships come from small lakes. Schindler's (1978) analysis of data from the Great Lakes indicates quite a different relationship between phosphorus inputs and chlorophyll to that observed in small lakes. The Great Lakes (and particularly the coastal zones of those lakes) are physically quite different from small lakes (Boyce 1974) so there is some suggestion in the literature that physics may play an important role in the ecology of phytoplankton in large lakes. These arguments concerning the relative roles of nutrients and physics in large lakes are not entirely academic because large-scale management programs in many lakes are predicated upon the models developed.

Many of the spring phosphorus/summer chlorophyll plots (such as that of Sakamoto (1966)) show that 1 μg of phosphorus is expressed as 2 μg of chlorophyll in the summer and it may be supposed that this is an intrinsic feature of algal growth. Such a relationship would in fact tend to give the phosphorus/chlorophyll correlations which are often observed in lakes--as long as, during the summer, the algae incorporate a significant fraction of the phosphorus available earlier in the year.

In a recent review (Harris 1978) I have considered the relationship of P_{max} to growth and nutrient uptake by phytoplankton. I concluded that as P_{max} was the maximum rate of carbon fixation (per unit biomass) that was sustained for 4 hours in a bottle in situ, then it might bear some relationship to growth rate of the population. There is certainly good physiological and ecological evidence to show that, over time periods of the order of a generation time, carbon fixation and nutrient uptake are controlled to produce new organisms with the correct ratios of cellular constituents (reviewed in Harris 1978). There are, however, relatively few simultaneous studies of carbon and nutrient uptake which would give some idea as to the variability of, say, C:P uptake ratios

which we might expect to find in the field in short-term experiments.

The data reported in this paper examine carbon fixation, nutrient uptake, chlorophyll turnover times, and the factors which influence these measures of algal performance and growth. We use data from all seasons to interpret the contributions of light, temperature, and nutrients to the growth of phytoplankton in the Harbour.

The methods of measurement of nutrients and physical factors have been published by Harris et al. (1979a) and the primary productivity methods in Harris et al. (1979b). Harris et al. (1979a) also contains details of the mass balance equation used to determine the in situ rates of nutrient uptake. In essence, the soluble reactive phosphorus (SRP) concentration in the water is a function of inputs, throughflow, exchange with Lake Ontario, and algal uptake. Harris et al. (1979a) used a total dissolved solids budget to estimate Lake Ontario exchange.

In 1978-79 the thermal structure of Hamilton Harbour was relatively stable compared to previous years, but the depth of the 18°C isotherm still oscillated from 5 to 11 meters during the stratified period. Such oscillations in mixing depth affected the photosynthetic performance of the algae from week to week and caused oscillations in photosynthetic capacity (P_{max}) from week to week. Thus temperature fixed an upper limit to P_{max} but physical perturbations destroyed the temperature effect during the stratified period. After fall turnover at 15°C, the P_{max}-temperature relationship became clear in a physically stable regime. In this respect, P_{max} and growth show parallel behavior. Eppley (1972) showed that temperature sets an upper limit for growth. This may be connected to the fact that photosynthesis rates are fixed by temperature (Harris and Piccinin 1977) at saturating irradiance and no seasonal adaptation occurs. So there was a seasonal temperature effect on P_{max}--obscured in summer by week-to-week changes in the light regime. Thermal regimes and light regimes interacted at a number of temporal scales from weeks to months.

Integral photosynthesis (ΣP $mgC \cdot m^{-2} \cdot h^{-1}$) fluctuated in response to changes in P_{max} (as in previous years, Harris et al. 1979b). But what relationship did ΣP have to growth? Growth rates are very difficult to determine in this physically variable regime due to extensive vertical redistribution of surface cells (Haffner et al. 1979) but from the mass balance, maximum chlorophyll turnover times reached 0.14 day^{-1} on a few occasions. This would indicate possible doubling times of approximately one week and would support previously published figures for the response times of the Harbour populations. Harris (1978) has postulated that the generation time of cells limits the response times for adaptation to new conditions and is also the fundamental integration period for fluctuating environmental conditions.

Growth rates were also estimated from nutrient uptake data. Depletion of surface SRP and surface total soluble nitrogen (TSN) was used in the mass balance equation to estimate P and N uptake rates.

Surprisingly, the use of SRP and TSN data gave reasonable estimates of P and N uptake, and estimates of algal P and N contents which were similar to previously published data. Presumably, in the presence of high SRP and TSN inputs from sewage treatment plants, interactions with particulate P and N in fractions other than the algal fraction were insignificant. Growth rates (as estimated by phosphorus and nitrogen uptake) fluctuated less than the P_{max} values. This indicated that although carbon metabolism fluctuated rapidly in response to changes in the light regime from day to day and week to week, growth of the cells tended to average out the short-term fluctuations. The relatively long doubling times of the populations (0.14 day^{-1}) would also tend to give good temporal averages if growth-related parameters were estimated on a weekly basis.

The nutrient uptake data are summarized below. These appear to be the first instances of in situ estimates of N and P uptake for free-floating, natural populations. The C:N:Chl:P ratios are very similar

to previously published data (cf. Giddings 1977; Jones et al. 1978; Perry 1976 and many others) indicating that most algae grow with the usual stoichiometric ratios. The week-by-week data, however, revealed more detail than just the mean ratios. The relationship between phosphorus uptake (P_u, $mgP \cdot m^{-2} \cdot h^{-1}$) and algal biomass per unit volume ($Chl \cdot mg \cdot m^{-3}$) was non-linear. P_u showed a saturation effect above 30 $mg \cdot m^{-3}$ Chl_a. This effect was largely removed if P_u was plotted against $\Sigma Chl_a (mg \cdot m^{-2})$, the biomass in the photic zone showing that self-shading was occurring and ΣChl was the major factor influencing the P_u rate. Carbon fixation (C_u, $mgC \cdot m^{-2} \cdot h^{-1}$) was line ly related to ΣChl_a with a mean slope of 1.05 mg $C \cdot mg\ Chl^{-1} \cdot h^{-1}$. P_u and C_u were not linearly related however as P_u showed saturation, so although the mean $P_u:C_u$ was 1:114 (gram:gram), the ratio actually varied from 1:75 over 1:2000 at high C_u. Clearly, in short-term experiments (4 hr) at high irradiance, C_u increased during the middle of the day. Overall, the best relationship was between P_u and ΣChl and, on a week-to-week basis, between increases in Chl and decreases in SRP (and vice versa). On a week-to-week basis 1 µg SRP became incorporated into 2 µg Chl. P_u and TSN uptake ($N_u \cdot mg\ N \cdot m^{-2} \cdot h^{-1}$) were not linearly related but N_u and C_u were linearly related with a mean $N_u:C_u$ ratio of 1:4.38.

This may be interpreted as follows: P_u appeared to be controlled, not by C_u, but by the growth of new biomass as Chl. Perhaps the P_u rate was more closely related to the requirements of P for energy transfer and metabolism per unit Chl than to the vagaries of C_u. The relationship of 1 µg P required for 2 µg Chl would explain all the usual relationships between P and Chl noted above. Because of the high inputs, however, and because of depressed growth rates due to physical perturbations, there was no relationship between P inputs and Chl in the Harbour. Uptake data show that P_u was never limited by the SRP concentration as we had surmised.

N_u was directly related to C_u which may be explained by a fairly close link between N and C metabolism. The mean $N_u:C_u$ ratio was low,

however, when compared to some previously published data (Perry 1976; Slawyk et al. 1977). Summer N_u:C_u ratios ranged from 1:5 to 1:15--more commonly observed ratios. The winter data, however, had N_u:C_u ratios of approximately 1:2.5--rather low ratios. When the N_u:C_u ratios were plotted against the I_K of the in situ populations, a significant regression resulted indicating that when the I_K of the population was low (75-100 $\mu E\ m^{-2}s^{-1}$, PAR) C_u was also relatively low. At high I_K (500-750 $\mu E\ m^{-2}s^{-1}$) the N_u:C_u ratio was within the usual range. What this might well indicate is that at low I_K (deep mixed populations), C_u, as measured by in situ techniques, was a serious underestimate due to severe photoinhibition in surface bottles. We have already suggested that such errors might occur on physiological grounds (Harris and Piccinin 1977; Harris 1978).

Thus the data indicate that the growth of phytoplankton in Hamilton Harbour was controlled by fluctuations in the light and temperature regimes, but at a variety of scales from weeks to months. Light regimes and thermal structures interact to produce some complex interactions between environment, physiology, and methodology. It would appear that fluctuations in C_u, brought on by fluctuations in the light and temperature regimes, are the mechanism by which P_u, N_u, and growth are limited. Primary productivity in the Harbour is lower than might be expected in an area of such high loadings (Harris et al. 1979b; Haffner et al. 1979), and carbon uptake seems to limit growth in this instance.

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NITROGEN FIXATION AND PHYTOPLANKTON INTERACTIONS IN SOUTHWESTERN RESERVOIRS

by

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INTRODUCTION

Nitrogen fixation is of unquestioned importance in the nutrient dynamics of many aquatic ecosystems (Keeney 1972) but relatively little is known about this phenomenon in reservoirs. This paper reports the occurrence of nitrogen fixation in the water column, the sediments, and the aufwuchs community of two southwestern reservoirs.

METHODS

A modification of the acetylene reduction technique (Dillworth 1966, Schollhorn and Burris 1966) was used to assay nitrogen fixation potential in Lake Arlington and Lake Ray Hubbard in North Texas. Both lakes are on the Trinity River drainage and are used for water supplies, flood control, and recreation and both receive power plant discharges. Water column fixation was measured by concentrating plankton through a 76-micron mesh net and washing the concentrate into a 40-ml bottle. A septum was placed over the bottle and the air phase was replaced with argon plus 10% acetylene. Incubation was from 30 minutes to one hour, at which time the sample was killed with TCA.

Sediment acetylene reduction samples were obtained by using SCUBA gear to go to the bottom of the reservoir, pushing a bottomless bottle into the sediments and stoppering both ends prior to removal from the sediments. Samples were then innoculated and incubated, the same as water column concentrates.

Aufwuchs and periphyton acetylene reduction samples were taken by scraping an area (e.g., 5 cm^2) and placing the scrapings along with filtered lake water in the 40-ml incubation bottles. Inoculation and incubation was *in situ*, the same as discussed for water column samples.

Nitrates and phosphates were measured according to Standard Methods (APHA 1971) and algal cell and volume counts were accomplished using a Palmer cell and Whipple eyepiece.

RESULTS AND DISCUSSION

Lake Arlington

Stations were monitored at the surface of locations near the center of the lake (Station A), and in the vicinity of the cooling water discharge (Station B). Another station was set up at the sediment surface below Station A which was called Station C. Results of acetylene reduction assays for these stations are shown in Table 1.

Varying amounts of nitrogen fixation occurred in the water column from February through October; there was essentially no difference between results from Stations A and B, indicating the passage of water through the power plant cooling system did not enhance or inhibit the ability to reduce nitrogen.

Sediment fixation occurred throughout the study period although the amount varied considerably with time; no real temporal trends were evident. Most of the sediment activity took place in the top two centimeters, vertical analyses revealed. Nitrates varied inversely with water column acetylene reduction rates (Figure 1), indicating that as nitrogen became scarce, the blue-greens responded with a physiological change and increased their fixation rate correspondingly.

Total phosphorus levels varied in proportion with blue-green algal volumes during the study (Figure 2) except for early in the sampling period when low temperature probably inhibited greater concentrations of blue-green algae.

Table 1. Acetylene reduction data for regular sampling dates on Lake Arlington.*

Date	Station A Surface	Station B Surface	Station C Sediments
2/24	0	0	22.5
3/23	2.0	0	8.1
4/12	2.4	6.6	15.0
5/17	2.7	3.0	15.0
5/29	10.5	8.0	18.0
6/10	5.5	5.5	92.0
6/26	0.8	4.9	34.4
7/18	6.0	1.2	69.0
8/08	5.5	6.8	15.0
9/12	0.4	0.4	48.0
10/6	0.3	2.2	3.4
Mean	3.3	3.5	30.9

* For samples at Station A and Station B, units are in n mole ethylene reduced per 100 liters per hour. For sediment samples, units are for 100 cm^2 of top sediment. All figures are averages of two samples.

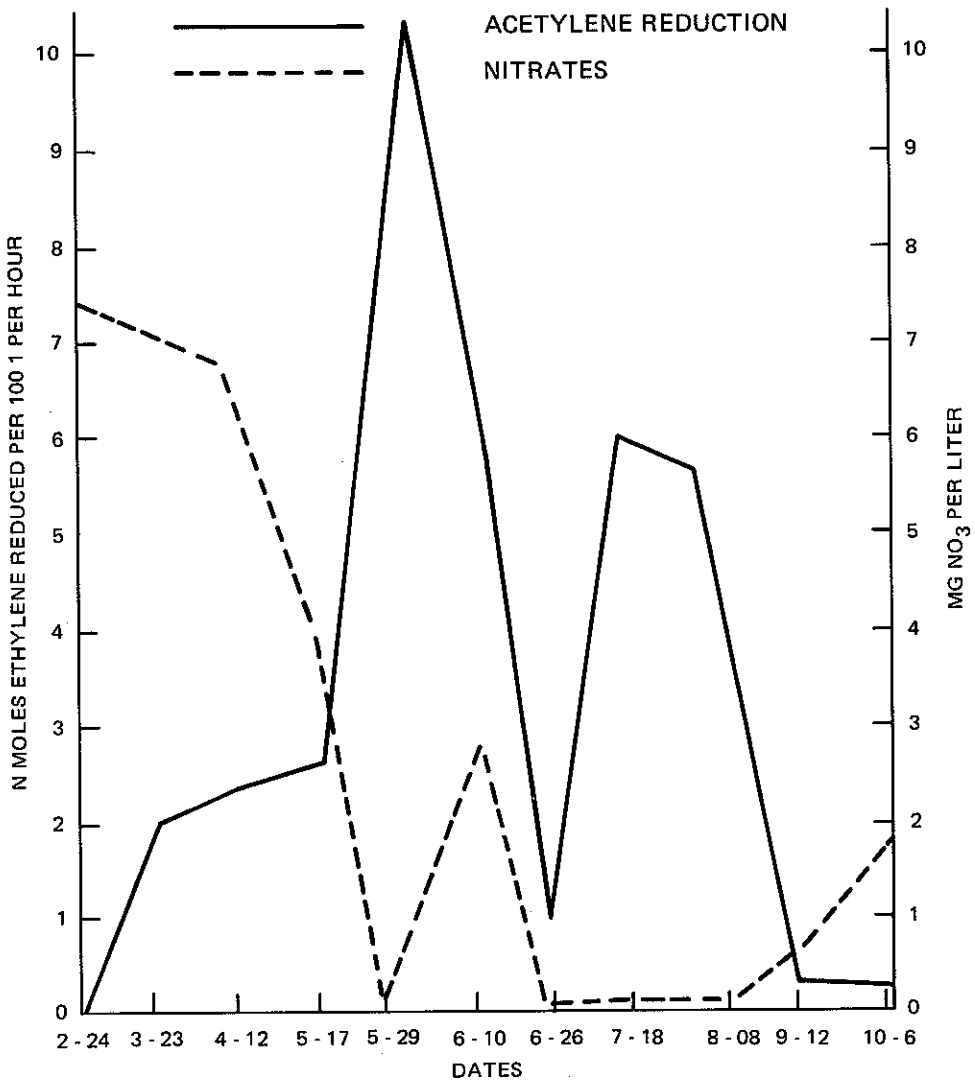

Figure 1. Comparison between nitrogen fixation and nitrate concentration.

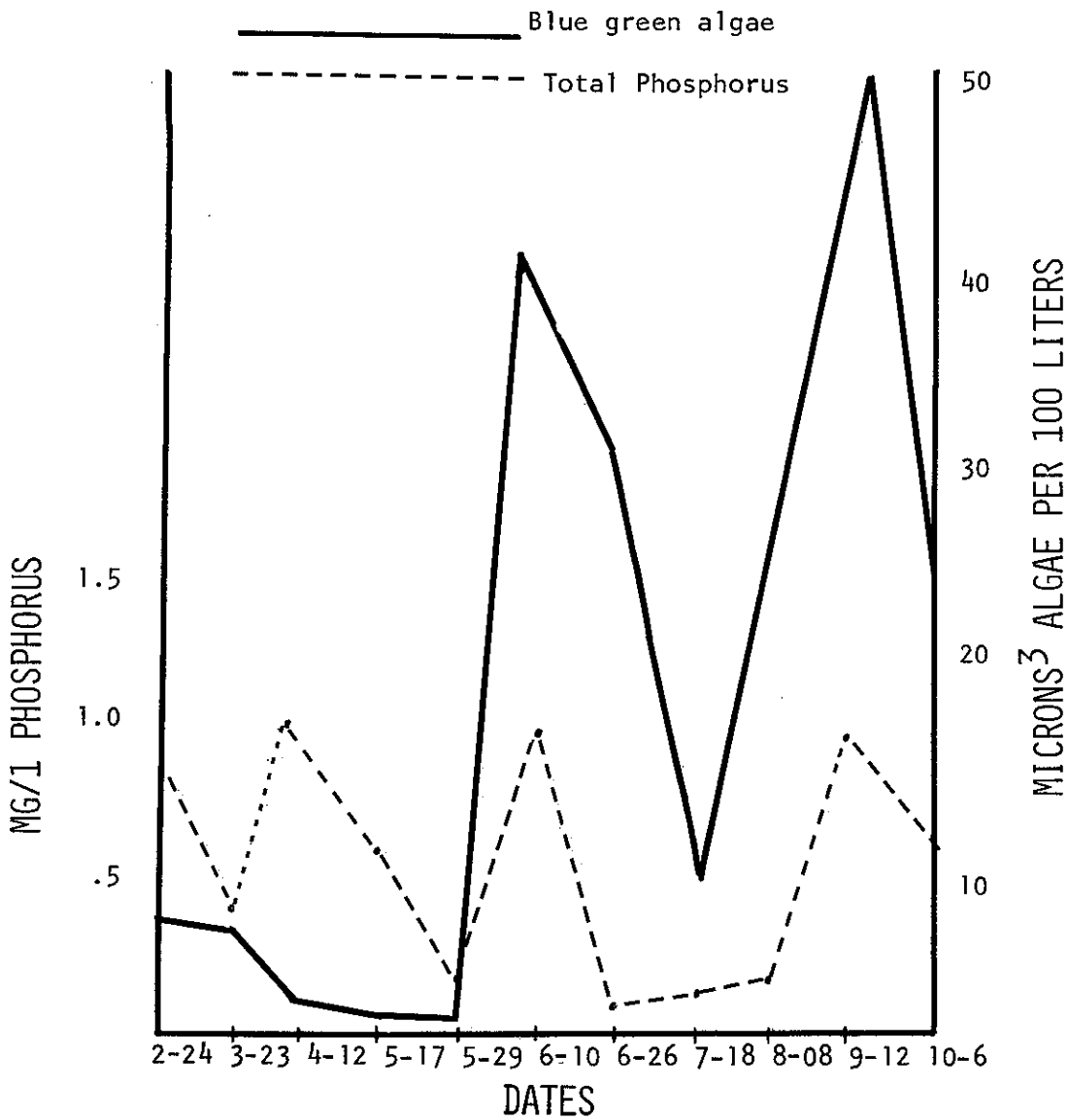

FIGURE 2. Comparison of blue-green algal volumes and total phosphorus at Station A on Lake Arlington for each sampling date.

Blue-green algal volumes corresponded quite closely with acetylene reduction rates at Station A (see Figure 3).

In addition to planktonic algae and sedimentary bacteria, epiphytic, epilithic, and aufwuchs (mats of algae growing at the sediment interface) may contribute reduced nitrogen to reservoirs. Little is known of the nitrogen fixation potential from these sources and the amounts they contribute are difficult to quantify. This study has found that potentially high nitrogen fixation rates were present among epiphytic populations at certain times of the year (Table 2). Goering and Parker (1971) and Carpenter (1972) have reported on epiphytic nitrogen fixation, Goering having found rates as high as 12.6 mg N m^{-2} hr^{-1} by *Nostoc* and *Anabaena* on gulf coast seagrasses. The nitrogen contributed by epiphytic algae in Lake Arlington cannot be estimated from one series of tests, but rates were similar to those found by Goering.

Approximately one third of the shoreline of Lake Arlington is rocky or bounded by concrete. During late summer, most of this stony area was covered with algae, primarily mixed blue-greens with an abundance of *Anabaena* which formed a mat more than 1 mm thick. The outermost layer was yellowed and dead; the inner layer contained live algae of many species. In an effort to quantify the nitrogen fixation potential of these mats, a cork borer was used to remove algae from flat areas. These samples were incubated in situ and results are shown in Table 2. The rate of 1.1 nm ethylene per two cm/hr is not constant, but this figure was used to make estimates of nitrogen contribution. These estimates indicated the rate of nitrogen reduced by the mats of algae to be nearly 1 g N/m^2 of rock surface/year.

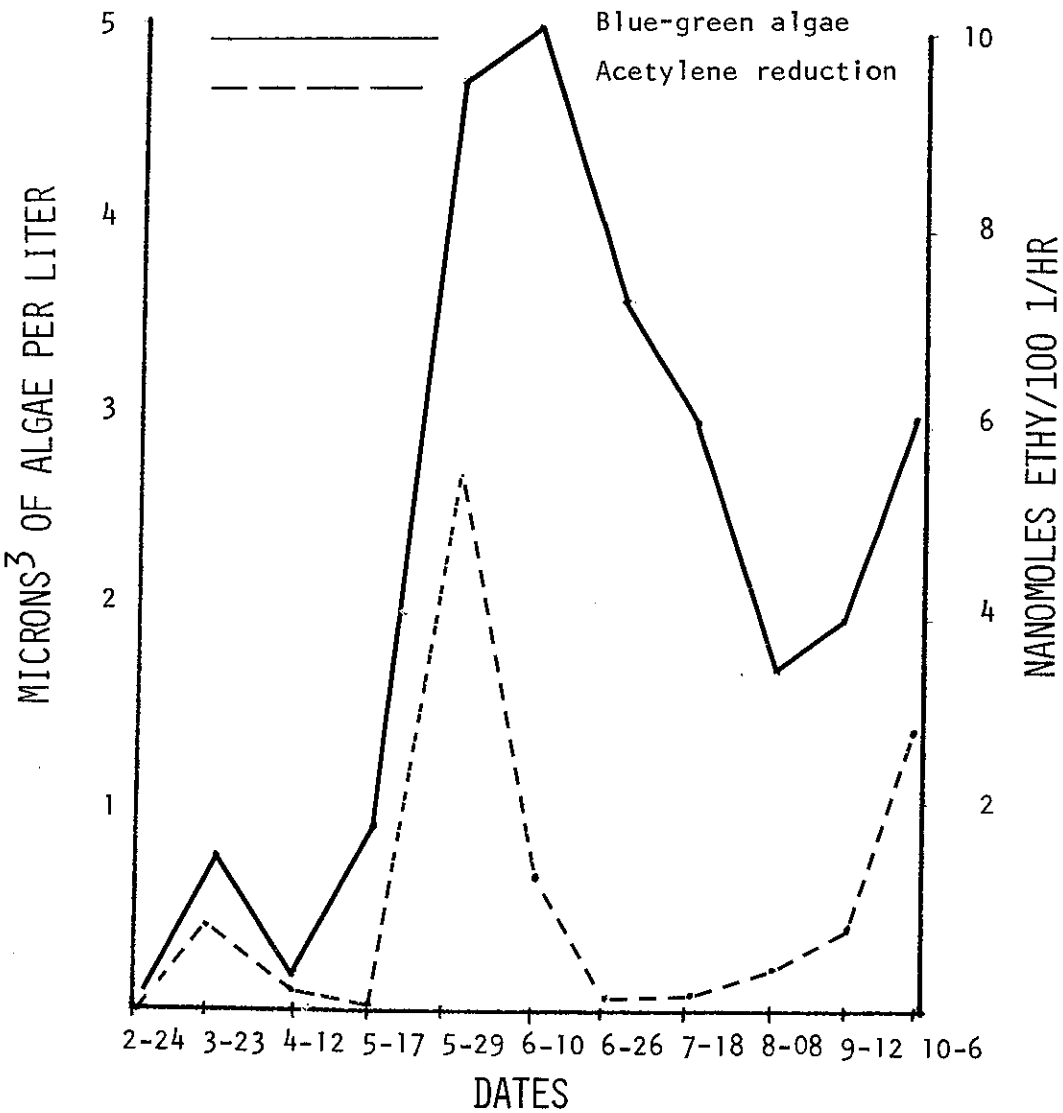

FIGURE 3. Comparison of blue-green algae volumes and acetylene reduction at the bottom of Station A.

Table 2. Other sources of nitrogen fixation in southwestern reservoirs.

Source	Quantity Unit	Dominant Algae Present	Ethylene Reduced
Epiphytic algae on willow stems, emergent aquatics, and miscellaneous objects	20 ml Wet Volume	*Nostoc* *Gloeotrichia*	1.5 n mole/hr
Epilithic algae on rocks and cement	20 ml Wet Volume	*Nostoc* *Anabaena* *Oscillatoria* *Scytonema*	3.2 n mole/hr
	2 cm	*Nostoc* *Anabaena* *Oscillatoria* *Scytonema*	1.1 n mole/hr
Aufwuchs on moist soil and in shallow water areas	2 cm Surface area	*Oscillatoria* *Lyngbya* *Anabaena*	2.2 n mole/hr
Floating mats	20 ml Wet Volume	*Oscillatoria* *Anabaena* *Lyngbya*	2.5 n mole/hr

Another seasonally important source of nitrogen fixation in area reservoirs is the aufwuchs community. Rapid shoreline fluctuation plus turbid waters normally are inhibitive to the formation of these thick mats of algae. Late in August, the reservoirs' shorelines recede at a steady pace from lack of rainfall and from evaporation. The winds were almost stilled at this time of year so the shoreline was not continually awash. The reservoir, being more quiescent, had lost some of its suspended particles and the trophogenic zone penetrated down to more than three meters. Under these conditions, tremendous areas of aufwuchs formed in all areas of the reservoir having a shallow soft bottom. Bottomless vials (mentioned previously) designed for sediment sampling were used to measure the acetylene reduction of this aufwuchs area *in situ*. The results depicted in Table 2 are averages of six replicates. The acetylene reduction rates were high even for pure cultures of blue-green algae. As the shoreline receded, the mats continued to reduce acetylene even when exposed to the air, until they became almost dry, forming a thin crust to be washed into the reservoir with the first rains. This process may be quite important in cycling sedimentary nutrients and introducing reduced nitrogen into the aquatic ecosystem. Some mats in the shallow water were observed to capture gas bubbles and float to the top, taking the top layer of sediment with them. These floating mats were quite abundant in the lake during late summer. Acetylene reduction rates by these mats also proved to be very high (Table 2). Although averages of three replicates were used for quantification, it is difficult to estimate the total nitrogen contribution by these mats. Waves gradually broke up the mats and helped to physically redistribute the nutrients and algae throughout the reservoir. Although floating mats occurred for only about four weeks during the summer, their fixation rates may have been important to the overall nutrient cycling and nitrogen budget of the reservoir.

These nebulous areas of nutrient cycling must be better understood before models of reservoirs can be constructed which closely approximate true nutrient dynamics.

From all the nitrogen fixation sources previously discussed, plus data on rainfall, fallout, and point-source discharges, a simple nitrogen contribution chart was constructed (Table 3). It is apparent from this table that no more than 10-15% of the total nitrogen budget comes from nitrogen fixation activities in the reservoir (although a great deal of the watershed runoff may be derived from nitrogen fixation) but this chart may not be indicative of the importance of fixed nitrogen to these reservoir ecosystems. Table 4 shows a potential importance index of the causes of problems in southwestern reservoirs. It is proposed that nitrogen fixation may be the single most important cause of many of the problems inherent to southwestern reservoirs.

Lake Ray Hubbard

Acetylene reduction analyses during blue-green algae blooms in Lake Ray Hubbard showed that nitrogen fixation was occurring in high quantities during the period of the bloom (April 1974). This may be the first instance of acetylene reduction taking place during an algal bloom in a southwestern reservoir. This bloom caused a subsequent taste and odor problem, killed fishes in two separate bays, and laboratory tests confirmed that it was composed of a toxic strain of *Aphanizomenon flosaquae*. Data from these assays will be the subject of a paper currently submitted for publication.

Table 3. Arlington Lake nitrogen budget.

Source	Contribution kg/year	% of Total
Nitrogen Fixation		
Water Column	620	1
Sediment	2,450	3
Periphyton	3,991	5
Aufwuchs	1,122	2
Total Nitrogen Fixation	8,183	11
Rainfall on Lake	8,720	11
Dry Fallout	7,000	9
Watershed Runoff	32,060	42
Point Source Discharges	21,160	27
Total Nitrogen	77,123	

Table 4. Problems in reservoirs (Estimates made by author).

Phytoplankton Blooms, Rapid Eutrophication, Fish Kills, Taste and Odor Problems, Restricted Recreation

Cause of Problems	% of Total
Nitrogen Fixation	45
Rainfall	3
Dry Fallout	2
Watershed Runoff	15
Point Source Discharges	35

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DCMU-ENHANCED CHLOROPHYLL FLUORESCENCE AS AN INDICATOR OF THE PHYSIOLOGICAL STATUS OF RESERVOIR PHYTOPLANKTON: AN INITIAL EVALUATION

by

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INTRODUCTION

Measurement of *in vivo* chlorophyll fluorescence has been widely applied to the investigation of phytoplankton distribution and abundance as an indicator of algal standing crop (e.g., Lorenzen 1966, Platt 1972, Powell *et al*. 1975, Fee 1976). However, algal fluorescence is variable and dependent on both the amount of chlorophyll present and algal physiological state as influenced by environmental conditions (Kiefer 1973, Heaney 1978). Recent studies suggest that DCMU[1]-enhancement of *in vivo* chlorophyll fluorescence may provide a method for (a) reducing variability in phytoplankton fluorescence measurements (Slovacek and Hannan 1977) and (b) assaying algal physiological state (Samuelsson and Öquist 1977, Samuelsson *et al*. 1978). A direct, convenient method for assessing the physiological status of natural phytoplankton communities would prove invaluable for distinguishing the major factors influencing phytoplankton biomass fluctuations and spatial distribution in aquatic systems. Thus, our purpose was to evaluate the applicability of DCMU-enhanced fluorescence measurements for such assessment. More specifically, our objectives were:

1) to test *in vivo* chlorophyll fluorescence response to DCMU-poisoning as an indicator of phytoplankton physiological state,

2) to determine the range of fluorescence response values to be expected in a variety of environmental conditions, and

3) to evaluate the utility of the fluorescence response technique for investigations of naturally occurring phytoplankton assemblages.

We thank Dr. L.G. Hill, Director of the University of Oklahoma Biological Station, for his support and encouragement. We also thank

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[1] 3-(3,4-dichlorophenyl)-1,1-dimethylurea, DCMU, inhibits non-cyclic photosynthetic electron transport and results in maximal fluorescence emission. Measurement of *in vivo* chlorophyll fluorescence before and after sample "poisoning" with DCMU permits a relative estimate of photosynthetic electron transport activity.

Corps of Engineers personnel from Lake Texoma and Broken Bow Lake projects for their cooperation; Dr. M.K. Patterson, Director of Foundation Research Laboratory for use of liquid scintillation counting facilities; and S.R. McComas and B.B. Looney for field and laboratory assistance.

METHODS

Laboratory Experiments

In vivo chlorophyll fluorescence parameters and photosynthesis rates of reservoir phytoplankton were compared in laboratory light-deprivation experiments. Near-surface Lake Texoma water was strained through 80-μm netting to remove large zooplankton, placed in a 4-l, foil-covered Pyrex flask, and incubated with gentle stirring at 25°C. Subsamples were removed periodically for photosynthetis and *in vivo* fluorescence measurements.

Photosynthesis rates were determined by radiocarbon uptake in 125-mℓ Pyrex light and dark bottles. Samples were inoculated with 1.0 μCi $NaH^{14}CO_3$ solution, incubated for 4 hr at 25°C and 64 μE m^{-2} sec^{-1}, and then vacuum-filtered on Whatman GFC filters. Sample activity was determined by liquid scintillation spectrometry.

In vivo chlorophyll fluorescence was measured with an AMINCO fluorocolorimeter equipped with a blue excitation lamp (GE F4T5-B, 4W), Corning glass primary (No. 5543) and secondary (No. 2030) filters, R136 photomultiplier tube and integrator-timer. Fluorescence of unpoisoned and DCMU-poisoned phytoplankton was determined over 5-sec integration periods initiated simultaneously with sample excitation for each of triplicate subsamples. The fluorescence of an unpoisoned 5-mℓ sample was determined, 0.2 mℓ of 10^{-4} M DCMU solution added with an automatic micropipet (final DCMU concentration = 10^{-5} M), the sample mixed by inverting the cuvette several times, and fluorescence of

the poisoned sample measured. Preliminary experiments showed that 1 hr dark storage, 5 min following DCMU addition, and 20 sec between excitation periods were sufficient intervals for avoiding photoinhibition effects, allowing DCMU penetration of cells and permitting cellular fluorescence recovery between readings, respectively. All measurements were conducted in dim red light to avoid unintentional activation of chlorophyll fluorescence.

Field Measurements

Water temperature, dissolved oxygen, pH, and conductance were measured *in situ* with a Hydrolab monitoring unit. Photosynthetically active radiation (400-700 nm) and relative light penetration were determined with a quantum sensor (Li-Cor 185A). Dissolved PO_4-P and NH_4-N analyses were by phosphomolybdate and phenolhypochlorite methods, respectively, as described by Strickland and Parsons (1972). NO_3-N was determined by modified hydrazine reduction method (Kamphake *et al.* 1967). Microbial biomass was estimated from adenosine triphosphate (ATP) levels as determined by the luciferin-luciferase assay (Holm-Hansen and Booth 1966). Phytoplankton productivity was measured *in situ* by the ^{14}C method of Steeman Nielsen (1952) as modified by Goldman (1963). Dissolved inorganic carbon availability was estimated from temperature, pH, and alkalinity data (Saunders *et al.* 1962). *In vivo* chlorophyll fluorescence and fluorescence response to DCMU poisoning was determined for field samples as described above for laboratory experiments.

In situ sample displacement experiments, in which photosynthetic ^{14}C uptake was measured in samples obtained from several water column depths (= light intensities) and incubated at a single depth, were conducted to provide an independent measure of phytoplankton photosynthetic potential for comparison to *in vivo* chlorophyll fluorescence data.

Expression of DCMU-Enhanced Fluorescence

Previous investigators have used a variety of methods for indicating *in vivo* chlorophyll fluorescence response to DCMU poisoning, with most employing some ratio of the unpoisoned initial fluorescence to either DCMU-enhanced fluorescence or extracted chlorophyll. Sample fluorescence yield depends on both algal physiological state and the amount of chlorophyll present. Slovacek and Hannan (1977) concluded that DCMU-enhanced fluorescence corresponded closely to total (extracted) chlorophyll for a variety of algal species and growth conditions. We were interested in evaluating fluorescence response as an indicator of physiological state; therefore, we chose to express our results as FRI values (previously used by Kiefer and Hodson (1974) and Cullen and Renger (unpublished)), where

$$\frac{F_d - F_i}{F_d} = FRI \qquad (1)$$

and F_i = initial (unpoisoned) sample fluorescence

F_d = DCMU-poisoned sample fluorescence

FRI = the fluorescence response index for the phytoplankton community samples

For our purposes, FRI possessed two advantages:

1) FRI is biomass independent (i.e., normalized relative to $F_d \cong$ algal chlorophyll) and, thus, should reflect the average physiological state of the phytoplankton assemblage, and

2) FRI has a discrete theoretical range of 0 ($F_d - F_i = 0$, no photosynthetic electron transport activity) to 1 ($F_i = 0$, all absorbed energy involved in photosynthetic electron transport).

RESULTS AND DISCUSSION

Laboratory Comparisons

In vivo chlorophyll fluorescence response to DCMU poisoning was directly related to phytoplankton photosynthetic potential in laboratory light-deprivation experiments. Photosynthetic carbon fixation and FRI values declined in a nonlinear, but parallel, manner in experiments I and II (Figure 1). Both parameters decreased rapidly during the initial 24 hr of darkness and then began to stabilize. Sample DCMU-induced fluorescence increases and carbon uptake rates were directly related and highly correlated ($r = 0.99$, $p < 0.01$) in both experiments (Figure 2). Our results for reservoir phytoplankton assemblages correspond to those of previous investigators (Blasco and Dexter 1972, Kiefer and Hodson 1974, Prézelin and Sweeney 1977, Slovacek and Hannan 1977, Samuelsson and Öquist 1977, Samuelsson *et al*. 1978) who have related DCMU-enhanced fluorescence to carbon uptake or oxygen evolution in algal cultures. Frey (1979) recently reported similar results from nutrient-enrichment experiments with marine phytoplankton.

Field Measurements

In vivo chlorophyll fluorescence, phytoplankton productivity, microbial biomass, and physical-chemical characteristics were compared in two limnologically dissimilar Oklahoma reservoirs. Lake Texoma, a large (360 km^2) but shallow ($\overline{Z} = 9$ m), 35-year-old impoundment of the Red River, is representative of many windswept reservoirs of the U.S. Southern Great Plains. It is nutrient rich, productive, and well mixed; thermal stratification is usually transitory. The euphotic layer is shallow (Secchi depth $\cong$ 1 m, 1% $I_0 \cong 3.5$ m) and exceeded in depth by the mixed layer. Figure 3 reflects typical late-summer productivity and mixing conditions. Although temperature and dissolved oxygen data do not clearly indicate the extent of mixing, vertical profiles of nutrients, *in vivo* fluorescence, and FRI show the mixed layer depth to be 10-12 m.

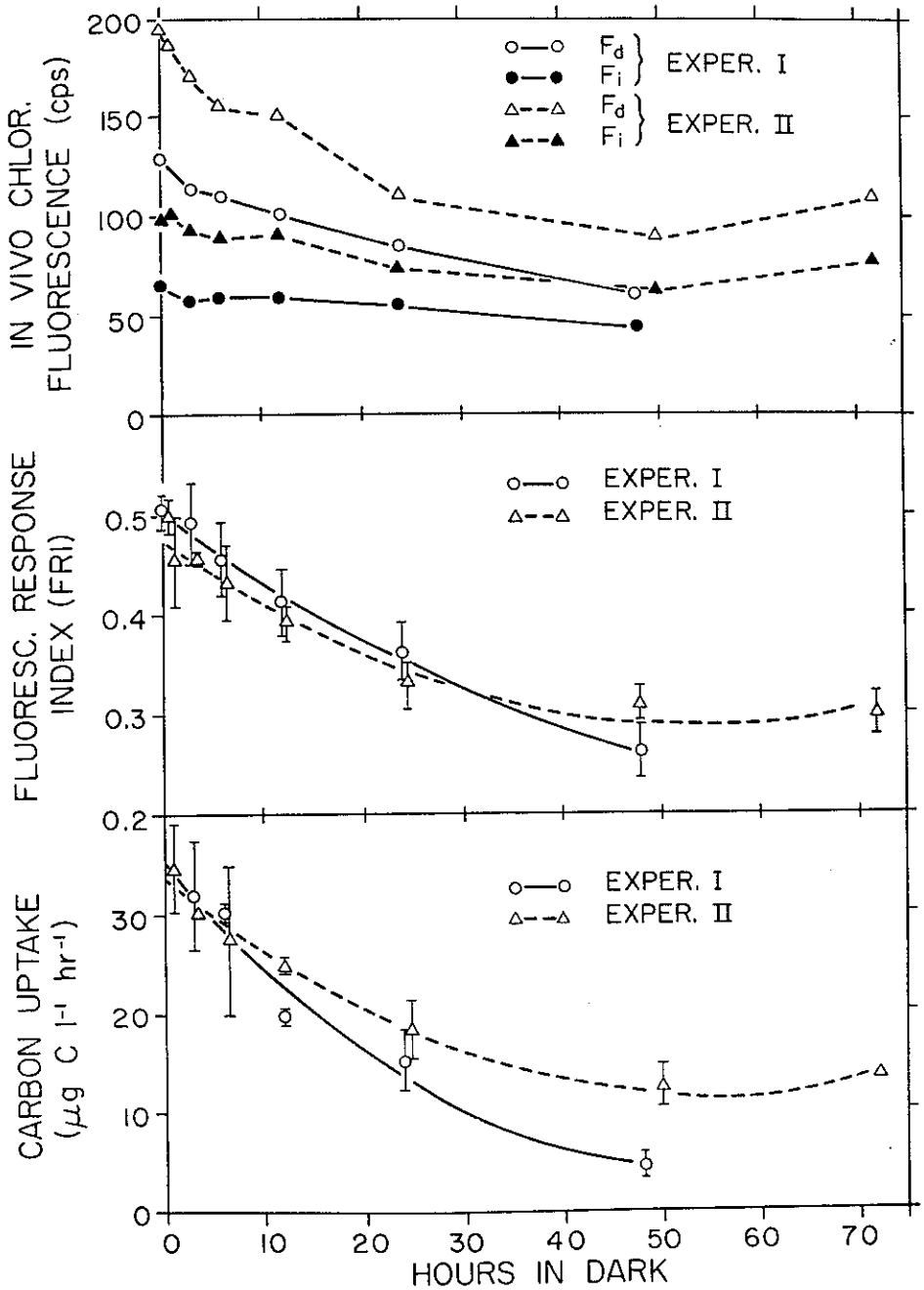

FIGURE 1. Decline of <u>in vivo</u> chlorophyll fluorescence (F_i = unpoisoned sample fluorescence, F_d = DCMU-poisoned sample fluorescence), the fluorescence response index (FRI), and photosynthetic carbon uptake in Lake Texoma phytoplankton assemblages during light-deprivation experiments.

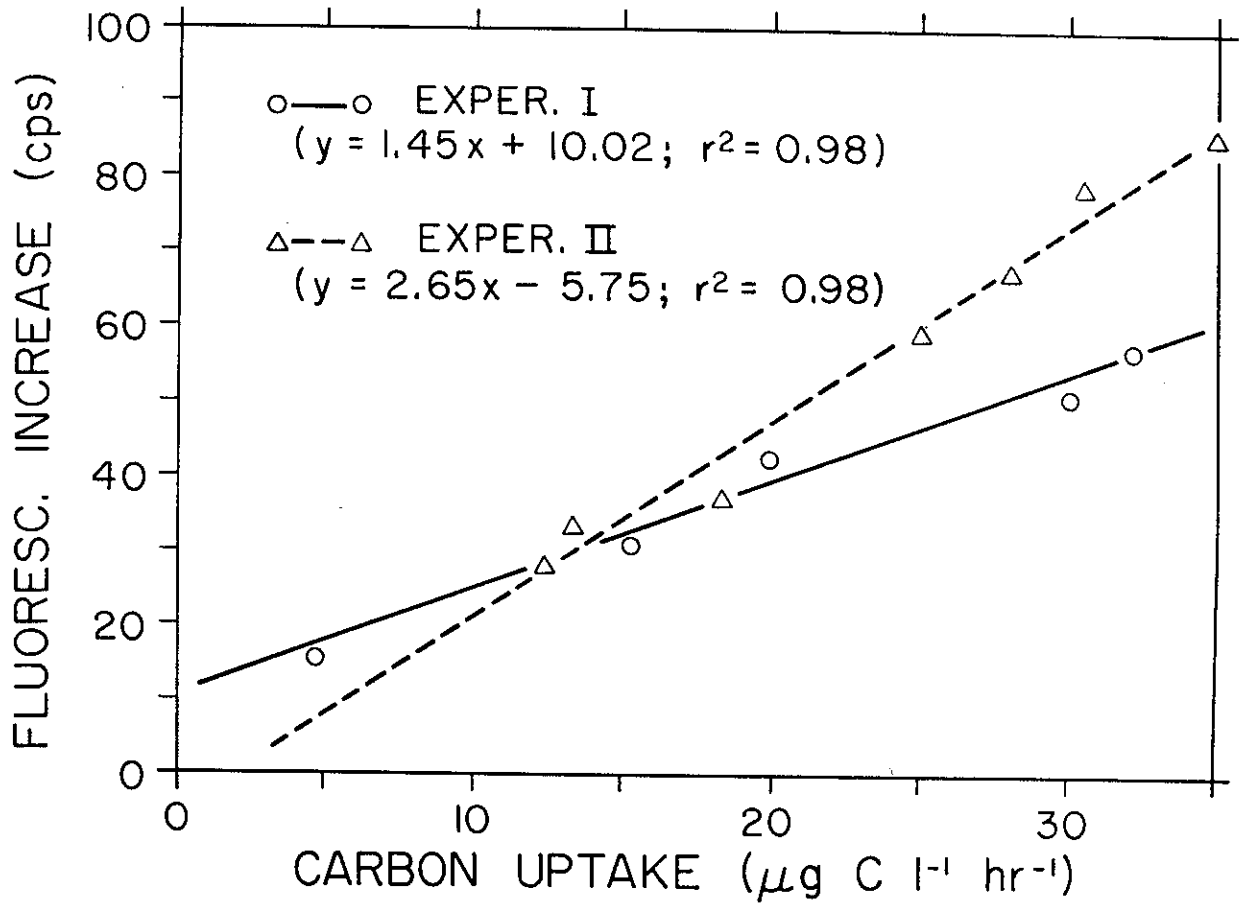

FIGURE 2. Relation between sample fluorescence increase (F_d - F_i) and photosynthetic carbon uptake in light-deprivation experiments conducted with Lake Texoma phytoplankton assemblages.

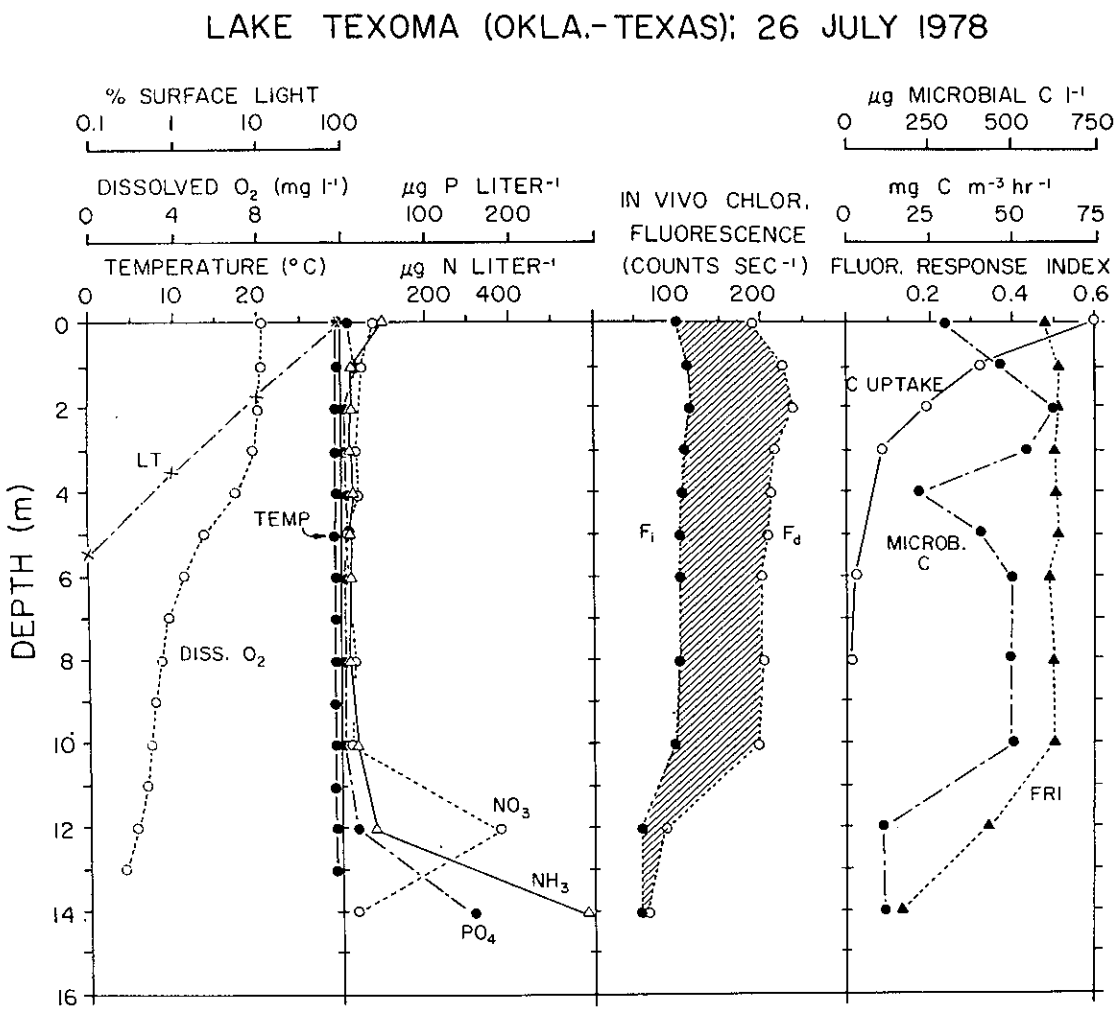

FIGURE 3. Late-summer vertical profiles of physical, chemical, and biological characteristics; in vivo chlorophyll fluorescence; and the flourescence response index (FRI) in Lake Texoma. Note the lack of thermal stratification; the extent of the mixed layer as indicated by nutrient, F_d, and FRI profiles; and the disparity of algal biomass (as reflected by F_d) and photosynthetic potential (as reflected by FRI) profiles to light and productivity distributions.

The photosynthesis-depth curve, derived from in situ ^{14}C-uptake measurements in light and dark bottles suspended at fixed depths, is characteristic of light-limited primary production and indicates that little photosynthesis occurs below 3-4 m. However, phytoplankton biomass (as reflected by F_d) is high throughout the mixed layer. Relatively constant FRI values (0.48-0.51) between 0 and 10 m suggest that the algal physiological state is maintained at depths exceeding the classical euphotic and trophogenic zones as delineated by light and productivity profiles. In situ sample displacement experiment results support this implication. Samples from 1, 3, and 8 m had similar biomass-specific photosynthetic carbon uptake rates when incubated at the same light intensity (Table 1).

Vertical mixing of algal cells through steep light gradients can enhance integral photosynthesis estimates (Marra 1978a, b). Thus, production measurements based on sample incubation at fixed light intensities probably underestimate phytoplankton productivity in "optically deep" (sensu Talling 1957) systems. Our data show that a major fraction of the viable phytoplankton biomass in Lake Texoma occurs in the aphotic portion of the mixed layer. Apparently, mixed layer circulation is sufficiently rapid that the photosynthetic capacity of "aphotic" phytoplankton is retained between intervals of exposure to light. Determination of vertical mixing rates in such environments is problematic; however, at water temperatures of 30°C, circulation must be rapid to prevent aphotic respiratory losses from producing deleterious effects on mixed layer phytoplankton.

Broken Bow Lake is a 10-year-old, 58-km^2 impoundment of the Mountain Fork River (southeastern Oklahoma) and representative of deep-valley impoundments occurring throughout eastern Oklahoma, western Arkansas, and southwestern Missouri. Relative to Lake Texoma, Broken Bow is oligomesotrophic, transparent (Secchi depth $\cong$ 5 m), and deep ($\bar{Z}$ = 20 m). The reservoir is thermally stratified throughout the growing season and its euphotic zone is deeper than the mixed layer. Data obtained on 14 August 1978 revealed the presence of strong thermal

Table 1. Comparison of phytoplankton photosynthetic potential as reflected by biomass-normalized photosynthetic carbon uptake (C uptake/F_d) and DCMU-enhanced *in vivo* chlorophyll fluorescence (FRI) in Lake Texoma and Broken Bow Lake sample displacement experiments. Incubation depths were 1 m (520 μE m^{-2} sec^{-1}) and 3 m (300 μE m^{-2} sec^{-1}) in Lake Texoma and Broken Bow Lake, respectively. F_d, reflecting algal biomass, is expressed in relative units (counts sec^{-1}).

Sampling Depth (m)	Fd	C Uptake (μg C l^{-1} hr^{-1})	FRI	C Uptake / F_d
		Lake Texoma, 26 Jul 1978		
1	226	46.86	0.51	0.21
3	215	43.25	0.50	0.20
8	202	44.66	0.50	0.22
		Broken Bow Lake, 14 Aug 1978		
3	19	4.04	0.38	0.21
8	47	25.14	0.41	0.54
12	30	18.89	0.46	0.64

stratification and a slight metalimnetic oxygen deficit (Figure 4). *In vivo* chlorophyll fluorescence and ATP determinations indicated metalimnetic concentrations of algal and total microbial biomass, and *in situ* phytoplankton productivity measurements showed a pronounced metalimnetic peak of photosynthetic activity. Epilimnetic FRI values were low (0.32-0.39), but increased to 0.44 at 5-6 m, probably in response to greater nutrient availability near the thermocline. FRI remained relatively constant (0.41-0.46) at metalimnetic depths corresponding to high algal and microbial biomass and phytoplankton productivity, then gradually decreased below 14 m ($\cong$ 0.1% I_0). Phytoplankton photosynthetic potential, as reflected by biomass-specific ^{14}C uptake in a sample displacement experiment, again corresponded to algal physiological status as indicated by FRI values (Table 1).

These data are of interest in regard to the origin of metalimnetic chlorophyll and production peaks in Broken Bow Lake. Such vertical distributions are common where euphotic depth exceeds mixed-layer depth (e.g., Findenegg 1964, Schindler and Holmgren 1971, Goldman *et al.* 1973, Fee 1976) and may be produced by (a) *in situ* growth of phytoplankton populations adapted to metalimnetic conditions, or (b) sedimentation of cells from overlying strata and accumulation in the metalimnion due to reduced settling velocities. The relative lack of vertical structure in the FRI profile, compared to those for algal biomass (F_d) and productivity (C uptake), suggests the importance of the latter mechanism in Broken Bow Lake during late summer. Experimental results also support this interpretation, as biomass-specific carbon uptake rates in 8- and 12-m samples incubated at 3 m suggest light-limited metalimnetic phytoplankton production rather than photoinhibition of shade-adapted populations (Table 1).

CONCLUSIONS

Our preliminary laboratory-field evaluation indicates that measurement of *in vivo* chlorophyll fluorescence response to DCMU is

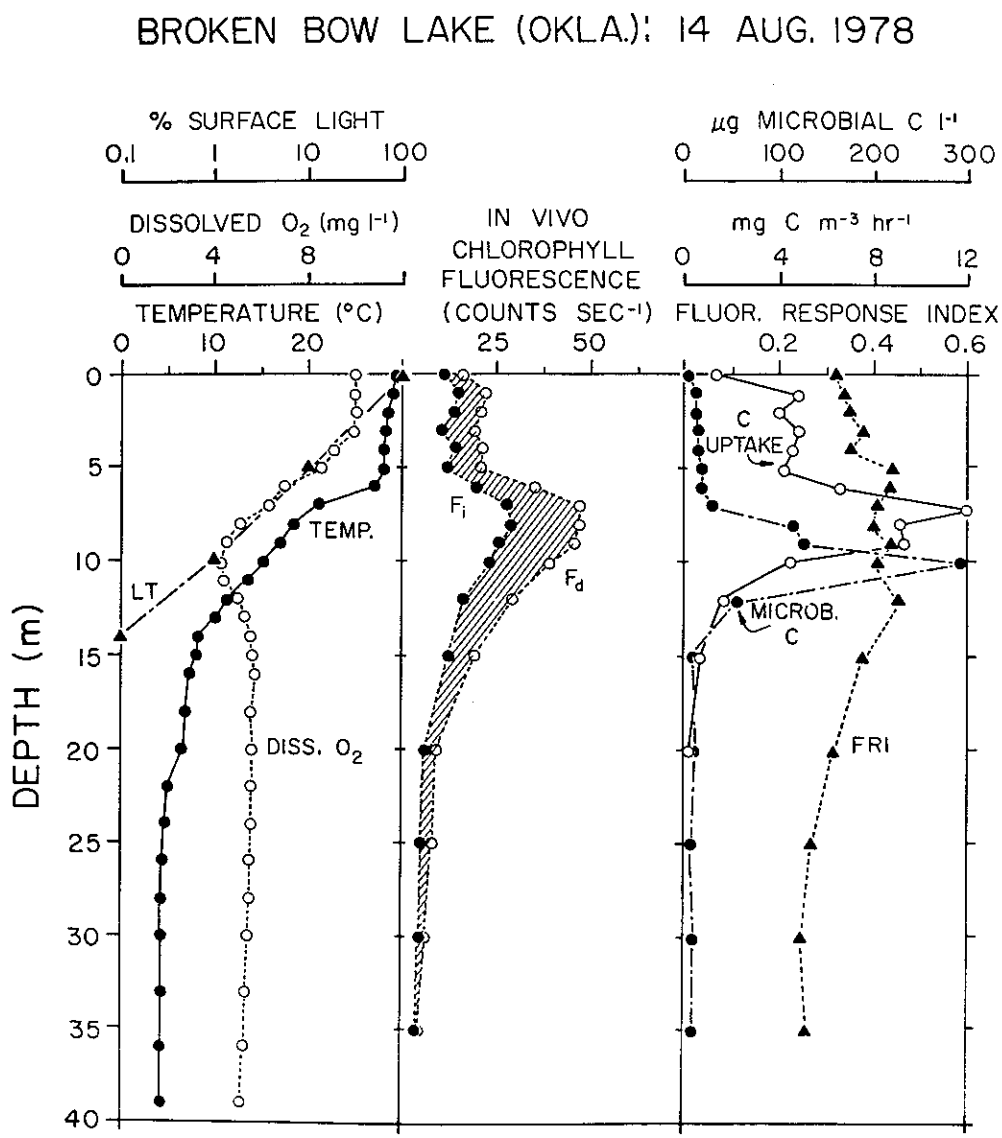

FIGURE 4. Late-summer vertical profiles of physical, chemical, and biological characteristics; in vivo chlorophyll fluorescence; and the fluorescence response index (FRI) in Broken Bow Lake. Note the pronounced thermal stratification, metalimnetic peaks of algal biomass (as reflected by F_d), microbial carbon and photosynthetic carbon uptake, and the lack of a corresponding peak in the fluorescence response index (FRI).

applicable to field investigations of naturally occurring phytoplankton communities. We have observed an FRI range of 0.11 to 0.68 in southern Oklahoma reservoirs and ponds. Blasco and Dexter (1972) reported FRI values of 0 and 0.6-0.7 for severely nitrogen-depleted and actively growing algal cultures, respectively. Cullen and Renger (unpublished) found a similar FRI range (ca. 0 to 0.7) in continuous vertical profiling of near-shore Southern California Bight waters. Our FRI profiles corresponded well to water column characteristics and the results of experiments conducted to provide independent estimates of phytoplankton photosynthetic potential. Comparison of FRI data to photosynthetic carbon uptake *in situ* and in displacement experiments clearly shows DCMU-enhanced fluorescence response to reflect phytoplankton physiological state or photosynthetic potential rather than *in situ* primary productivity.

Numerous uncertainties are associated with the DCMU-enhanced fluorescence response technique. Diel fluctuations in fluorescence response and photosynthetic capacity (Prézelin and Sweeney 1977), the relationship of F_d to algal chlorophyll (McMurray 1978, Esaias 1978), and effects of community species composition (Kiefer 1973, Heaney 1978) and high light intensities (W.F. Vincent and G.F. Harris personal communication) on fluorescence and fluorescence response all require clarification. However, our initial results indicate that *in vivo* fluorescence response has utility as a physiological assay and may be of particular value as an indicator of the extent of vertical mixing in "optically deep" environments. Certainly, by virtue of the simplicity of the fluorimetric analysis and the ecologically integrative nature of the information obtainable, DCMU-enhanced fluorescence response appears worthy of further evaluation and application to field investigations.

ACKNOWLEDGEMENT

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PHYTOPLANKTON EFFECTS ON RESERVOIR USE

by

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INTRODUCTION

Phytoplankton play an intimate role in governing the overall desirability of multiuse reservoirs. Reservoirs used principally for power supply, navigation, and flood control often also support recreation, fisheries, and water supply systems. Algal blooms have been found to be directly responsible for fish kills (Prescott 1948, Moshiri et al. 1978) and pungent odor and taste problems in water supply systems (Hixson, personal comm.), and they have often frustrated boaters, fishermen, and swimmers.

Predictive models, based on nutrient input, temperature changes, and light conditions have been developed to describe potential growth and yield under various conditions. Managers of reservoirs and water supply systems, however, are committed to coping with existing problems, which affect all reservoir biota and the day-to-day routines of the citizens and industries that use the reservoir as a source of water.

This paper details the history of water supply problems associated with nuisance algae and describes treatments for abating or curtailing excessive algal growth. Reservoir water supply management strategies, as they apply to multiuse reservoirs, are also discussed.

HISTORY OF TASTE AND ODOR RESEARCH

Much speculation exists as to which group of biological organisms cause taste and odor problems in water supplies. Baker (1962) claimed that algae were probably the single most important cause of taste and odor. His statement was based on the assumption that either the algae produced the nutrients required by taste- and odor-causing organisms, or the algae themselves produced the metabolites causing the problem. MacKenthun and Keup (1970) stated that poor water quality was caused

by the decay or decomposition of fungi and/or bacteria. Sigworth (1957) identified industrial wastes, decaying vegetation, and algae as contributors to taste and odor problems.

The compounds most often reported as causing earthy or musty odors are geosmin, musidone, and 2-exo-hydroxy-2-methylborane. Geosmin ($C_{12}H_{22}O$) was first isolated from the actinomycete *Streptomyces griseus* by Gerber and Lechevalier (1965). It is characterized as a colorless, viscous, neutral oil with a boiling point of 270°C. Work by Wasserman (1966) indicated that geosmin was also produced by *Streptomyces fradiae, S. odorifer,* and *S. antibioticus*. Medsker et al. (1968, 1969) verified Gerber's findings and noted that geosmin is produced by certain actinomycetes as well as by algae.

Musidone ($C_{12}H_{18}O_2$), isolated by Dougherty et al. (1966), also produces an earthy smell. Musidone is oxidized by carboxylic acid when exposed to large amounts of a given oxidant. Medsker et al. (1969) identified 2-exo-hydroxy-2-methylbornane ($C_{11}H_{20}O$). This compound is an extremely volatile, white solid with a melting point of 158° to 160°C.

One of the earliest works to specifically associate algae with taste and odor problems was a report by Jackson and Ellms (1897). They observed a bloom of *Anabaena* in a contaminated water supply in Massachusetts that was experiencing a severe taste and odor problem. Later work by Rushton (1929) indicated that diatoms also produced taste and odor, although their metabolites were unknown. Only recently have specific metabolites been identified. Maloney (1958) was one of the first to associate a particular odor with a group of compounds. This work was expanded on by Saffermann et al. (1967), who identified geosmin as an odor-causing compound that could be produced by organisms other than actinomycetes. Safferman noted that a compound produced by *Symploca muscoruun* imparted an earthy smell similar to the compound (geosmin) reported earlier by Gerber and Lechevalier (1965). This work

was later substantiated by Henley (1970), who isolated geosmin from *Anabaena circinalis*. Henley also pointed out that geosmin acted as a potential control mechanism for algal blooms by first inhibiting, then enhancing, heterocyst formation.

While many researchers consider algae to be the most important contributor to taste and odor problems, Silvey (1953a) has identified actinomycetes as the major cause of taste and odor problems in southwestern reservoirs. The genus *Streptomyces* has been particularly common in producing isoamyl amine, isovaleric acid, isobutyl amine, valeric acid, betahydroxy butyric acid, and isovaleraldehyde. In an early study, Silvey (1953a) reported that blooms of *Anabaena* and *Melosira* preceded odor problems. However, when these algae were cultured in the laboratory, no odor was produced. This led to the possibility of algae interacting with actinomycetes to produce tastes and odors. Subsequent work tended to support this hypothesis when actinomycetes spores were found in *Anabaena, Aphanizomenon, Cladophora, Chlamydomonas, Chlorella, Gleocapsa, Melosira, Navicula, Nostoc,* and *Pediastrum* (Silvey 1953b). This work and other observations led Silvey to introduce the hypothesis that an imperfect symbiotic relationship existed between taste- and odor-producing algae and actinomycetes (i.e., as long as the algae were healthy and the actinomycete populations were controlled). However, when nutrients became limiting, the relationship shifted to a parasite-host relationship, to the detriment of the algae. Silvey claimed that this mechanism was the reason algal blooms and taste and odor problems did not always coincide.

CONTROL METHODS

A wide array of algal control methods have been proposed, ranging from nutrient limitation to ultrasonic radiation.

Biological Control

Several organisms in the aquatic food web have been used experimentally to control excessive algal growth. Species of *Plectonema*, *Phormidium*, and *Lyngbya* were shown to be sensitive to a blue-green algal virus, labeled BGA and LLP-1 (Safferman and Morris 1964a, 1964b). These experiments also indicated that viral algicides increase in concentration during treatment (i.e., algal control in one system could theoretically coincide with production of the virus for use in another affected system), thus eliminating the need for continuous culture maintenance in the laboratory. Although this appears to be a reasonable solution to growth control for algae susceptible to the BGA virus, several strains of viruses would be necessary to control all classes of nuisance algae.

The effects of zooplankton grazing on naturally occurring phytoplankton communities have been extensively studied and are outlined in general terms by Hutchinson (1967). The complexities of phytoplankton species succession and the grazing habits of specific consumers would probably eliminate the use of artificially induced grazing to reduce phytoplankton standing crop. Bishop (1970) did observe that natural rotifer communities would significantly affect the photosynthetic rate. However, the algae that are responsible for degrading the water quality may prove to be toxic to the zooplankton, which would normally be actively grazing (Schmitz, personal comm.)

Several fish species have been evaluated for vascular plant control (Avault et al. 1968), but few, if any, of these fish species can be considered as phytophagus. The eating habits of the Chinese grass carp *Ctenopharyngodon idella* (Val.) have been extensively studied to determine whether it could significantly reduce phytoplankton standing crops (Avault 1965; Kingen and Smitherman 1971; Opuszynski 1972). Using this fish to control growth, however, might present more problems (i.e., disturbance of spawning areas for game fish) than benefits.

Chemical Treatment

Chemical algicides are commonly used to purify undesirable water. One of the most serious problems associated with chemical treatment, however, is the toxicity of the chemical to all the aquatic organisms in the system and not just the target organisms. Historically, copper sulfate has been a preferred treatment method because of its low cost and effectiveness (Sledeckova and Sladecek 1968; Gratteau 1970; Muchmore 1978). Potassium permanganate (Kemp *et al*. 1966) has also been used effectively to control some algal blooms, but it is not applicable as a universal control (Fitzgerald 1966). Other researchers (Hiltibran 1972; Otto 1970; Fitzgerald *et al*. 1952) have tested numerous algicides for effectiveness on a target organism, but few have been studied to determine their overall environmental effects.

Nutrient Limitation

Nutrient input and associated phytoplankton yields have been extensively studied by using various stochastic and deterministic models (Vollenweider 1975; Dillon and Rigler 1974; Imboden 1974; Lorenzen 1973; Lung *et al*. 1976). A reduction in algal yield (biomass, chlorophyll, etc.) accompanies a reduced nutrient load, regardless of the model used.

Controlling both point- and nonpoint-source nutrient inputs to reservoir systems will obviously reduce algal growth. In some cases, however, high treatment costs or lack of input information prohibits the reservoir manager from regulating or quantifying nutrients entering the system. Dilution with nutrient-poor river water has been used successfully as an alternative to special waste treatment to control nuisance algal blooms (Welch *et al*. 1972; Goldman 1968). This is a special type of treatment, which would not be applicable in many cases because dilution water is not readily available.

Mechanical Disruption

Ultrasonic radiation (Fogg 1969) and a shockwave technique (Menday and Buck 1972) have been proposed as potential controls for blue-green algae. These techniques have been shown to be relatively ineffective and, in some cases, harmful to the fisheries.

Reservoir destratification by air injection (Fruh 1967) appears to have a negative effect on algal growth, but it may also have a hazardous effect on the entire system by disrupting life cycles of other organisms in the food web.

MANAGEMENT STRATEGIES

Ultimately the managers of water supply systems face all the problems associated with nuisance algal growth (i.e., taste, odor, color, and filter clogging). Although several methods for controlling algal growth are available to managers of reservoirs and water supply systems, they are often neither practical nor cost-effective. Two management techniques that are gaining popularity in areas of chronic algal blooms are multilevel water intakes and system flushings.

Use of multilevel water intakes may eliminate many of the taste and odor problems caused by algae in water supply systems, simply by drawing water from levels not affected by a bloom. This solution may be reasonable for planned facilities, but it does not solve the problem at fixed intakes. Also, water drawn from the hypolimnium may be high in manganese, iron, copper sulfate, and other undesirable chemical compounds, which can significantly increase water treatment costs (Iwanski, personal comm.). However, the trade-off between algal problems and the treatment cost due to heavy metal contamination must be measured before implementing a variable depth intake program.

Water treatment of some type is the only tool a manager can rely on if a water intake is in a fixed position in a reservoir. If, however, the intake is downstream from the reservoir, a change in reservoir release operations may alleviate taste, odor, and color problems associated with algal growth. This management technique has been demonstrated for water supply systems below Normandy Reservoir in Tennessee (Hixson, personal comm.). Algal communities that had developed in Normandy Reservoir were released through the dam and carried downstream to water supply holding ponds, where they continued to proliferate. This growth caused taste and odor problems and filter clogging at three municipalities downstream from the reservoir. The problem was solved by releasing a plug flow of hypolimnetic water. As the water flowed downstream, the nuisance algal growth was decimated by the abrupt temperature changes and increased streamflow. In this way a serious water quality problem was eliminated without costly chemical treatment, simply by adjusting the water release level. Such a reservoir release operation would be especially effective in a large water basin with more than one reservoir. Releases could be timed to effectively eliminate foul water supply problems witnout hindering flood control and navigation purposes of the reservoirs.

RESEARCH AND MANAGEMENT NEEDS

Managers of reservoirs and water supply systems will continue to rely on previously tested techniques to ensure the aesthetic quality and safety of reservoir water. Continued research in the area of reservoir release operations could significantly enhance the biological and chemical properties for downstream water use. Biological control by grazing zooplankton appears to be a desirable method for controlling algal growth, but insufficient testing to date has limited its use on a practical basis.

Nutrient limitation, and hence low algal standing crops, appears to be a reasonable method for eliminating nuisance reservoir phytoplankton. If models can be developed to accurately predict phytoplankton response to nutrient input, then the manager can make a confident decision about appropriate reservoir operations. However, until the causes of excessive phytoplankton growth are quantified and modeled, the reservoir manager will have to rely on existing techniques.

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THE USE OF BIOASSAY APPROACHES FOR ASSESSING PHYTOPLANKTON GROWTH IN LAKES AND RESERVOIRS

by

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INTRODUCTION

Although laboratory algal cultures were used to assess the nutritional status of water and other water quality variables as long ago as 1910 (Allen and Nelson 1910), only in recent years have methods been standardized for using algae as test organisms to assess water quality of fresh and marine waters (PAAP 1969; U.S.EPA 1971, 1974; Miller et al. 1978; APHA 1976).

Definition of Bioassay

The application of algal bioassay techniques is dependent on several definitions. Primary productivity in lakes and reservoirs refers to the initial biological steps of fixing energy for the food chain. Generally, macrophytes, phytoplankton, benthic algae, and photosynthetic and chemosynthetic bacteria are each a part of the primary productivity of lakes. The concept of bioassay in this application assumes that representative species can be used to assess the effects of growth-controlling factors on primary production. Because bioassays integrate the effects of many variables, they can be used to evaluate the effects of toxicants and growth-promoting materials in relation to laboratory manipulation of environmental factors and ecological factors. In this sense they are used to evaluate the accuracy of models of lakes and reservoirs. Because of ease of culture, rapid growth rate, and relative ease of measurement, algae (generally phytoplankton species) have been selected for use in bioassays to represent the effects of factors affecting primary production. For specific problems concerning other primary producers, it is best to develop specific procedures for individual species or assemblages of species. In this review we restrict our attention to algal bioassays (U.S. EPA 1971; APHA 1976).

Algae respond to chemicals in the water and to environmental variables (light, temperature, carbon dioxide, mixing, and other biota). These environmental variables are exogenous variables, i.e., variables external to a specific water sample. The chemical quality of the water depends on compounds and elements that are classified as dissolved salts (calcium, magnesium, sodium, potassium, chloride, sulfate, and bicarbonate), other dissolved chemicals (dissolved organic compounds, gases - O_2, N_2, CO_2), nutrients (nitrogen, phosphorus, trace elements, inorganic carbon), and particulates. Algae, organisms that graze on algae, decomposers, and other plants and animals constitute biological variables. These chemical and biological variables are endogenous variables. The only variables relating to the natural system that can be tested using bioassay approaches are the chemical variables. The other variables should be assessed only in relation to the natural or prototype system.

Carbon dioxide occupies a special role in this system. Carbon dioxide can be part of the endogenous system when it is derived from the aqueous phase (CO_2, bicarbonate, carbonate--inorganic carbon) as illustrated by Goldman et al. (1972, 1974) or it can be supplied as CO_2 from the atmosphere, from degradation of organics in the water column and the sediments (Schindler and Fee 1973; Rudd and Hamilton 1978; Sonzogni et al. 1977; Mortimer 1971). Schindler (1971) and colleagues have shown that when other nutrients are supplied in adequate or excess amounts, the carbon dioxide invasion rate from the atmosphere is adequate to provide sufficient carbon for algal blooms. Consequently, one would conclude that algal bioassays should not be used for the analysis of carbon requirements. Carbon dioxide should be treated as an exogenous variable and, except for physiological, algal chemostat culture, or other laboratory-related relationships with carbon dioxide, CO_2 should not be assessed in a bioassay context.

Bioassay Methods

Bioassay means the assessment of the concentration of material with a biological measuring system. Bioassays themselves can be conducted in a variety of ways. One of the goals of the U.S. EPA-sponsored algal bioassay program was to develop standardized algal assay procedures that would allow laboratories to compare their results. Two methods were identified (PAAP 1969) as: 1) batch culture systems (Fogg 1975) and 2) continuous culture systems (Malek and Fencl 1966). So far, the batch culture systems have been used as a screening test and to assess large numbers of water bodies with different chemical composition. Kalff and Knoechel (1978), in a relevant critical review, state that bioassays are last in order of declining realism of experimental methods to study lakes; they rank batch as last and continuous culture with artificial media as next to last. Generally, continuous culture systems have been used more as a research tool to understand phytoplankton growth dynamics than as a bioassay approach (Eppley and Renger 1974; Fuhs et al. 1972; Goldman et al. 1974; Goldman and McCarthy 1978; Reynolds et al. 1975a,b; Rhee 1973, 1978; Toerien et al. 1971).

Although continuous culture has excellent application to bioassay (Porcella et al. 1970; Toerien et al. 1971), its use has not been widespread due to poor understanding in using the technique and in interpreting results. Continuous culture methodology is not as simple as batch methods. Although the data are more meaningful, interpretation is difficult because of sample preparation problems, replication, and because the application of the data to actual situations has been so minimal that managers have not encouraged its use. Batch cultures have widespread use. This use has resulted in broad acceptance of batch cultures and in some cases to use in management decisions (Kotai et al. 1978; Miller et al. 1978). Although much of the theory and understanding of

growth of algal cultures has been derived from continuous culture work, the remainder of this paper is devoted to the analysis and interpretation of batch culture results. The specific procedure discussed includes only the various modifications of the Algal Assay Procedure: Bottle Test (AAP:BT; U.S. EPA 1971).

In laboratory algal bioassays the change in amount of algae relative to the concentrations of material of interest is assessed over periods of time and these measurements are used to estimate the chemical quality of the water. Essentially, two concepts are applied in interpreting the measurements: biostimulation and toxicity. Generally, biostimulatory chemicals increase and toxic chemicals decrease the growth of algae. The concentration of the material of interest causes a change in the amount of growth compared to a control.

Evaluation of effects involves several different groups of variables: 1) the assessment of growth, 2) the relationship of different measures of biomass to growth, and 3) the relationship of growth to concentration of material or materials of interest. It is this last aspect that is of most importance to interpreting bioassay results. However, biomass/growth and measurement relationships must be understood before attempting to interpret bioassay results.

MEASUREMENT OF BIOMASS

Which Variables Are Measured?

In batch cultures microbiological populations typically follow a growth curve which progresses through a lag phase, an exponential growth phase (geometric increase), and a stationary phase (Figure 1). This growth curve can be described mathematically (Pearl 1925; Gates

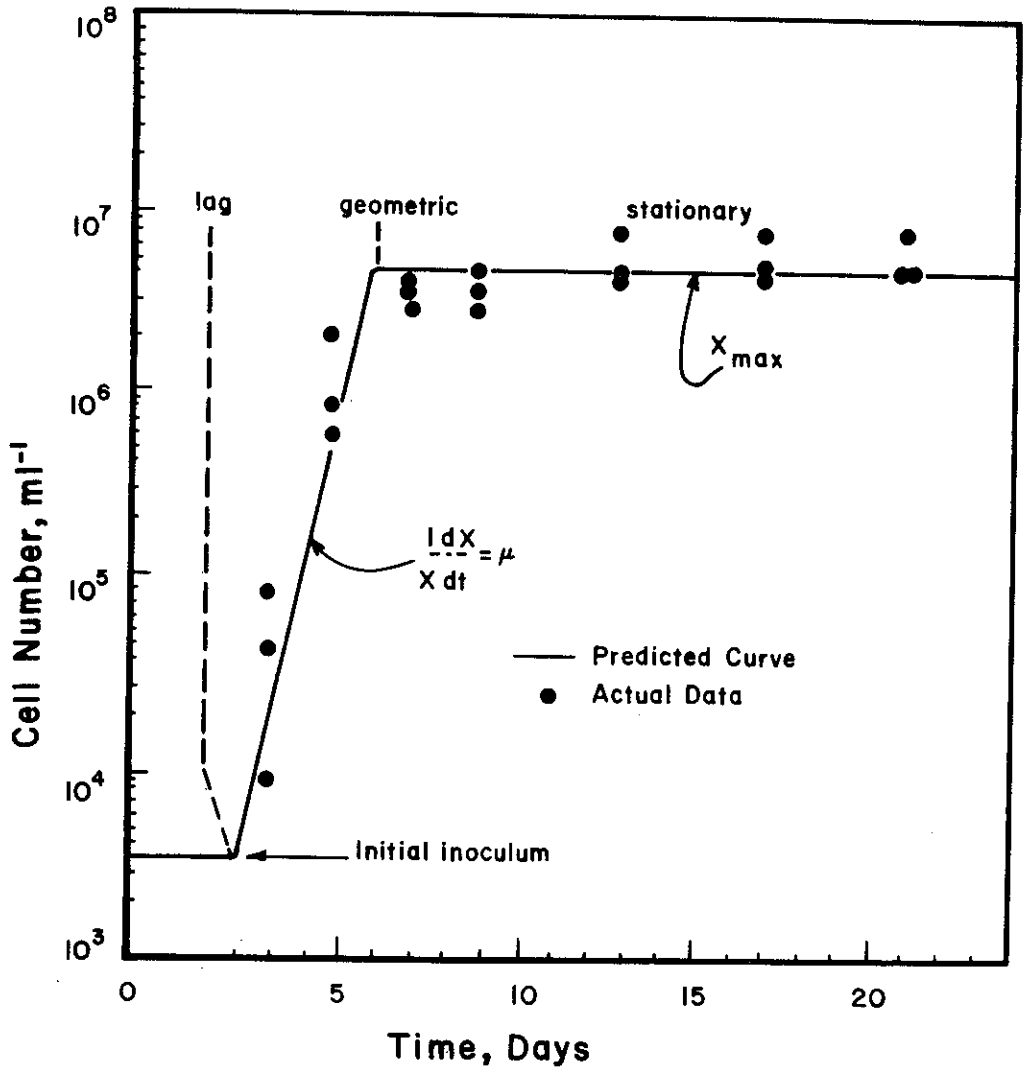

FIGURE 1. Comparison of predicted growth curve (batch) for *Selenastrum capricornutum* for 100 percent AAM with data points of actual batch assays (adapted from Toerien and Huang 1973).

and Marlar 1968) and growth responses interpreted in relation to chemical conditions (Toerien and Huang 1973; O'Brien 1974). The stationary phase is succeeded by a senescent phase in which biomass decreases. The lag phase is that period of time where the culture does not grow as the cells adjust to their new environment. At present, the effect of varying chemical concentrations and compositions on lag time is not adequately explained and lag time is not evaluated in bioassays.

The period of geometric increase is when each cell grows at a constant rate (μ) and divides into constant numbers and sizes of cells. The variables in this growth pattern are the biomass concentration (X) and time (t). The equation describing growth for that interval is:

$$dX/dt = \mu X \qquad (1)$$

The cell population can be described in terms of a doubling time ($t_{\frac{1}{2}}$):

$$t_{\frac{1}{2}} = (1/\mu)\ \ell n\ 2 \qquad (2)$$

The stationary phase is attained when the organism runs out of materials required for growth, that is, when materials become limiting to growth.

We define algal biomass as the elemental composition of algae grown under optimal conditions expressed as moles; for example, Stumm and Morgan (1970) define algae stoichiometrically as $C_{106}H_{263}O_{110}N_{16}P_1$ (3550g/mole) (minor elements are neglected). Dry weight of cells reasonably approximates biomass and is considered equivalent to biomass. The maximum biomass (Xmax) attained (at the stationary phase) relates to the initial concentration of the limiting material:

$$Xmax = Y(So) \tag{3}$$

where Y is a yield coefficient and So is the initial concentration of the element controlling the maximum growth. Also, the rate of change of biomass is related to the concentration of limiting material. The relationship between growth rate and concentration can be visualized as follows:

$$\mu = f(S) \tag{4}$$

where S is the concentration of the limiting factor and μ is the growth rate of the organism under the particular environmental conditions of the bioassay.

These concepts apply very well to biostimulation. To assess the effects of toxicity, the estimates of biomass and the growth variables (Xmax,μ) are compared to a control. Controls include measurements of receiving water (synthetic or natural) without any pollutants, receiving water with known pollutants, and algal assay medium (APHA 1976; Miller et al. 1978; U.S. EPA 1971).

Selection of actual variables for comparison requires some judgment. For the maximum biomass (Xmax), the peak measurement is usually used (APHA 1976; Miller et al. 1978). The specific growth rate of a batch culture (μb) is calculated from biomass measured over a period of time and actually varies with time (Figure 2):

$$\mu_b, 1.0 \text{ days}^{-1}, = \frac{1}{t_{n+1}-t_n} \ln \frac{X_{n+1}}{X_n} \tag{5}$$

The peak (μbmax) measured specific growth rate (Figure 2) is simplest to use as the growth rate variable (Middlebrooks et al. 1971).

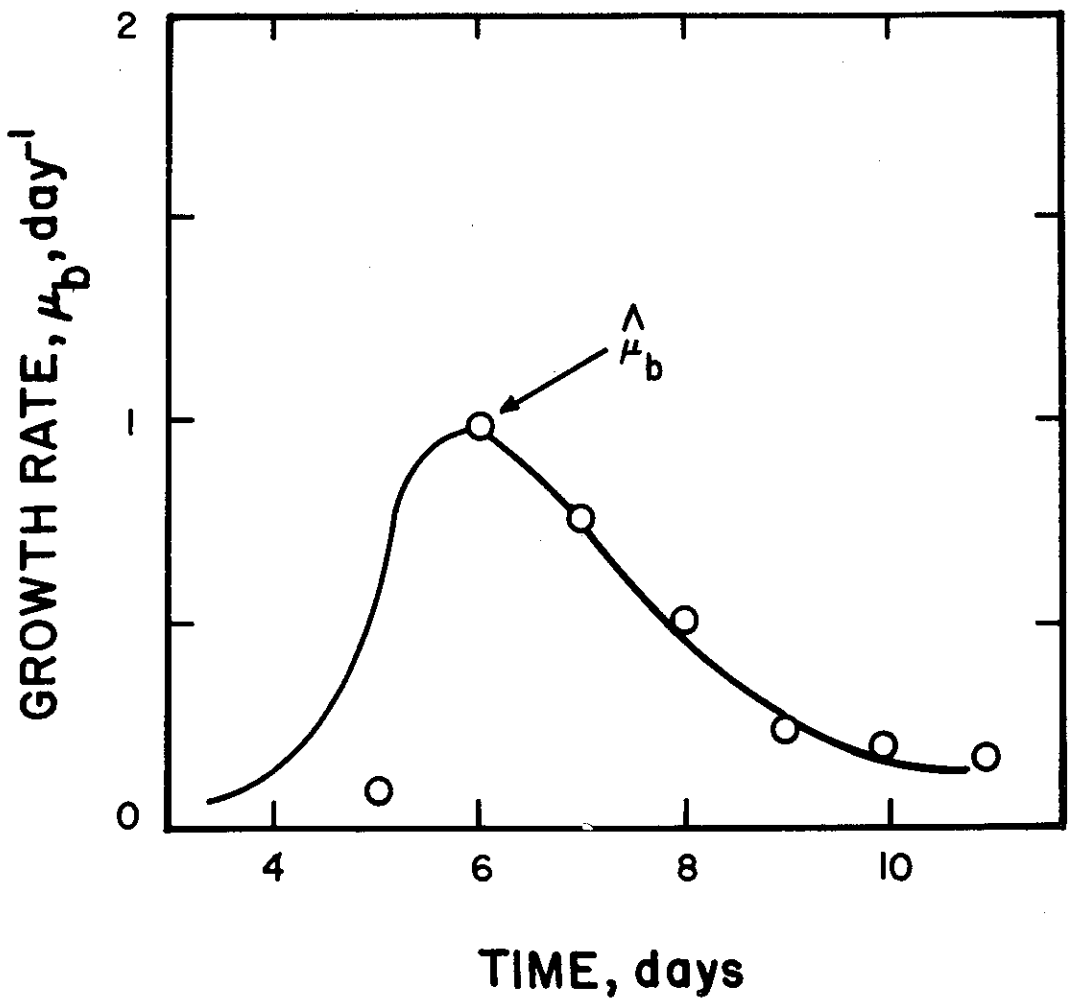

FIGURE 2. Change of batch culture growth rate with time (Porcella et al. 1970).

Only one measurement of each variable for each bioassay flask is obtained using Xmax and μbmax. A statistical approach that can be used to expand the degrees of freedom is to use Duncan's Multiple Range Test (Duncan 1955; Middlebrooks et al. 1971) and treat each biomass measurement as a replicate in time.

How is Biomass Measured?

Methods of measuring biomass must be evaluated in terms of accuracy, precision, sensitivity, cost, and convenience. Qualitative judgment about previous methods is summarized in Table 1. Different investigators would use one or several methods, as appropriate, depending on available facilities and staff and bioassay objectives. If biomass values are compared to a control, then the method is not as important as when the results are compared to other investigators and other sample sites and sampling times.

Accuracy is a term that means the truth of the measurement; that is, how close is the measurement to measuring what is really of importance? This is difficult to assess and most investigators have concluded that dry weight of cells is the measurement of biomass closest to the truth (Kalff and Knoechel 1978). Dry weight is the measurement most appropriate for use in models. This assumes that the cells being measured are totally cells and not contaminated with debris and other materials. Also, dry weight may be difficult to evaluate because of precision and sensitivity problems. Many investigators argue that more than one measurement is important because no one measurement is truly a measure of the variable of interest.

If we accept that biomass is the most important growth variable and that dry weight is the best estimation of biomass and yet

Table 1. Qualitative evaluation of different methods of estimating biomass in algal cultures.

Biomass Variable Measured	Reference[a/]	Evaluation[b/] Accuracy	Precision	Sensitivity	Cost	Convenience
Cell counts						
microscopy	(1)	low	low	high	low	low
displacement	(2)	low	high	high	high	high
Volume						
microscopy	(1)	low	low	high	low	low
displacement	(2)	moderate	high	high	high	high
Absorbance	(1)	low	low	low	low	high
Dry weight						
SS on filter	(1)	high	moderate	low	low	low
tared dish	(2)	high	low	low	low	low
Chemical composition						
particulate carbon	(3)	high	moderate	moderate	high	low
chlorophyll	(1)	low	moderate	high	low	high

a/ (1) = APHA 1976; (2) = Miller *et al*. 1978; (3) = Porcella *et al*. 1970.

b/ Accuracy is considered in relationship to the mass of elements contained in cells of composition $C_xN_yP_zH_aO_b\ldots$

Precision is in terms of coefficient of variation for $n \geq 3$ samples ($CV = 100\ Sx/\bar{x}$).

Sensitivity is precision at low concentration.

Cost includes technician time and equipment cost. Generally if equipment cost is < $5,000 and technician time is not excessive, it is marked low; otherwise high.

Convenience embodies minimal training and simple procedures.

there are experimental difficulties in measuring dry weight, then it is important to define measurements that relate to dry weight precisely and sensitively (Table 1). By assuming that the total variance of the biomass estimation procedures for a bioassay is the sum of the variance attributed to the measurement and that of the variance of the bioassay itself, it is possible to calculate the precision of the bioassay itself to be in the range of 6.5 to 26 percent with a median of about 13 percent (Porcella et al. 1970). Therefore, reproducibility of replicate assay flasks is reasonably good. The actual biomass estimates themselves are highly variable depending on the mean value. Low concentrations have high coefficient of variation (CV) while a limit is reached for higher concentrations (Table 2).

In a comparison of results from eight different laboratories and three different media, Weiss and Helms (1971) showed that reasonable precision could be obtained (Table 3). The measurement of Xmax was more precise than μbmax. However, a low precision technique (hemacytometer) was used to assess biomass for determining μbmax. Because this growth parameter is measured at low biomass concentrations where precision is less, a measurement that is both precise and sensitive should be used. Estimation of Xmax does not suffer from this type of precision problem because, except in low nutrient waters, biomass is usually in a range where precision is more acceptable.

In comparing the two growth parameters, μbmax can be ascertained sooner (0-5 days) while Xmax is determined after a much greater time interval (10-21 days); both parameters must be measured frequently over most of the growth curve. The trade-off is one of time and cost versus precision. If equivalently precise biomass techniques were used, μbmax would often be the only measurement.

Table 2. Overall precision[a] of different parameters measured in batch culture assays (Porcella *et al.* 1970).

Analysis	Range of Concentrations	Coefficient of Variation (%) Range	Coefficient of Variation (%) Mean	Number of Observations
Absorbance OD/one-inch cell	0.005 to 0.05	16.0 to 28.0	20.2	5
	0.051 to 0.15	4.0 to 37.0	13.2	13
	0.151 to 0.30	2.0 to 19.0	8.3	20
	> 0.30	4.0 to 9.0	6.5	8
Cell Counts No. x 10^6/mℓ	0.5 to 1.5	4.0 to 60.0	23.2	4
	1.51 to 4.0	7.0 to 28.0	13.8	10
	4.01 to 9.0	7.0 to 14.0	10.8	4
	> 9.0	7.0 to 13.0	10.0	2
Suspended Solids mg/ℓ	> 30.0	8.0 to 33.0	17.7	3
	30.1 to 60.0	2.0 to 32.0	13.9	11
	60.1 to 100.0	5.0 to 26.0	14.3	6
	>100.0	4.0 to 7.0	5.5	2
Suspended Carbon mg/ℓ	> 10.0	15.0 to 40.0	27.5	2
	10.1 to 20.0	6.0 to 17.0	10.2	4
	20.1 to 30.0	5.0 to 18.0	13.0	6
	> 30.0	5.0 to 16.0	9.5	6

[a]Overall precision = variance of analytical method plus variance of batch bioassay procedure. Coefficient of variation = 100 ($Sx/\overline{x}$).

Table 3. Comparison of bioassay results from eight different laboratories using different media (Weiss and Helms 1971).

Biomass Measurement	Percent CV	
	Xmax (21 days)	μbmax (0-5 days)
Cells/volume		
Hemacytometer	17.9	24-31*
Coulter Counter	9.3	not done
Dry Weight	10.4	not done

*High concentration media only.

For interpretive reasons, both parameters should be measured. The choice of which method of biomass estimation to use depends on facilities available and the unique features of each method of estimating biomass.

Cell counting procedures suffer from the disadvantage that cells have different sizes throughout their life cycle. Rapidly growing populations are composed mostly of smaller cells while slow-growing populations are composed mostly of larger cells. To correct for size variation the biomass can be estimated by calculating the cell volume or otherwise measuring the volume of cells. This correction is simple and accurate with high technology instrumentation such as the Coulter Counter® and other particle counters that work on displacement principles; but low technology alternatives, such as microscope counting and calculation of mean cell volumes assuming spherical shapes for cells, etc., are tedious and have significant problems with precision.

Light-scattering techniques have been used and because of their convenience and the ubiquity of spectrophotometers these techniques have received wide application. However, they are often inaccurate because of background light scattering, light absorption due to colored particles and other materials, and/or they are imprecise at low concentrations (insensitive). In terms of convenience they are nondestructive and require very little sample volume or time and training of technicians.

There are several chemical techniques for measuring biomass. These include measurements such as COD (chemical oxygen demand), chlorophyll (whether by extraction and spectrophotometric measurement or by *in vivo* fluorescent measurements; Tunzi *et al.* 1974);

ATP (Brezonik et al. 1975) particulate organic carbon, and other elemental measurements.

If an investigator has the methodology to use one or the other of these variables, then it is possible using parallel measurements to correlate any variable with the dry weight variable (for example, Porcella et al. 1970, 1973; Kotai et al. 1978; Miller et al. 1978). Regression equations do not give much weight to low values and give greater weight to high values. Also, nonuniform cell size during growth will alter relationships. Thus regression equations apply better to biomass measurements obtained at times later during the bioassay growth curve. In no case should transformed data be used for calculating growth rate; original data are used.

THE RELATIONSHIP BETWEEN BIOASSAY VARIABLES AND THE CONCENTRATIONS OF CHEMICALS OF INTEREST

Limiting Factors

Two growth variables have been defined, maximum specific growth rate and batch (μbmax) and maximum standing crop (Xmax), for the algal assay bottle test. It is assumed that μbmax and Xmax are a function of the concentration of limiting nutrient(s). A limiting nutrient is defined as the element (N,P, ...) that is in lowest supply relative to needs for elements. Limiting nutrients are determined because of their value in directing control measures. Algal bioassays measure the concentrations of limiting nutrients. Two types of limiting nutrients have been defined that relate to the AAP:BT, growth rate limiting and maximum biomass limiting (Figure 3). This occurs because the maximum growth rate is attained at low nutrient concentrations early in the growth curve while total standing crop

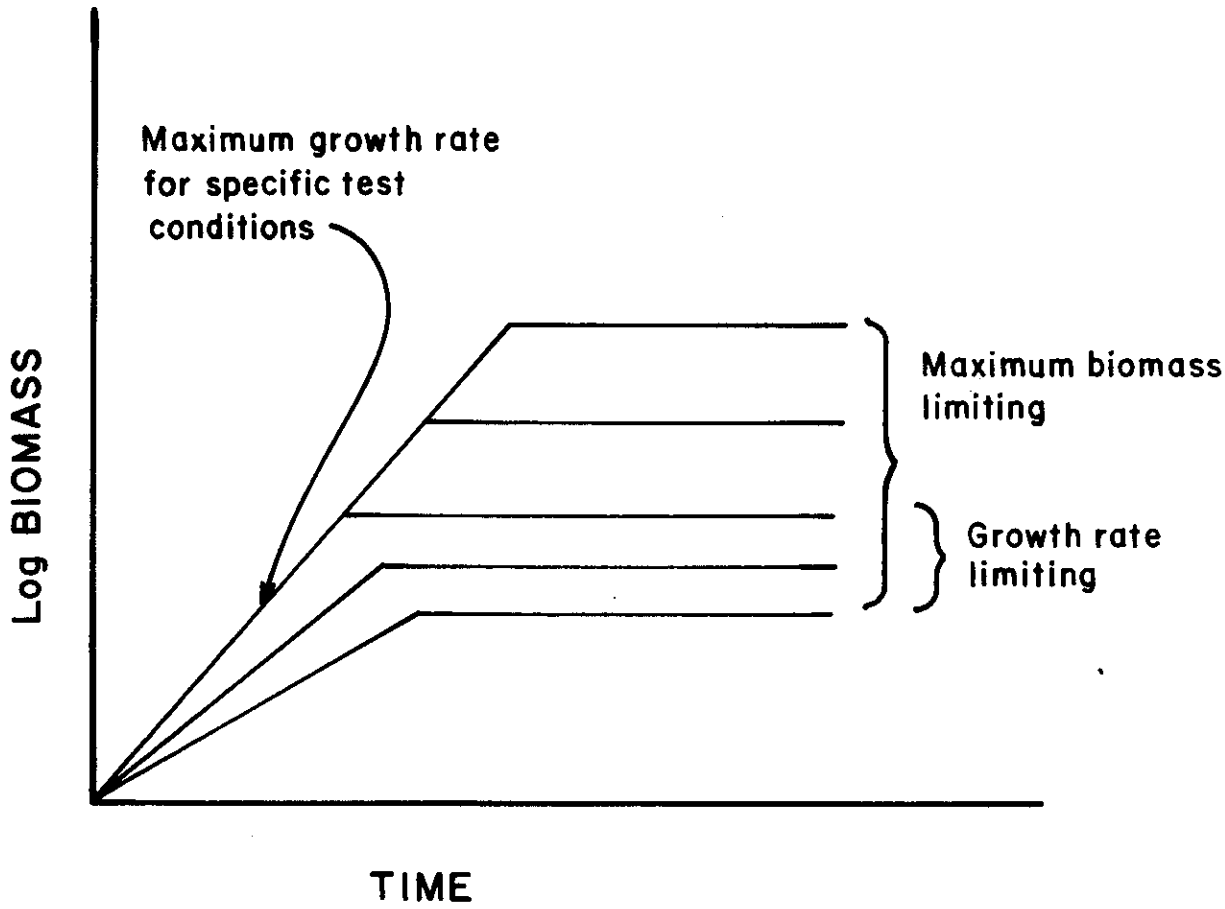

FIGURE 3. Analyzing growth response relationships to limiting nutrients.

can be attained over a long period of time for higher nutrient concentrations. Because many samples have enough nutrients to attain maximum growth rate in the laboratory, Xmax is frequently the only parameter useful to bioassay those samples.

Essentially two methods are used for determining which limiting nutrient controls algal growth in a water sample: comparing chemical nutrient ratios or comparing the effects of nutrient standard additions ("spiking"). Generally, nutrient ratios are based on typical cell composition measurements, e.g., N/P molar ratios of 16:1. Bioassay responses to spiking conform generally to cell composition measurements when N/P ratios are considered. As a rule, N/P molar ratios of 16:1 (7:1 by weight) provide the point where nitrogen limits growth (<16:1) or phosphorus limits growth (>16:1). Shiroyama et al. (1975) provide a value of 25:1; Kotai et al. (1978) provide 18:1; Chiaudani and Vighi (1974) concluded that below 11:1 nitrogen was limiting, above 22.1 phosphorus was limiting, and in between both were limiting. However, in continuous culture experiments Rhee (1978) showed that N/P ratios of 30:1 were the transition point for *Scenedesmus*. Also, he argued that there is no simultaneous limitation of growth, i.e., where both N and P limit growth. In batch bioassays it is common to see no additional growth in water samples to which spikes of N and P alone are added, but considerable added growth when both N and P are added. The significance of these results relate to growth rate measurements as in the chemostat studies by Rhee and the yield relation of Xmax and initial nutrient concentration. Interpretation and application of these concepts to natural waters needs further research.

Toxic Factors

Toxicity is exerted on metabolic processes as a function of toxicant concentration. Various toxicity models have been applied

to algae (Reynolds et al. 1975b) and the relationships between concentration and growth are well established. Procedures for assessing toxicity in the algal assay have been defined but differences of opinion exist on the best means of assessing toxicity effects (Miller et al. 1978; APHA 1976). One of the most useful techniques for assessing toxicity is comparing growth of a test sample with a control. Fitzgerald (1971) has defined useful algistatic and algicidal concepts for evaluating toxicity in batch cultures. Many investigators have used the algal assay for evaluating samples from mixed chemical systems where the chemical composition precludes assessment of effects on biota.

Different Species and Other Methodological Choices

The use of a single algal species (*Selenastrum capricornutum*) of well-understood physiological response and biomass measurement is suggested by Miller et al. (1978). In general the use of a single species to represent many species is probably an acceptable concept. Shuter (1978) showed that nitrogen and phosphorus cell quotas for 28 different species were remarkably constant when corrected for size of the cells. Similarly, Banse (1976) has shown that growth rates and photosynthesis and respiration rates are a function of cell size for unicellular algae.

Some functions are not represented by a single algal species. Nitrogen fixation is restricted to blue-green algae; silica requirements are bioassayed using diatoms. Trace elements and toxicants affect different species uniquely. Payne (1975, 1976) suggested that *Microcystis* was sensitive enough to zinc that the standard algal nutrient medium approached toxic levels. Generally, Miller et al. (1978) are correct for routine monitoring. As they suggest, growth of other algal species should be bioassayed where appropriate,

but growth should be related to that of *Selenastrum capricornutum*. Although Goldman (1978) discusses natural assemblages, the loss of precision is not balanced by gains in accuracy and standardization.

Although generally the specific bioassay environmental conditions (APHA 1976) are considered nonvariant (temperature: 24°C; vertical illumination cool-white, fluorescent: 400 ft-C or 1300 uW/cm^2, visible light at sample surface; borosilicate glass flasks: 500 ml vol, 100 ml of sample with nontoxic closures that permit some air exchange), measurement precision (± 10 percent) prevents complete adherence to the conditions. This is particularly critical because small variations in temperature, light, CO_2 supply, and diffusion rates can have significant effects on growth. Some variations in conditions are permitted to provide for special assays, species requirements, and project objectives; for example, blue-green species are generally grown under lower light intensities (200 ft-C). All such variations and changes in conditions should be reported.

In addition to variation in the algal assay procedures, sample collection can vary in time and space according to the objectives of the study. Flow rates, geological and climatic differences, chemical variation, and biological factors should be assessed in determining a sampling schedule. After sample collection, treatment of the sample prior to bioassay can vary. Again, depending on the objectives, sample treatment can affect the presence and availability of chemicals subject to bioassay. The possible effects should be carefully assessed because such treatment can significantly affect results (Lee 1973). Selection of growth parameters and biomass variables depends on objectives. The relationship between objectives or protocol and bioassay growth parameters is summarized in Table 4.

Table 4. Summary of probable responses for algal assay growth parameters.

Assay Protocol	μbmax	Xmax
Initial concentration of limiting nutrient	Defines rate rate limiting	Defines biomass limiting
Standard additions of limiting and other nutrients	Generally equal to maximum-no effect	Increased biomass
Toxic materials	Decreases	Decreases
Growth-rate stimulating chemicals	Increases	No effect

EXAMPLES OF ALGAL BIOASSAYS IN LAKES AND RESERVOIRS

The algal assay and its various modifications have been widely applied (review in Miller et al. 1978; also see several symposia edited by Middlebrooks et al. 1969, 1975; Glass 1973; U.S. EPA 1975; Nordforsk 1973; Soltero 1976). In this paper specific studies have been selected to illustrate the use of bioassays in lake and reservoir water quality assessments.

Nutrients, Biostimulation, and Eutrophication

Miller et al. (1974) used *Selenastrum capricornutum* to assay waters in 49 U.S. lakes. They used standard algal assay procedures and estimated biomass as calculated dry weight measured from displacement counts and mean cell volume measurements. They concluded that the maximum biomass produced (Xmax) was correlated with the reported trophic state for those lakes having available data. The ranges for low, moderate, moderately high, and high productivity lakes were 0 to 0.1 mg/ℓ, 0.11 to 0.8 mg/ℓ, 0.81 to 6.0 mg/ℓ, and 6.1 to 20.0 mg/ℓ dry weight (calc.), respectively. Based on standard additions, 35 lakes were P limited, eight were N limited, and six were both N and P limited. In general, P-limited lakes were less prevalent as lakes tended to be more productive. Thus greater concentrations of P occur with eutrophication and P is therefore less likely to be limiting. Because nitrogen fixation occurs and can make up the N requirement (Schindler 1977; Liao and Lean 1978), high phosphorus lakes under natural conditions are either not nutrient limited or are limited by trace elements.

Miller et al. (1974) compared the effects of autoclaving samples on P assay results and showed autoclaving effects similar to those discussed by Gerhold and Weiss (Middlebrooks et al. 1975,

p. 349-361). Sample pretreatment techniques have significant effects on assay results and therefore interpretation must include an assessment of sampling and treatment biases.

Wastewater Evaluation

Middlebrooks et al. (1971) evaluated the algal assay response to raw sewage and primary, secondary, and tertiary effluents from the South Tahoe Public Utilities District using an early modification of the AAP:BT. Growth rates and standing crop measurements on the fifth day based on cell counts (hemacytometer) of *Selenastrum gracile* were used to show effects of treatment level. Some toxicity was observed in all samples; toxicity was determined by comparing growth in several dilutions of wastewater.

Similarly, Forsberg et al. (1978) used a modified algal assay to show that waste water treatment plant effluents were toxic. They concluded that algal assays provide data related to toxicity that ordinary chemical analysis does not provide. However, they also suggested that assays may not be necessary for determining limiting nutrients and the potential for algal growth; these data can be calculated from chemical analyses.

However, Cowen and Lee (1976) used algal bioassays to assess algal availability of different phosphorus forms contained in storm water runoff from urban Madison, Wisconsin. Various chemical fractionations failed to provide an estimation of total available P. Based on bioassays with *Selenastrum capricornutum*, Cowen and Lee showed that the probable upper boundary for available total P was total soluble P plus 30% of the particulate P.

Toxicity

The Toxic Substances Control Act and regulations associated with product toxicity will result in broad application of toxicity assays. Assessment methodology exists for algal toxicity measurements (APHA 1976; Miller *et al*. 1978) and application to product testing in potential receiving waters has received some attention (Sturm and Payne 1973; Payne 1976).

The effects of heavy metals and many toxicants on batch algal assay results are not simple to assess. Bartlett *et al*. (1974) made minor modifications of the AAP:BT (nonstandard light spectra) and measured growth in standard medium (containing trace elements, iron, and chelator) as affected by Cu, Zn, and Cd. Growth was measured by packed cell volume and then transformed to dry weight. Results were related to algistatic (will regrow in fresh medium) and algicidal (no growth in fresh medium) concepts (Fitzgerald 1971). Algistatic and algicidal concentrations were established in standard medium and then compared to algicidal samples collected from heavy metal polluted reaches of the Couer d'Alene River, Idaho. The authors showed that Zn concentrations were high enough to cause the observed growth inhibition.

Miller and colleagues have developed algal assay protocols based on displacement biomass measurements of maximum standing crop (Xmax) for determining heavy metal toxicity in water samples. Greene *et al*. (1976) showed that samples from Long Lake contained high and inhibitory zinc concentrations from upstream drainage (Couer d'Alene River) and nutrients from sewage effluents discharged by the City of Spokane. Added EDTA complexed Zn and other metals making it possible for the test algae to express growth as a function of phosphorus concentration (the limiting nutrient) in the

samples. Also, Greene et al. (1976) showed that the biomass produced correlated linearly with unit slope of phytoplankton (standing crop) contained in water samples. Presumably, these phytoplankton were species that were resistant to the Zn levels toxic to *Selenastrum* and *Anabaena*; an indigenous alga, *Sphaerocystis schroeteri*, produced its greatest growth under assay conditions when no EDTA was added.

Salts and Organics

The presence of salts and organic materials in water samples can both interfere with assay results as well as affect algal growth. Waters draining limestone regions frequently have high hardness and alkalinity concentrations ($\geq$ 200 mg/ℓ as $CaCO_3$). As CO_2 is removed from the alkalinity system, pH increases and most alkalinity is present as $CO_3^{=}$. The $CaCO_3$ solubility product is exceeded, $CaCO_3$ precipitates and phosphate and trace elements are frequently co-precipitated reducing the availability of nutrients or toxicants in the sample to less than would be expected based on initial chemical measurements. This can lead to erroneous interpretations because productivity in the natural lake may have a less severe effect since CO_2 is replenished by natural mechanisms. Interference in the test is caused by resultant "sticking" of cells on $CaCO_3$ crystals. Also, particles of $CaCO_3$ can prevent use of many of the typical biomass measurements.

A series of bioassays were performed on samples from eutrophic Deer Creek Reservoir, Utah (Porcella and Merritt 1976) using the AAP:BT and measuring growth as it is affected by nutrient standard additions to the samples. Filtered epilimnetic samples were collected at summer peak bloom, fall overturn, and spring overturn to characterize reservoir dissolved available nutrients dynamics based

on assay response (Figure 4). A variety of standard additions were made (N, P, trace elements, complete assay medium, $NaHCO_3$). It was found that Deer Creek Reservoir was initially P limited during the bloom, and that nitrogen and trace elements additions (secondary and tertiary limitation) could increase the growth after P was added. Similar conditions existed at spring overturn. The fall overturn sample was initially nitrogen limited. Some evidence of trace element toxicity was observed in the overturn samples that may have been caused by transport of metals from the anaerobic hypolimnion.

Assays of the first sample (September) showed that the high hardness/alkalinity levels interfered with the test; the interference caused "sticking" in the December sample and reduced growth in the September sample. The addition of $NaHCO_3$ to later samples helped reduce but not eliminate these problems.

Salinity can be toxic to *Selenastrum capricornutum* at high concentrations. Oil shale development in Colorado, Utah, and Wyoming may impact Colorado River drainage with salinity and organic compounds. Chemical data alone to assess ecological impacts of these compounds in the Colorado River would not be feasible and algal assays were chosen as an approach. The first step was to assess salt effects on assay growth parameters using *Selenastrum capricornutum*. For example, although $MgSO_4$ is a common algal culture medium salt (0.24 meq/ℓ) and Mg^{++} is a component of chlorophyll and other biomolecules, at higher concentrations ($\geq$ 4 meq/ℓ; 48 mg/ℓ) $MgSO_4$ inhibited algal growth (Figure 5).

To assess the effects of oil shale leachates on algal growth, standard elutriate extracts from a sample of a specific type and source of spent oil shale (other samples often give different responses) were added to algal assay medium (AAM). The assay organism

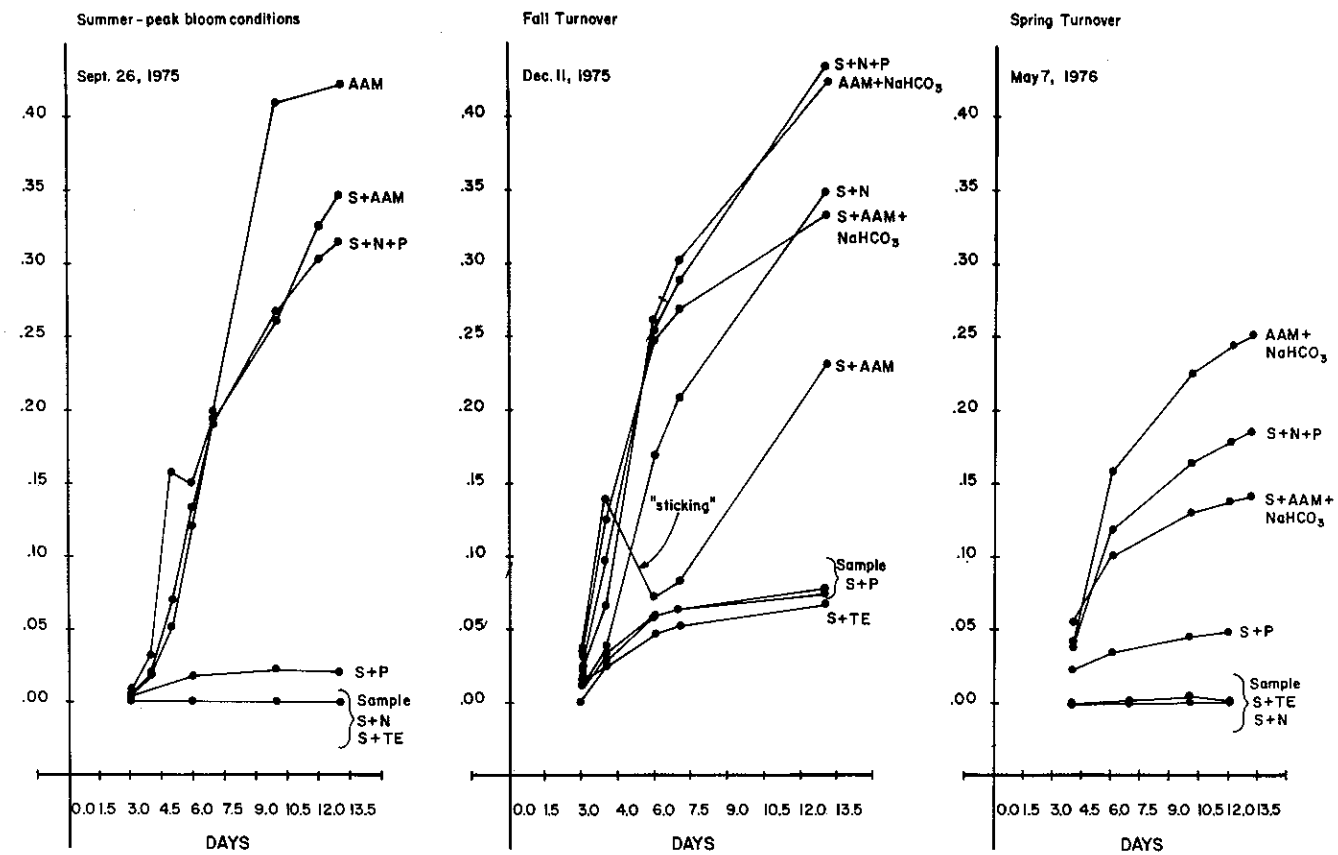

FIGURE 4. Algal assay (*Selenastrum capricornutum*) of eutrophic Deer Creek Reservoir (C-2, midlake sample) illustrates trace element toxicity and effects of $CaCO_3$ precipitation (Additions: AAM = algal assay medium, N = nitrogen, P = phosphorus, TE = trace elements, S = sample; standard additions in May were 50 percent of earlier dates).

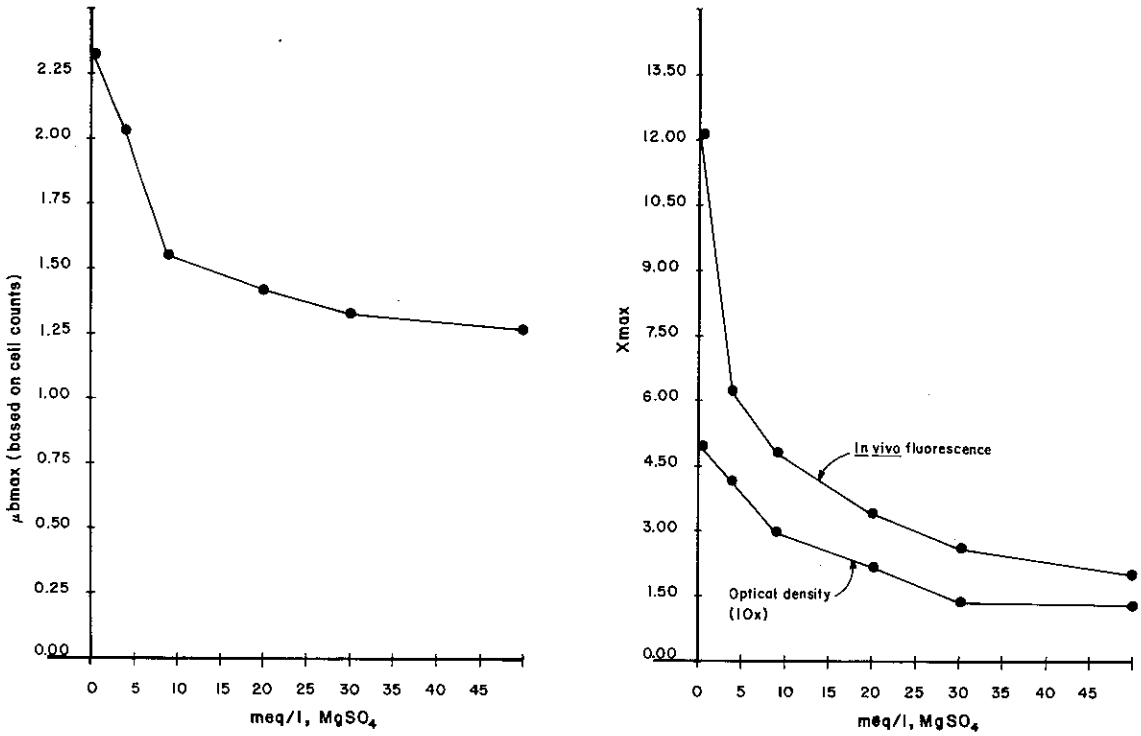

FIGURE 5. The effects of increasing concentrations of $MgSO_4$ on growth of *Selenastrum capricornutum* in AAM.

(*Scenedesmus* sp.) was isolated from Lake Powell. Controls consisting of AAM and AAM plus salts equivalent to the salinity of the extract (determined by analysis) were used for isolating the effects of the shale elutriate on the different growth responses (Figure 6). Some differences in pH were observed during the bioassay and these were not attributable to chemical differences in the waters being assayed. Significant differences (P>0.95) in growth rate measured by optical density and in vivo fluorescence were observed; the culture medium control had lower growth rate (AAM alone) than the other samples. Although no significant differences in maximum standing crop (Xmax) could be detected, the biomass (optical density treated as replicates in time) was significantly lower for AAM plus spent shale. The results indicate that salt increased growth rate but had no effect on maximum standing crop. An apparently delayed effect of chemicals contained in the leachate significantly reduced the final biomass in the assay.

PREDICTIVE USE OF ALGAL ASSAY RESULTS IN EVALUATION OF RESERVOIRS

Some Management Uses

Algal assays are a biological tool for assessing the effects of specific chemicals in aquatic systems. Specific growth parameters have been observed to respond to the set of chemical variables that constitute a water sample. Thus, the bioassay serves to conveniently and inexpensively integrate the effects of biostimulatory and toxic chemicals, some of which may not be defined or are difficult to evaluate in combination with other factors. The bioassay has no direct ecological application but can be useful to predict impacts of certain management decisions. Some example decisions could involve: 1) determining the effects of new effluent discharges,

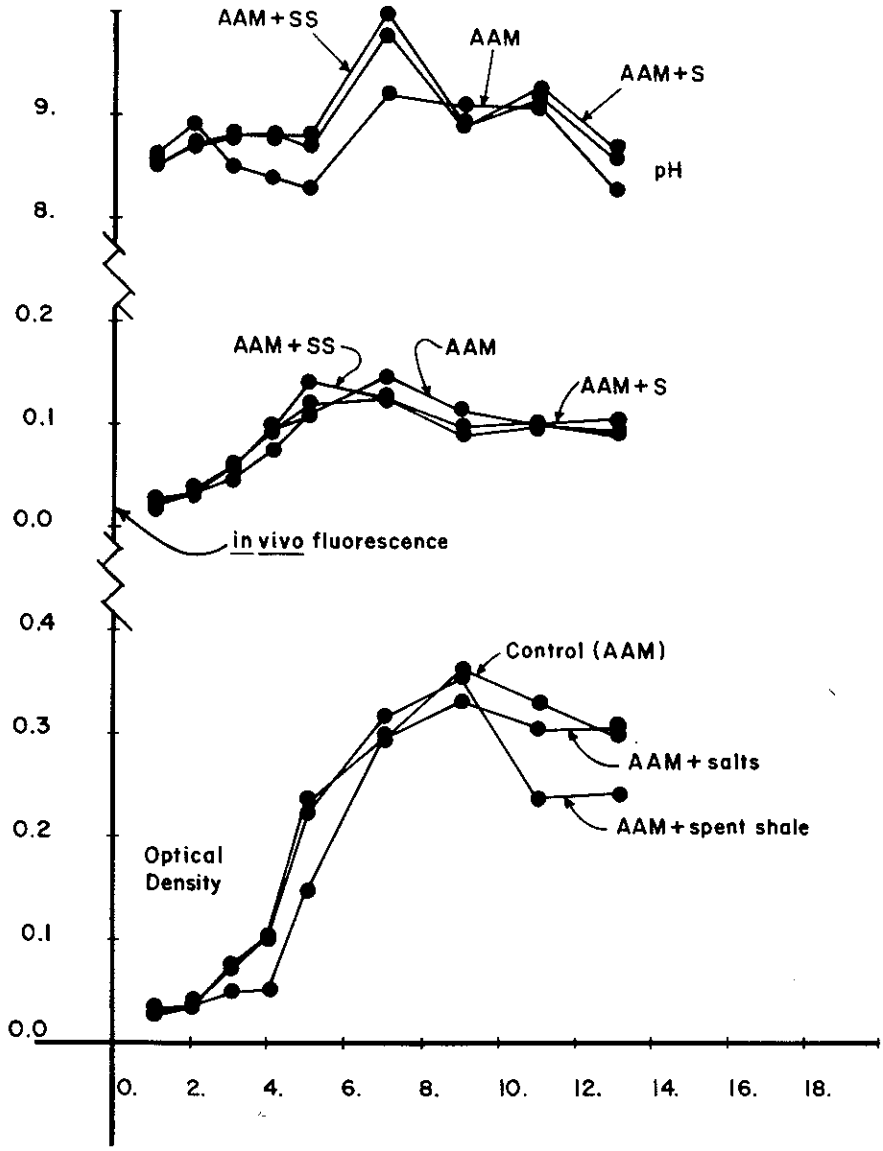

FIGURE 6. Algal assays to differentiate salt impacts of spent oil shale.

tributary diversions and/or new combinations, and changes in reservoir outlet structure depth on reservoir and downstream water quality; 2) determining the potential productivity of new reservoirs; 3) evaluating effects of changes in watershed management (land uses) and reservoir operation (mixing, discharge timing, and restoration techniques).

The Utah Water Research Laboratory has been extensively involved in algal assays to assess the effects of impounding waters in U.S. Army Corps of Engineers reservoirs (Kickapoo, Redstone, Blackhawk, and other potential reservoir systems) and Bureau of Reclamation (USDI) Colorado River drainage reservoirs (Strawberry Reservoir system, San Miguel, Colorado, Animas, Gunnison). In most cases apparent biostimulation was sufficient to indicate excessive algal productivity in the potential reservoirs. Assay results have shown the presence of heavy metal toxicity in the Colorado River drainage.

Gerhold and Otto (1976) used algal assays to assess possible treatment options and to define operational techniques in a potential cooling pond for a proposed power plant. The authors concluded that considerable operational savings could result from implementation of their conclusions.

In discussing regional management of a river/lake drainage system in Norway, Kotai et al. (1978) concluded that algal assays were invaluable in assessing management decisions as to location of waste discharges, diversions, and other activities. In Sweden, Forsberg et al. (1978) reported using algal assays as a routine monitoring analysis to evaluate phosphate removal from wastewater treatment plants.

Research Recommendations

Prediction implies modeling at least at a primitive level. The assay itself is a biological model but it has no predictive value alone. Thus the application of algal assays in reservoir modeling does require some additional research. However, interpretation of the effects of various mixtures of waters and operations (stream/reservoir waters/effluent discharges/pest control chemicals/effect of land use alternatives on runoff) would be aided significantly by algal assay results. Mass balance models and ecologic models that involve chemical variables often depend on chemical measurements. Algal assays could be used to determine the biological availability of those chemicals and the effects of combining those chemical variables.

The modeling of potential biomass based on algal assays has not yet been attempted. Although some researchers have shown a correlation between assay results and phytoplankton standing crop (Greene et al. 1976), such a correlation may be misleading. Algal assays only measure the production aspect of growth; they do not measure the consumption or other loss of produced material and these variables are equally as important in determining phytoplankton succession and biomass production (Kalff and Knoechel 1978). Further research may improve model prediction by expanding the role of algal assay procedures. In our opinion the following areas need most research:

Recommendation 1. Continuous culture (chemostat) techniques should be applied to reservoir operations. This would seem especially valuable because of the rapid and unique flow-through times typical of most reservoirs which may be somewhat analogous to

chemostats. Some questions relevant to algal assays still exist and comparison of chemostat and batch assays may provide some answers to the roles of growth rates and nutrient ratios and of the effects of nonlimiting nutrient concentrations on phytoplankton growth dynamics.

Recommendation 2. The relationship between potential (algal assay) and actual phytoplankton standing crop in reservoirs should be determined. A first step would be to model algal assay response parameters as a function of various inputs of chemicals and environmental variables. Further evaluation would include the effects of succession (different algal species) and algal removal (grazing, sinking, etc.). This approach differs from the development of ecologic models because bioassay approaches are more exactly defined. The results from such an attempt would provide a further basis for interpreting algal assay results. Another aspect is that it would provide a different way of looking at ecologic models which could have serendipitous results. An example of such an approach without the formalism of a mathematical model is the study of a lake and river system by Miller and Maloney (1971). An important step in the development of such a model would be comparison of expected and observed results in an actual reservoir.

CONCLUSIONS

This review has shown that the Algal Assay Procedure: Bottle Test is useful for bioassaying water samples to assess chemical constituents. The AAP:BT should not be used directly to interpret ecological relationships. However, the evaluation of chemical constituents by algal growth has many advantages. It is a single,

integrated, biological measurement of constituents in a sample that exerts impact as a function of chemical concentration. The algal bioassay measures the effects of biostimulatory and toxic compounds.

Examples illustrating the application of the algal bioassay to management questions about effects of nutrients, toxic compounds, and salts show that the test can be used for determining the relative effects of these substances. The algal bioassay can be used in reservoir studies to assess the effects of changes in effluent discharges, tributary diversion and/or combination, evaluating water quality of potential reservoirs, changes in reservoir operation (mixing, discharge timing and location, restoration), effects of differing land uses, downstream effects, and seasonal variation in inflow/outflow.

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RELATIONSHIP OF COMMON DOMINANT PHYTOPLANKTON TO WATER TEMPERATURE AND SEASON

by

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INTRODUCTION

Much of the solar radiation entering lakes and reservoirs is accumulated in the form of heat energy. Water temperatures follow the seasonal patterns of available light and normally are at maximum in late July or early August and minimum in February. Similarly, phytoplankton biomass increases with light intensity and temperature. Maximum biomass levels often coincide with the warmest periods. The influence of temperature as a controlling factor, for the growth and development of phytoplankton, is difficult to separate from other environmental factors such as light, nutrition, grazing, and parasitism. The interactions of these factors are complex, and the effect of one factor on the growth of algae is likely to be influenced by the others.

During spring, summer, and fall of 1972 through 1975, 815 lakes and reservoirs were sampled throughout the 48 contiguous United States. About 2.5 million physical, chemical, and biological data points were obtained. The purpose of this paper is to describe the occurrence of the 20 most common phytoplankton genera observed as related to water temperature and season in lakes sampled in 1973, 1974, and 1975.

MATERIALS AND METHODS

Lakes were sampled as part of the U.S. EPA's National Eutrophication Survey. Lakes and reservoirs included in the survey were selected through discussion with State water pollution agency personnel and U.S. Environmental Protection Agency Regional Offices (U.S. EPA 1975). The number of lakes sampled and the sampling periods for each season are given by sampling year in Table 1.

Table 1. Sampling periods.

Sampling Year	No. of Lakes	Season		
		Spring	Summer	Fall
1973	250	3/7 - 7/1	7/5 - 9/18	9/19 - 11/4
1974	180	3/4 - 5/12	5/13 - 9/5	9/11 - 11/14
1975	154	2/21 - 6/10	6/11 - 9/3	9/4 - 12/11

Aside from using a much expanded data base, the methods employed for lake sampling, phytoplankton analysis, and data storage and manipulation reported in this paper are identical to those described by Lambou et al. (1979) at this workshop and by Taylor et al. (1978). Only temperature data from the photic zone, i.e., the water zone from which the phytoplankton were collected, were utilized.

In this paper, data associated with the 20 phytoplankton genera that most frequently accounted for at least 10 percent of the total cell count of samples (dominant occurrence) are used. These data are compared with those from corresponding samples in which the specific genera were not detected at all (nonoccurrence). For example, temperature data associated with the dominant occurrence of *Aphanizomenon* represent seasonal or annual means for those lakes or reservoirs from which samples were taken that showed the genus at a level of 10 percent or more of the total numerical cell count. Nonoccurrence data represent the seasonal or annual means from lakes and reservoirs from which samples contained no detectable levels of *Aphanizomenon*.

RESULTS AND DISCUSSION

A list of the 20 phytoplankton genera that appeared most frequently as dominants is given in Table 2. Most of the genera (15) are either blue-green algae (Myxophyceae) or diatoms (Bacillariophyceae). *Melosira* was by far the most common genus. The number of dominant occurrences of the two flagellates *(Chroomonas* and *Cryptomonas)* was underestimated because of their small size and problems associated with identification of preserved material.

Diatoms dominated equally throughout the three seasons (Table 2). The only important exception was *Asterionella,* which was more frequently dominant in spring. The blue-green genera, as expected, were most important in summer and fall. However, they were not restricted to those seasons. Averaged for 1973-75, 11 percent of blue-green dominant occurrences were during the spring. The cryptomonad flagellates *(Cryptomonas, Chroomonas)* occurred equally through the seasons while the chrysophytan flagellate *(Dinobryon)* was dominant in spring samples 50 percent of the time. The two chlorophytan genera *(Scenedesmus, Ankistrodesmus)* differed in their dominant occurrence patterns. *Scenedesmus* occurred equally through the seasons, while *Ankistrodesmus* occurred 60 percent of the time in spring samples.

Seasonal mean temperature values for dominant occurrence and non-occurrence of the 20 most common dominant phytoplankton genera are given in Table 3. The genera are organized by major algal groups (e.g., diatoms, blue-greens, etc.).

Trends for genera within both the blue-green algal group and the diatom group were similar enough that mean temperature values (weighted by the frequency of dominant occurrence of each representative genus) were calculated for each group to show group trends (Figures 1 and 2,

Table 2. Phytoplankton genera most commonly occurring as numerical dominants in U.S. lakes and reservoirs and their seasonal distribution.

Genus	Number of Dominant Occurrences	Percent of the Dominant Occurrences of a Genus (rounded)		
		Spring	Summer	Fall
* *Melosira*	480	34	31	35
Chroomonas	369	37	31	32
Cryptomonas	305	36	30	34
** *Oscillatoria*	197	17	46	37
* *Stephanodiscus*	191	43	30	27
** *Aphanizomenon*	185	5	45	49
* *Fragilaria*	162	24	44	31
* *Cyclotella*	155	30	38	32
** *Dactylococcopsis*	129	20	32	48
** *Lyngbya*	129	12	56	32
* *Asterionella*	115	57	26	17
* *Nitzschia*	99	29	38	32
** *Microcystis*	98	9	44	47
* *Synedra*	96	46	41	14
Scenedesmus	83	30	35	36
Dinobryon	76	50	26	24
** *Anabaena*	72	10	56	35
** *Merismopedia*	62	14	42	44
** *Raphidiopsis*	61	5	62	33
Ankistrodesmus	55	60	20	20

*Diatom

**Blue-green algae

Table 3. Seasonal mean temperature (°C) values for dominant occurrence and nonoccurrence of the 20 most common dominant phytoplankton genera. (The number of observations upon which the means are based is in parentheses.)

Algae Group	Dominant Occurrence				Nonoccurrence			
	Spring	Summer	Fall	Annual	Spring	Summer	Fall	Annual
Blue-greens								
Anabaena	21.1 (7)	22.5 (40)	18.4 (25)	20.9 (72)	12.6 (376)	23.5 (262)	17.6 (301)	17.2 (939)
Aphanizomenon	17.6 (10)	22.1 (84)	15.8 (91)	18.7 (185)	13.7 (441)	24.5 (379)	18.7 (351)	18.7 (1171)
Dactylococcopsis	16.2 (26)	27.5 (41)	20.0 (62)	21.6 (129)	12.9 (327)	23.2 (447)	16.9 (362)	18.2 (1136)
Lyngbya	23.0 (15)	27.6 (72)	21.0 (42)	24.9 (129)	13.1 (411)	22.9 (420)	17.0 (400)	17.7 (1231)
Merismopedia	19.4 (9)	26.2 (26)	18.2 (27)	21.7 (62)	12.6 (408)	22.3 (340)	16.7 (340)	16.9 (1088)
Microcystis	19.1 (9)	24.7 (43)	18.6 (46)	21.3 (98)	13.1 (388)	22.8 (297)	17.2 (294)	17.3 (979)
Oscillatoria	15.6 (34)	26.1 (90)	19.0 (73)	21.7 (197)	12.5 (273)	22.7 (312)	17.0 (272)	17.6 (857)
Raphidiopsis	22.3 (3)	26.8 (38)	22.0 (20)	25.0 (61)	13.5 (462)	23.4 (490)	17.4 (475)	18.2 (1427)
Diatoms								
Asterionella	11.0 (66)	18.7 (30)	13.9 (19)	13.5 (115)	15.2 (244)	25.2 (443)	18.4 (451)	20.4 (1138)
Cyclotella	13.8 (46)	24.9 (59)	18.5 (50)	19.6 (155)	12.5 (278)	23.1 (331)	17.2 (324)	17.9 (933)
Fragilaria	11.3 (39)	21.8 (72)	15.5 (51)	17.3 (162)	15.2 (297)	25.1 (385)	18.8 (365)	20.1 (1047)
Melosira	15.1 (162)	24.7 (148)	18.2 (170)	19.2 (480)	12.2 (127)	22.7 (170)	16.7 (130)	17.7 (427)
Nitzschia	13.1 (29)	25.1 (38)	18.3 (32)	19.4 (99)	13.4 (203)	23.0 (325)	17.5 (299)	18.7 (827)
Stephanodiscus	12.0 (82)	24.3 (58)	16.3 (51)	16.9 (191)	15.1 (237)	24.4 (357)	18.3 (314)	19.8 (908)
Synedra	12.9 (44)	23.4 (39)	18.6 (13)	17.9 (96)	13.2 (174)	23.4 (321)	17.5 (299)	18.9 (794)
Greens								
Ankistrodesmus	12.8 (33)	23.5 (11)	16.3 (11)	15.6 (55)	13.8 (253)	23.6 (380)	17.7 (360)	18.9 (993)
Scenedesmus	19.2 (24)	26.5 (29)	20.1 (30)	22.1 (83)	11.6 (205)	21.4 (211)	15.5 (191)	16.3 (607)
Cryptomonads								
Chroomonas	11.5 (136)	21.7 (116)	15.4 (117)	15.9 (369)	15.8 (284)	25.4 (370)	19.3 (353)	20.6 (1007)
Cryptomonas	13.3 (110)	23.3 (92)	16.3 (103)	17.3 (305)	15.0 (84)	25.0 (170)	20.0 (163)	21.0 (417)
Chrysophytan flagellate								
Dinobryon	11.9 (38)	20.0 (20)	16.6 (18)	15.2 (76)	13.8 (318)	24.4 (454)	18.0 (435)	19.3 (1207)

respectively). In Figure 1, the blue-green algae can be seen to dominate in waters of higher temperature during each season. The greatest difference between mean values for dominant occurrence and nonoccurrence was in the spring, when nearly 4.5°C separated the two categories. The relatively low frequency of occurrence of blue-greens as dominants in the springtime may be related to the lower water temperatures, but the possible effects of light limitation should not be overlooked.

The diatoms are similarly summarized in Figure 2. The temperature observed for dominant occurrence is only slightly lower than the temperature observed for nonoccurrence. *Asterionella* was the only diatom genus that deviated drastically from the general relationship. It dominated in much colder waters, particularly in summer and fall. Since light attenuation (by other than phytoplankton) would be less likely a problem in summer and early fall than in spring, temperature may be a significant factor for the relative success of this genus.

Seasonal temperature data associated with the occurrence of the two green algae are presented in Figure 3. There is about a 6°C difference between the dominant occurrence and nonoccurrence values for *Scenedesmus* for each of the seasons. This is the highest temperature difference observed for the 20 genera under discussion. *Asterionella* had a similarly wide temperature spread but dominated in cooler water, while *Scenedesmus* dominated in much warmer water.

The trend for *Ankistrodesmus* was opposite that of *Scenedesmus*, i.e., dominant occurrence was associated with lower water temperatures than those of water bodies where it did not occur (Figure 3).

Waters in which *Cryptomonas* and *Chroomonas* exhibited dominant occurrence were cooler than those in which they were not found (Figure 4). *Dinobryon*, another flagellated genus, showed a similar preference

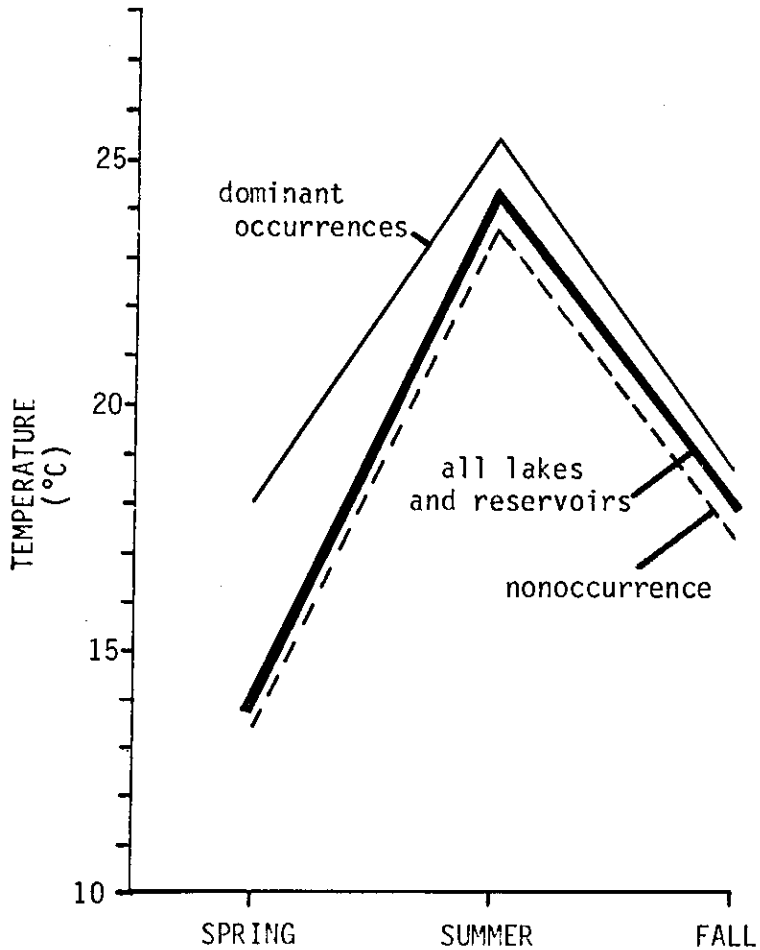

FIGURE 1. Mean seasonal temperature values associated with dominant occurrence and nonoccurrence of blue-green algae.

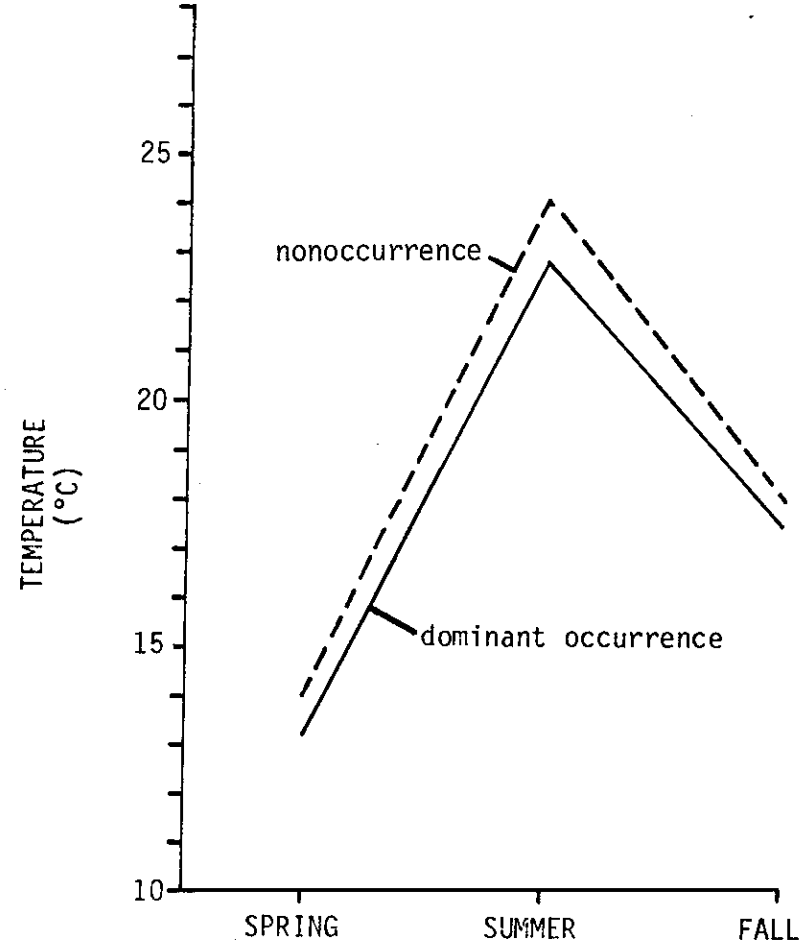

FIGURE 2. Mean seasonal temperature values associated with dominant occurrence and nonoccurrence of diatoms.

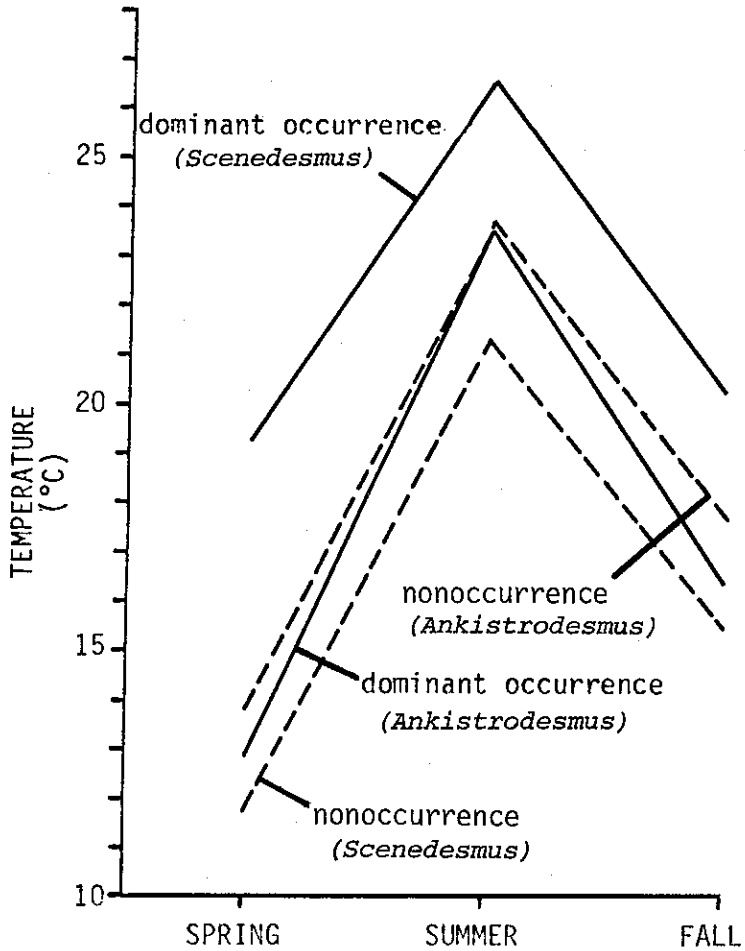

FIGURE 3. Mean seasonal temperature values associated with dominant occurrence and nonoccurrence of *Scenedesmus* and *Ankistrodesmus*.

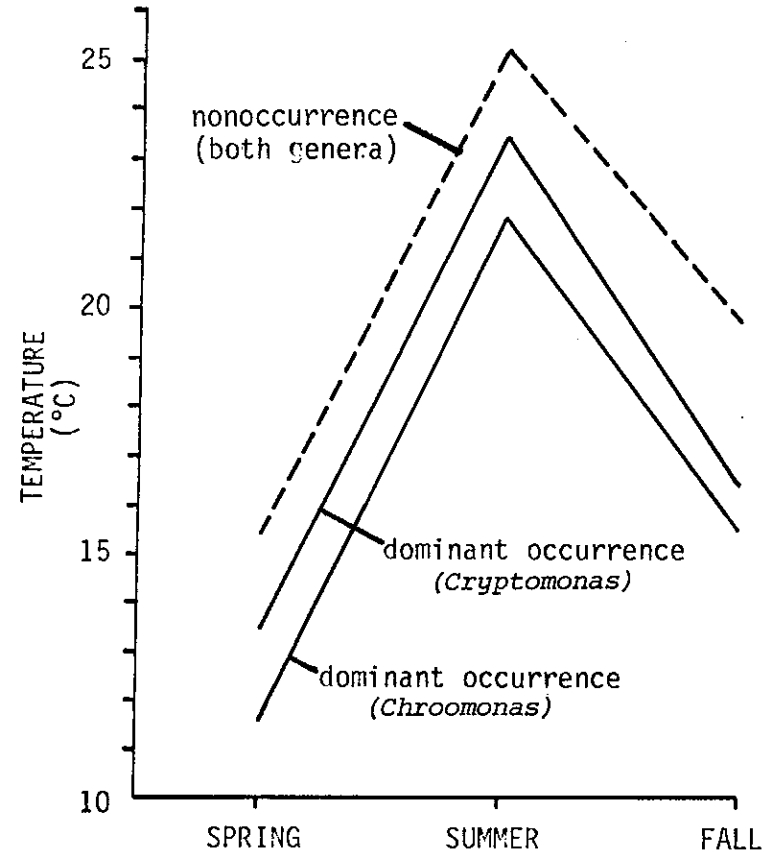

FIGURE 4. Mean temperature values associated with dominant occurrence and nonoccurrence of *Cryptomonas* and *Chroomonas*.

for cooler water as a dominant (Figure 5).

Most of the temperature data illustrated in Figures 1-5 show about a 10°C change between spring and summer dominant occurrences. This difference is greater than the within-season temperature spread between dominant occurrence and nonoccurrence for any of the genera discussed. Obviously these genera are adaptable to wide ranges in water temperatures.

To further illustrate this point, the seasonal temperature range and 95 percent confidence intervals for *Lyngbya* and *Asterionella* are shown in Figure 6. Differences between the mean temperature values for these two genera were greater than for any other pair. Obviously the range of values for each genus was very large, and the ranges overlapped one another for each of the seasons. This phenomenon cannot entirely be explained by the "genus" level approach taken in this paper. Most of the data on *Asterionella* are for a single species, *A. formosa,* and yet the genus exhibited dominant occurrence with about a 14°C temperature spread in each of the seasons. The mean temperatures associated with the dominant occurrence of the two genera were significantly different during each season. Whether the difference in distribution is truly a function of temperature rather than a consequence of complex temperature-related or other manifestations cannot be determined from the data. Temperature values for each genus closely paralleled the seasonal temperature regime of the entire group of lakes and reservoirs sampled, even though some genera showed considerably higher or lower temperature means than others.

Temperature, per se, appears to limit few of the genera studied, although particular temperature ranges may confer a greater or lesser opportunity for genus to compete successfully in the phytoplankton community. The inability, in most cases, to clearly discriminate

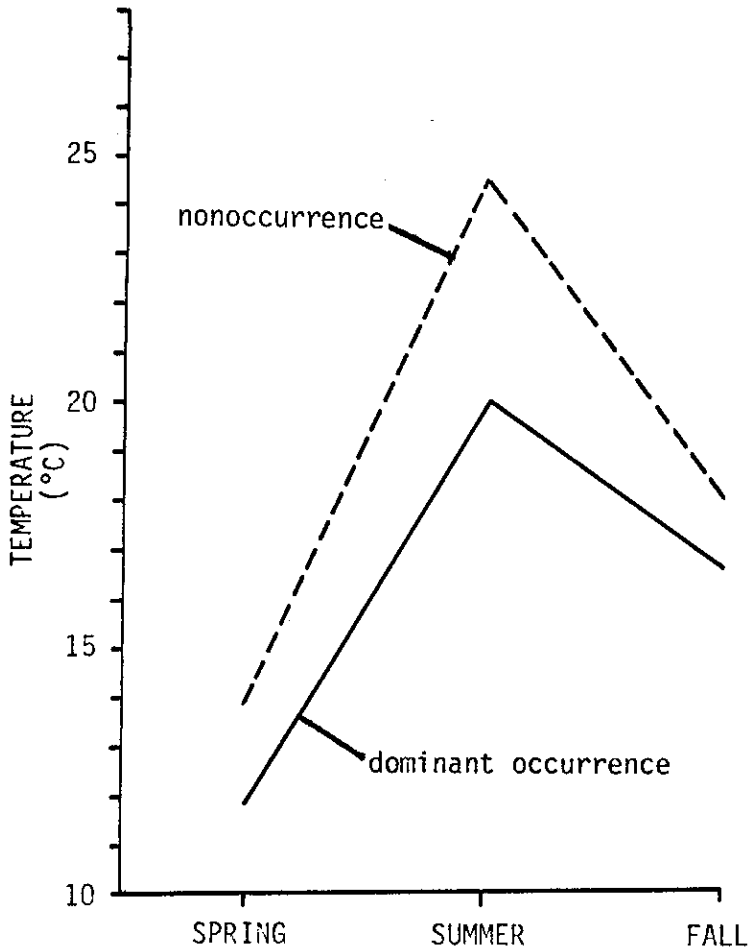

FIGURE 5. Mean temperature values associated with dominant occurrence and nonoccurrence of *Dinobryon*.

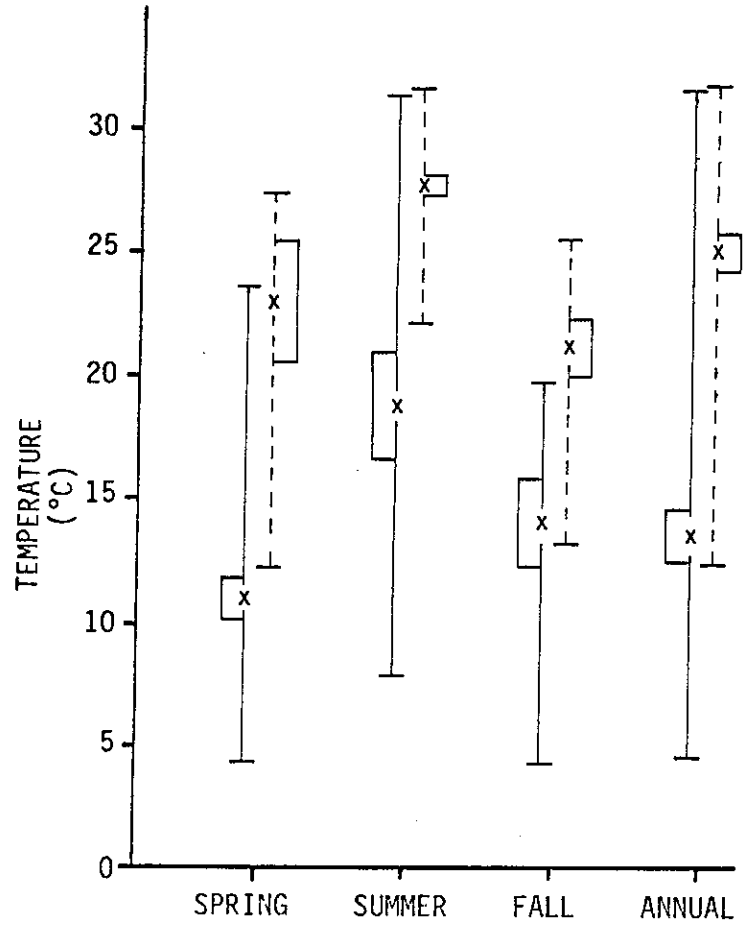

FIGURE 6. Mean, range, and 95 percent confidence intervals for mean temperature values associated with dominant occurrence of *Asterionella* (solid line) and *Lyngbya* (dashed line).

between those conditions which will support various components of the phytoplankton community makes it difficult to make definitive statements about the effect of the temperature conditions on the basis of the mere occurrence, or even the dominance, of a single genus. However, temperature differences do exist, and an approach which takes into account the cumulative probabilities of each major component of the community to succeed under a given set of environmental conditions should prove to have predictive value.

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RELATIONSHIP OF COMMON PHYTOPLANKTON GENERA TO NUTRIENTS IN EASTERN AND SOUTHEASTERN LAKES

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INTRODUCTION

During the spring, summer, and fall of 1973, 250 lakes were sampled in 17 eastern and southeastern states. Approximately 180 genera and over 700 phytoplankton species and varieties were observed in 692 water samples, resulting in nearly 25,000 phytoplankton occurrence records. The purpose of this paper is to describe the relationship between the occurrence of the common phytoplankton genera observed and nutrient levels in the lakes.

MATERIALS AND METHODS

Lake Sampling

Lakes were sampled as part of the U.S. Environmental Protection Agency's (EPA) National Eutrophication Survey. Lakes and reservoirs included in the survey were selected through discussion with State water pollution agency personnel and U.S. Environmental Protection Agency Regional Offices (U.S. EPA 1975). Details of the lake sampling and quality assurance methods are presented elsewhere (U.S. EPA 1975; Taylor *et al*. 1978).

Sampling was accomplished by two teams, each consisting of a limnologist, pilot, and sampling technician, operating from poontoon-equipped helicopters. With few exceptions, each lake was sampled under spring (Round 1), summer (Round 2), and fall (Round 3) conditions. Sampling for Rounds 1, 2, and 3 took place between March 7 and July 1, July 5 and September 18, and September 19 and November 14, respectively. Sampling locations were chosen to define the character of the lake water as a whole and to investigate visible or known problem areas, e.g., algal blooms, and sediment or effluent plumes. The number of sampling stations was limited by the survey nature of the program and varied in accordance with lake size, morphological and

hydrological complexity, and practical considerations of time, flight range, and weather. At each station, appropriate sampling depths were selected by the limnologist. At each sampling depth, two water samples were collected for nutrient determinations.

At each sampling station, a depth-integrated phytoplankton sample was taken. These samples were uniform mixtures of water from the surface to a depth of 4.6 meters (15 feet) or from the surface to the lower limit of the photic zone, whichever was greater. The lower limit of the photic zone was defined as the depth at which 1 percent of the surface incident light could be measured. If the depth at the sampling station was less than 4.6 meters (m), the sample was taken from just off the bottom to the surface.

Nutrient and Phytoplankton Analysis

Nutrient analyses were made on the water samples for total phosphorus (total P), dissolved orthophosphorus (ortho P), ammonia nitrogen (NH_3), nitrite-nitrate nitrogen (NO_2 + NO_3), and total Kjeldahl nitrogen (KJEL). All of the analyses were performed utilizing adaptions of automated procedures described by Mullins *et al*. (1975). Further details are given by U.S. EPA (1975) and Taylor *et al*. (1978).

Four milliliters (ml) of Acid-Lugol's preservative solution (Prescott 1970) was added to each site-specific 130-ml phytoplankton sample at the time of collection. The samples were shipped to our laboratory in Nevada, where equal volumes for each station were mixed to form two 130-ml composite samples for a given lake and sampling round. One composite sample was placed in storage; the other was used for the examination.

Prior to examination, the composite samples were concentrated by allowing the solids to settle for at least 24 hours and drawing off the supernate. Final concentration varied from 15 to 40 times the

original, depending upon the density of the phytoplankton in the sample. Wet mounts and heat-treated Hyrax-mounted diatom slides were prepared for species identification.

The phytoplankton samples were examined with the aid of binocular compound miscroscopes. A preliminary examination was performed to identify and list the forms encountered. The duration of this examination varied depending on the complexity of the sample. An attempt was made to find and identify all of the forms present in each sample. Diatom slides were examined with a standard light microscope. When greater resolution was essential to accurately identify the diatoms, a phase-contrast microscope was used.

After the species list was compiled, phytoplankton were enumerated at 400X magnification (40X objective lens) using a Neubauer Counting Chamber. All forms within each field were counted. The count was continued until a minimum of 100 fields had been viewed, or until the most numerous form had been observed a minimum of 100 times. Counts were reported in algal units (cells, filaments, or colonies) per ml.

Further details on both nutrient and phytoplankton analyses, as well as quality assurance procedures, are given by U.S. EPA (1975), Taylor *et al*. (1978), and Taylor *et al*. (1977).

Data Storage and Manipulation

The nutrient data collected were entered into STORET (STOrage and RETrieval), the U.S. EPA computer system by which water quality data are processed and maintained. Phytoplankton data (species lists and differential counts) were stored on disc packs accessible through ALPHA, a text editor. Data manipulation was as described by Bliss *et al*. (1976).

In this paper, only nutrient data collected from the photic zone were utilized so as to eliminate the extreme conditions found at greater depths, which have little or no short-term effects on the phytoplankton community structure. Nutrient data were manipulated to provide equivalent weight to each depth samples at a station and to each sampling station on an individual lake during a sampling round.

Mean parameter values for each sampling station were calculated as follows (Lambou et al. 1976):

$$\overline{Par}_j = \sum_{i=1}^{D} Par_i/D \qquad (1)$$

where $\overline{Par}_j$ = mean value for a parameter at the jth sampling station during a sampling round (lake-date)

Par_i = value for the ith depth

D = number of depths for which a parameter was measured at the jth sampling station during a sampling round

Mean parameter values for each sampling round on a given lake were calculated as follows:

$$\overline{Par}_k = \sum_{j=1}^{S} \overline{Par}_j/S \qquad (2)$$

where $\overline{Par}_k$ = mean value for the kth sampling round on a given lake

S = number of sampling sites

Equations 1 and 2 were used to determine mean parameter values for total P, ortho P, NH_3, $NO_2 + NO_3$, inorganic nitrogen ($NO_2 + NO_3 + NH_3$ = IN), and KJEL, all expressed in micrograms per liter (μg/ℓ). The ratio of

inorganic nitrogen to total phosphorus (N/P) for each sampling station was calculated as follows:

$$\overline{N/P} = \overline{IN}/\overline{total\ P} \qquad (3)$$

However, at the Equation 1 level, a total phosphorus value was deleted if either nitrogen complement was missing. Values for each round were calculated using Equation 2.

During any given round [Round 1 (spring); Round 2 (summer); and Round 3 (fall)], phytoplankton samples from stations within a lake were composited in such a way as to give each station equal weight. After examination the resulting data were placed in computer storage. The phytoplankton data were then aggregated into genera-based files and the percent composition of each genus was determined from its concentration relative to the total cell count in the sample. The genera were sorted to determine the combination of lake and date in which a specific genus attained 10 percent or more of the total numerical cell count (dominant occurrence); was detected at levels below 10 percent (nondominant occurrence); was detected, without respect to level (occurrence); or was not detected at all (nonoccurrence). Table 1 provides criteria for each occurrence category.

The nutrient and phytoplankton data were interfaced by computer techniques as described by Taylor et al. (1978).

Table 1. Genus occurrence categories and definitions.

Occurrence Category	Definition
OCC (occurrence)	Genus was detected in each lake-date sample represented in this category.
NONOCC (nonoccurrence)	Genus was not detected in any of the lake-date samples represented in this category.
DOM (dominant occurrence)	Genus constituted 10 percent or more of the numerical total cell concentration of each lake-date sample in this category.

Table 1 (continued)

Occurrence Category	Definitions
NONDOM (non-dominant occurrence)	Genus constituted less than 10 percent of the numerical total cell concentration of each lake-date sample in this category.

COMMON PHYTOPLANKTON GENERA

Fifty-seven genera were designated as "common," based on their occurrence in at least 10 percent of the 692 samples. An alphabetical listing of the 57 genera, including the number of samples within which each occurred, organized by season (spring, summer, fall, and annual) and occurrence category, is given in Table 2.

Melosira was the most common genus encountered in the lakes sampled (Table 2). Other genera of importance, in descending order of total sample occurrences, were *Scenedesmus, Synedra, Cyclotella, Oscillatoria, Euglena, Cryptomonas, Navicula, Nitzschia, Anabaena, and Microcystis*. All occurred in 50 percent or more of the samples examined. *Pediastrum, Merismopedia, Tetraedron, Coelastrum, Dactylococcopsis,* and *Lyngbya* occurred in 40 to 50 percent of the samples examined.

The number of samples in which a genus is detected is not necessarily an indication of its ability to attain community dominance. While *Melosira* occurred more frequently than any other genus both as a dominant and nondominant, *Scenedesmus*, the most frequently encountered genus, attained dominance in only 9 percent of the samples in which it occurred. Several other genera *(Euglena, Navicula, Pediastrum, Tetraedron,* and *Coelastrum)* are of special interest because they occurred in more than 40 percent of the samples ($\geq$ 277/692), but were dominant in less than 2 percent of the samples. *Pediastrum* never occurred as a numerical dominant.

Table 2. The number of lake-date composite samples in which a common genus occurred as a dominant (DOM), nondominant (NONDOM), and irrespective of dominance (OCC) during three sampling seasons and cumulatively (annual) (A ranking (OCC rank) of the genera by OCC, highest to lowest, is presented for each seasonal grouping.)

	Spring (202 samples)				Summer (243 samples)				Fall (247 samples)				Annual (692 samples)			
Genus	DOM	NON DOM	OCC	OCC Rank	DOM	NON DOM	OCC	OCC Rank	DOM	NON DOM	OCC	OCC Rank	DOM	NON DOM	OCC	OCC Rank
Achnanthes	0	41	41	31	5	44	49	40	1	53	54	38	6	138	144	40
Actinastrum	2	26	28	47	0	29	29	51	0	38	38	46	2	93	95	47
Anabaena	5	62	67	17	14	133	147	8	14	128	142	7	33	323	356	10
Anabaenopsis	2	8	10	56	4	36	40	46	1	32	33	49	7	76	83	51
Ankistrodesmus	5	71	76	14	1	84	85	24	3	91	94	24	9	246	255	20
Aphanizomenon	7	19	26	48	19	45	64	34	15	49	64	34	41	113	154	38
Asterionella	27	87	114	9	6	38	44	43	2	38	40	42	35	163	198	28
Ceratium	0	16	16	52	0	77	77	28	2	63	65	33	2	156	158	37
Chlamydomonas	0	33	33	42	2	44	46	41	2	59	61	36	4	136	140	41
Chlorogonium	0	11	11	53	0	29	29	52	0	36	36	48	0	76	76	55
Chroococcus	0	30	30	45	7	67	74	31	12	63	75	28	19	160	179	32
Closterium	1	44	45	28	1	90	91	22	2	100	102	20	4	234	238	23
Cocconeis	0	45	45	29	0	39	39	47	0	31	31	53	0	115	115	45
Coelastrum	0	47	47	26	5	118	123	14	1	116	117	16	6	281	287	15
Coelosphaerium	0	11	11	54	2	32	34	49	4	35	39	45	6	78	84	52
Cosmarium	1	34	35	40	1	103	104	18	1	96	97	22	3	233	236	24
Crucigenia	1	38	39	35	0	104	104	19	1	98	99	21	2	240	242	22
Cryptomonas	36	100	136	4	16	112	128	12	19	110	129	13	71	322	393	7
Cyclotella	18	105	123	6	38	130	168	3	27	123	150	5	83	358	441	4
Cymbella	0	77	77	13	0	42	42	44	0	51	51	39	0	170	170	33
Dactylococcopsis	7	69	76	15	20	72	92	21	31	88	119	15	58	229	287	16
Dictyosphaerium	0	41	41	32	1	66	67	33	0	77	77	26	1	184	185	29
Dinobryon	15	71	86	12	7	53	60	35	9	66	75	28	31	190	221	26
Euastrum	0	11	11	55	0	26	26	54	0	40	40	43	0	77	77	56
Euglena	3	103	106	10	2	142	144	9	3	155	158	3	8	400	408	6
Fragilaria	15	61	76	16	16	61	77	29	14	48	62	35	45	170	215	27
Glenodinium	0	33	33	43	3	43	46	42	1	31	32	51	4	107	111	46
Golenkinia	2	20	22	50	0	59	59	36	0	45	45	40	2	124	126	42
Gomphonema	0	38	38	36	1	18	19	57	0	20	20	57	1	76	77	57
Gymnodinium	2	34	36	38	0	22	22	55	0	29	29	55	2	85	87	50
Gyrosigma	0	30	30	46	0	28	28	53	0	22	22	56	0	79	80	54
Kirchneriella	1	31	32	44	2	54	56	37	5	70	75	29	8	155	163	34
Lagerheimia	0	21	21	51	0	31	31	50	0	32	32	52	0	84	84	53
Lyngbya	15	39	54	21	49	70	119	15	35	78	113	17	99	187	286	17
Mallomonas	2	49	51	23	1	51	52	38	3	56	59	37	6	156	162	36
Melosira	92	87	179	1	74	132	206	1	89	133	222	1	255	352	607	1

Table 2 (continued)

Genus	Spring (202 samples)				Summer (243 samples)				Fall (247 samples)				Annual (692 samples)			
	DOM	NON DOM	OCC	OCC Rank	DOM	NON DOM	OCC	OCC Rank	DOM	NON DOM	OCC	OCC Rank	DOM	NON DOM	OCC	OCC Rank
Merismopedia	1	46	47	27	10	138	148	6	11	122	133	12	22	306	328	13
Microcystis	6	43	49	24	22	126	148	7	25	124	149	6	53	293	346	11
Navicula	3	134	137	3	2	115	117	16	1	136	137	10	6	385	391	8
Nitzschia	4	119	123	7	11	117	128	13	13	108	121	14	28	344	372	9
Oocystis	2	38	40	34	2	71	73	32	1	68	69	31	5	177	182	35
Oscillatoria	21	99	120	8	51	103	154	5	33	121	154	4	105	323	428	5
Pandorina	0	38	38	37	0	41	41	45	0	37	37	47	0	116	116	44
Pediastrum	0	61	61	19	0	130	130	11	0	142	142	8	0	333	333	12
Peridinium	2	34	36	39	3	75	78	26	1	39	40	44	6	148	154	39
Phacus	0	44	44	30	0	98	98	20	2	109	111	18	2	251	253	21
Raphidiopsis	2	24	26	49	25	53	78	27	18	55	73	30	45	132	177	30
Scenedesmus	12	124	136	5	17	186	203	2	21	193	214	2	50	503	553	2
Schroederia	1	33	34	41	1	75	76	30	0	69	69	32	2	177	179	33
Staurastrum	0	52	52	22	0	108	108	17	1	110	111	19	1	270	271	19
Stephanodiscus	30	66	96	11	26	56	82	25	17	80	97	23	73	202	275	18
Surirella	0	48	48	25	0	20	20	56	0	31	31	54	0	99	99	48
Synedra	18	137	155	2	22	143	165	4	8	134	142	9	48	414	462	3
Tabellaria	7	34	41	33	10	28	38	48	3	40	43	41	20	102	122	43
Tetraedron	1	56	57	20	1	130	131	10	3	133	136	11	5	319	324	14
Trachelomonas	2	60	62	18	2	84	86	23	0	80	80	25	4	224	228	25
Treubaria	0	10	10	57	0	51	51	39	0	33	33	50	0	94	94	49

All 57 genera occurred during each season. In fact, many of the genera exhibited dominant occurrence in all three of the seasons. Only five genera *(Asterionella, Gomphonema, Surirella, Cymbella,* and *Gymnodinium)* had at least 40 percent of their occurrences in spring samples. This was in sharp contrast with summer and fall samples where 21 and 25 genera, respectively, had at least 40 percent of their occurrences.

Asterionella and *Radhidiopsis* are the only forms, among those showing strong seasonal preferences in their general occurrence, which frequently exhibited dominant occurrence. Seventy-seven percent of the *Asterionella* dominant occurrences were in spring samples. By comparison, *Oscillatoria* did not show strong seasonal preference in general occurrence, but as a dominant was an important summer form. Similarly, the preference of *Dinobryon* for spring conditions was only apparent in data from its dominant occurrence.

Flagellates and diatoms were the most common springtime plankton genera while blue-green and chlorococcalean genera were most common in the summer and fall. Diatoms were quite important in all three seasons.

NUTRIENT REQUIREMENTS

Most genera were found to occur over an extremely wide range of nutrient conditions. To illustrate this point, range diagrams for the respective occurrence categories of each genus have been prepared for the following parameters: total P, Kjeldahl nitrogen, and N/P ratio (Appendix A, Figures A-1 through A-3). Direct comparisons of the ranges of conditions in which a genus occurred or attained dominant occurrence with those conditions under which it was not detected at all clearly demonstrate the breadth of both the conditions favorable to the phytoplankton genera and the overlap of conditions supporting widely dissimilar genera. In many cases, the ranges of conditions

supporting a given genus were no different from those under which that genus was not detected. The same patterns were found for the other nutrient species. The range of ortho P, $NO_2 + NO_3$, and NH_3 values associated with dominant occurrence, nondominant occurrence, and occurrence of *Anabaena*, *Cryptomonas*, and *Dinobryon* is presented in Table 3 to illustrate this pattern.

Table 3. Range of ortho P, $NO_2 + NO_3$, and NH_3 values within three occurrence categories for three genera

Parameter	Category		*Anabaena*	*Cryptomonas*	*Dinobryon*
	Occur.	Range			
Ortho P (μg/liter)	DOM	MIN	2	2	1
		MAX	2009	851	85
	NONDOM	MIN	1	1	1
		MAX	1189	1189	555
	OCC	MIN	1	1	1
		MAX	2009	1189	555
$NO_2 + NO_3$ (μg/liter)	DOM	MIN	20	21	19
		MAX	3429	9745	989
	NONDOM	MIN	17	17	17
		MAX	9745	7557	7557
	OCC	MIN	17	17	17
		MAX	9745	9745	7557
NH_3 (μg/liter)	DOM	MIN	35	31	31
		MAX	3024	532	164
	NONDOM	MIN	30	20	22
		MAX	569	979	979
	OCC	MIN	30	20	22
		MAX	3024	979	979

To illustrate the nutrient range overlap typically encountered when making comparisons between genera, the two genera associated with the largest and smallest mean total phosphorus values were

examined. *Actinastrum* had the highest mean total P (287 μg/ℓ) associated with its distribution, while *Tabellaria* was associated with the lowest mean total P (42 μg/ℓ) of the 57 genera considered in this report (Figure A-1). Even though they represent the extremes in mean total phosphorus, enough overlap occurred in their ranges to substantially reduce their usefulness as general indicators of either high total phosphorus in the case of *Actinastrum* or low total phosphorus in the case of *Tabellaria*.

Considering only the genera exhibiting dominant occurrence in more than 10 samples, *Scenedesmus* and *Tabellaria* were associated with the largest and smallest total P values, 351 and 22 μg/ℓ, respectively (Figure A-1). One might expect ranges to narrow appreciably, since dominant occurrence presumably requires near-optimal conditions for growth and reproduction. What was found, however, is that the range of total P values for the two genera overlapped. Although the upper end of the *Tabellaria* range was well below the mean value of *Scenedesmus*, the entire range of *Tabellaria* was encompassed by the range of *Scenedesmus*.

A number of genera appear to have a narrow range of total P values associated with dominant occurrence (e.g., *Achnanthes, Actinastrum,* and *Gymnodinium)*. The narrow ranges may have resulted from the small number of dominant occurrences recorded rather than truly restrictive requirements. If an organism has such unique requirements, or is able to outcompete other organisms only under very unusual conditions, it will generally be quite rare in the "normal" range of lake conditions and therefore relatively useless in classifying most lake waters.

It is desirable to identify trends in nutrient conditions associated with specific genera and to provide means for comparative analysis among genera. To accomplish this, a series of tables was constructed which ranks the 57 genera by mean nutrient parameter values

(Tables 4 and 5). The first column in Table 4 presents, in rank order, the total number of occurrences of each of the genera. There were a total of 692 sample possibilities in which each genus could have occurred. In subsequent columns the genera are ranked by their mean values on a parameter-by-parameter basis.

The seven genera associated with levels of total P greater than 200 μg/ℓ (see Table 4) were tracked through the other rankings. Similarly, five genera associated with levels of total P less than 700 μg/ℓ were tracked. These two groups will be referred to as the nutrient-rich and nutrient-poor groups, respectively. The final group, specifically tracked through the various rankings of mean parameter values, is comprised of the blue-green algae.

The nutrient-rich group consists of four chlorococcaleans (Chlorophyta), one green flagellate (Chlorophyta), and two filamentous blue-green (Cyanophyta) genera. While *Lagerheimia* has about 10 species reported in the United States, the other genera have very few species and not all of these were detected in the samples. Therefore, data trends suggested at the genus level oftentimes may be attributed to the influence of only one or two species. All seven genera were summer and fall forms, while *Actinastrum* and *Lagerheimia* also occurred equally in spring.

There was a strong tendency for the nutrient-rich group to cluster at or near the top of the nutrient parameter lists. The outstanding exception was with nitrite-nitrate nitrogen (NO_2 + NO_3) where the genera were scattered from top to bottom. Lake NO_2 + NO_3 concentrations were found to be considerably higher in spring than in summer or fall. This may explain the scatter of the nutrient-rich group in this parameter since they were primarily summer and fall forms.

The nutrient-poor group consisted of *Asterionella, Dinobryon, Tabellaria, Peridinium,* and *Ceratium*. *Asterionella* was the only genus which occurred primarily in spring. The two dinoflagellates, *Peridinium*

Table 4. Phytoplankton genera ranked by frequency of occurrence and associated mean nutrient values.

Genus	Frequency of Occurrence	Genus	Total P (µg/l)	Genus	Ortho P (µg/l)
Melosira	607	*Actinastrum	287	*Actinastrum	149
Scenedesmus	553	*Chlorogonium	271	*Chlorogonium	147
Synedra	462	*Golenkinia	245	*Golenkinia	142
Cyclotella	441	*Lagerheimia	243	*Lagerheimia	126
‡Oscillatoria	428	*‡Anabaenopsis	238	*Schroederia	115
Euglena	408	*Schroederia	227	*‡Anabaenopsis	114
Cryptomonas	393	*‡Raphidiopsis	212	*‡Raphidiopsis	109
Navicula	391	Chlamydomonas	199	‡Chroococcus	107
Nitzschia	374	Dictyosphaerium	197	Chlamydomonas	105
‡Anabaena	356	Phacus	192	Dictyosphaerium	105
‡Microcystis	346	‡Chroococcus	191	Kirchneriella	94
Pediastrum	333	Kirchneriella	184	‡Merismopedia	87
‡Merismopedia	328	‡Merismopedia	176	‡Dactylococcopsis	87
Tetraedron	324	‡Microcystis	167	‡Microcystis	83
Coelastrum	287	Pediastrum	166	Tetraedron	81
‡Dactylococcopsis	287	Tetraedron	165	Pediastrum	80
‡Lyngbya	286	‡Dactylococcopsis	164	Phacus	79
Stephanodiscus	275	Closterium	156	Closterium	71
Staurastrum	271	Euglena	153	Pandorina	70
Ankistrodesmus	255	Treubaria	146	Treubaria	64
Phacus	253	Coelastrum	142	Euglena	63
Crucigenia	242	Pandorina	138	Scenedesmus	63
Closterium	238	Scenedesmus	135	Coelastrum	63
Cosmarium	236	Surirella	135	‡Oscillatoria	62
Trachelomonas	228	‡Oscillatoria	135	Cyclotella	60
†Dinobryon	221	Crucigenia	133	‡Anabaena	58
Fragilaria	215	Ankistrodesmus	129	Surirella	57
†Asterionella	198	Oocystis	129	Crucigenia	57
Dictyosphaerium	185	‡Ababaena	127	Ankistrodesmus	56
Oocystis	182	Cyclotella	126	Cosmarium	53
‡Chroococcus	179	Stephanodiscus	126	Oocystis	52
*Schroederia	179	Cosmarium	125	‡Lyngbya	50
*‡Raphidiopsis	177	Trachelomonas	118	Stephanodiscus	49
Cymbella	170	Cryptomonas	116	Cocconeis	49
Kirchneriella	163	Nitzschia	116	Cryptomonas	48
Mallomonas	162	Glenodinium	113	Nitzschia	47
†Ceratium	158	Cocconeis	112	Melosira	45
‡Aphanizomenon	154	‡Lyngbya	110	Glenodinium	43
†Peridinium	154	Melosira	109	Euastrum	41
Achnanthes	144	‡Aphanizomenon	103	Trachelomonas	41
Chlamydomonas	140	Gymnodinium	101	‡Coelosphaerium	40
*Golenkinia	126	Synedra	98	‡Aphanizomenon	38
†Tabellaria	122	Gyrosigma	95	Staurastrum	35
Pandorina	116	Navicula	94	Navicula	34
Cocconeis	115	‡Coelosphaerium	93	Cymbella	34
Glenodinium	111	Staurastrum	91	Synedra	34
Surirella	99	Cymbella	91	Fragilaria	31
*Actinastrum	95	Gomphonema	91	Gyrosigma	30
Treubaria	94	Euastrum	89	Achnanthes	29
Gymnodinium	87	Mallomonas	85	Mallomonas	29
‡Coelosphaerium	84	Fragilaria	82	Gomphonema	28
*Lagerheimia	84	Achnanthes	74	Gymnodinium	27
*‡Anabaenopis	83	†Peridinium	66	†Peridinium	26
Gyrosigma	80	†Ceratium	62	†Ceratium	24
Euastrum	77	†Dinobryon	60	†Dinobryon	24
Gomphonema	77	†Asterionella	56	†Asterionella	17
*Chlorogonium	76	†Tabellaria	42	†Tabellaria	14

Table 4 (continued)

Genus	NO_2+NO_3 (µg/l)	Genus	NH_3 (µg/l)	Genus	KJEL (µg/l)
Surirella	1146	*Actinastrum	157	*Lagerheimia	1717
Gomphonema	963	Surirella	154	*‡Anabaenopsis	1697
Gyrosigma	925	*Lagerheimia	149	*Chlorogonium	1592
Stephanodiscus	850	*‡Raphidiopsis	145	‡Chroococcus	1529
*Actinastrum	799	*Schroederia	137	*Schroederia	1526
Gymnodinium	714	Pandorina	136	*Actinastrum	1523
Trachelomonas	701	Coelastrum	133	*Golenkinia	1515
Euglena	693	Phacus	132	Dictyosphaerium	1398
Cryptomonas	683	Chlamydomonas	132	*‡Raphidiopsis	1386
Synedra	634	Pediastrum	130	Oocystis	1380
Navicula	634	Dictyosphaerium	130	‡Microcystis	1367
Nitzschia	629	Trachelomonas	128	‡Merismopedia	1363
Cyclotella	611	‡Merismopedia	128	Kirchneriella	1347
†Asterionella	605	Oocystis	128	Tetraedron	1326
Glenodinium	599	Euglena	126	Phacus	1307
Cymbella	572	*Golenkinia	125	Pediastrum	1307
Chlamydomonas	568	‡Aphanizomenon	124	Treubaria	1300
Phacus	565	‡Oscillatoria	124	Cosmarium	1285
Pandorina	558	Gyrosigma	123	Closterium	1279
Melosira	531	Closterium	122	Chlamydomonas	1232
‡Dactylococcopsis	523	‡Microcystis	122	Coelastrum	1207
Cocconeis	520	‡Dactylococcopsis	121	‡Lyngbya	1202
Closterium	512	‡Anabaena	119	‡Aphanizomenon	1175
Ankistrodesmus	508	Cyclotella	119	Crucigenia	1155
Fragilaria	499	Tetraedron	118	‡Coelosphaerium	1146
‡Oscillatoria	496	Cryptomonas	117	‡Dactylococcopsis	1141
Coelastrum	492	Staurastrum	116	‡Ababaena	1138
*Schroederia	489	‡Chroococcus	116	Glenodinium	1133
Scenedesmus	481	Navicula	116	Scenedesmus	1125
†Dinobryon	478	Melosira	116	Euglena	1109
‡Aphanizomenon	464	Scenedesmus	116	Staurastrum	1104
Achnanthes	456	Cocconeis	115	Ankistrodesmus	1087
*Chlorogonium	453	Kirchneriella	115	‡Oscillatoria	1081
Kirchneriella	434	Gomphonema	114	Gymnodinium	1032
Crucigenia	425	Crucigenia	114	Cyclotella	1018
*Lagerheimia	423	Ankistrodesmus	113	Stephanodiscus	1016
Pediastrum	422	Synedra	113	Trachelomonas	1006
‡Merismopedia	413	Cymbella	113	Cryptomonas	1001
Mallomonas	406	Nitzschia	113	Melosira	999
†Ceratium	383	Glenodinium	113	Surirella	996
Oocystis	379	*‡Anabaenopsis	112	Fragilaria	990
Treubaria	371	Cosmarium	111	Nitzschia	975
†Tabellaria	363	Fragilaria	110	Cocconeis	958
*‡Raphidiopsis	361	*Chlorogonium	108	Euastrum	930
‡Anabaena	351	Stephanodiscus	108	Gyrosigma	923
Dictyosphaerium	348	‡Coelosphaerium	106	Mallomonas	923
‡Microcystis	347	Mallomonas	106	Navicula	921
Tetraedron	335	‡Lyngbya	106	Synedra	870
†Peridinium	334	†Ceratium	103	†Ceratium	850
*Golenkinia	330	Gymnodinium	103	Gomphonema	845
Staurastrum	325	Achnanthes	100	Pandorina	830
‡Lyngbya	310	†Dinobryon	100	†Peridinium	828
Cosmarium	287	Treubaria	99	Achnanthes	818
‡Coelosphaerium	274	†Asterionella	96	Cymbella	807
‡Chroococcus	239	†Tabellaria	95	†Dinobryon	707
*‡Anabaenopsis	197	Euastrum	91	†Asterionella	627
Euastrum	145	†Peridinium	91	†Tabellaria	582

Table 4 (continued)

Genus	N/P
*‡Anabaenopsis	3.3
Euastrum	4.7
‡Chroococcus	6.0
*Golenkinia	6.0
*‡Raphidiopsis	7.1
Dictyosphaerium	7.1
*Lagerheimia	7.6
Treubaria	7.9
Tetraedron	7.9
Cosmarium	8.1
*Schroederia	8.3
Pediastrum	8.4
Kirchneriella	8.6
*Actinastrum	8.9
Chlamydomonas	9.1
‡Merismopedia	9.1
‡Microcystis	9.3
‡Lyngbya	9.4
*Chlorogonium	9.7
‡Anabaena	9.8
‡Dactylococcopsis	9.9
Staurastrum	9.9
Oocystis	10.1
Phacus	10.2
Closterium	10.3
Crucigenia	10.6
Pandorina	10.6
‡Oscillatoria	10.6
Cocconeis	10.9
Scenedesmus	11.1
Coelastrum	11.3
Ankistrodesmus	11.3
Euglena	12.2
‡Aphanizomenon	12.2
‡Coelosphaerium	12.3
Achnanthes	12.3
Trachelomonas	12.5
Nitzschia	12.8
Melosira	13.0
Mallomonas	13.4
Gyrosigma	13.4
Gymnodinium	14.3
Fragilaria	14.3
Cryptomonas	14.6
Navicula	14.6
Cymbella	14.7
†Peridinium	14.7
Stephanodiscus	14.9
Cyclotella	14.9
Synedra	15.1
Surirella	15.2
Glenodinium	15.4
†Ceratium	15.7
Gomphonema	16.3
†Asterionella	16.9
†Tabellaria	18.0
†Dinobryon	19.2

*nutrient-rich group: mean Total P > 200 μg/ℓ
†nutrient-poor group: mean Total P < 70 μg/ℓ
‡blue-green algae

Table 5. Selected genera* ranked by their frequency of dominant occurrence and the mean parameter values associated with their dominant occurrence

Genus	Frequency of Dominant Occurrence	Genus	Total P (μg/l)
Melosira	255	Scenedesmus	351
Oscillatoria	105	Cyclotella	185
Lyngbya	99	Anabaena	183
Cyclotella	83	Merismopedia	183
Stephanodiscus	73	Dactylococcopsis	178
Cryptomonas	72	Stephanodiscus	166
Dactylococcopsis	58	Chroococcus	163
Microcystis	53	Microcystis	148
Scenedesmus	50	Aphanizomenon	147
Synedra	48	Oscillatoria	125
Raphidiopsis	45	Cryptomonas	115
Fragilaria	45	Raphidiopsis	106
Aphanizomenon	41	Lyngbya	99
Asterionella	36	Melosira	94
Anabaena	33	Nitzschia	92
Dinobryon	31	Synedra	82
Nitzschia	29	Fragilaria	64
Merismopedia	22	Asterionella	36
Tabellaria	20	Dinobryon	27
Chroococcus	19	Tabellaria	22

Genus	Ortho P (μg/l)	Genus	NO_2+NO_3 (μg/l)
Scenedesmus	194	Stephanodiscus	1201
Cyclotella	110	Cryptomonas	970
Dactylococcopsis	108	Synedra	905
Anabaena	92	Melosira	715
Merismopedia	89	Asterionella	621
Chroococcus	76	Fragilaria	601
Stephanodiscus	66	Nitzschia	592
Aphanizomenon	63	Cyclotella	587
Microcystis	62	Merismopedia	510
Cryptomonas	53	Scenedesmus	502
Synedra	43	Oscillatoria	381
Oscillatoria	41	Aphanizomenon	311
Melosira	38	Raphidiopsis	303
Lyngbya	38	Microcystis	302
Raphidiopsis	27	Dinobryon	298
Fragilaria	26	Anabaena	252
Nitzschia	25	Dactylococcopsis	186
Dinobryon	11	Chroococcus	161
Asterionella	11	Tabellaria	133
Tabellaria	5	Lyngbya	107

*Each genus selected achieved dominance at least 10 times in samples from eastern and southeastern lakes.

Table 5 (continued)

Genus	NH_3 (µg/l)	Genus	KJEL (µg/l)
Anabaena	208	Scenedesmus	1826
Oscillatoria	127	Chroococcus	1630
Cyclotella	120	Lyngbya	1488
Stephanodiscus	120	Microcystis	1457
Synedra	120	Aphanizomenon	1437
Raphidiopsis	119	Merismopedia	1387
Scenedesmus	117	Oscillatoria	1356
Fragilaria	115	Stephanodiscus	1112
Cryptomonas	112	Raphidiopsis	1073
Aphanizomenon	112	Cyclotella	1053
Lyngbya	110	Dactylococcopsis	1041
Merismopedia	110	Anabaena	1015
Melosira	103	Nitzschia	883
Nitzschia	101	Fragilaria	843
Microcystis	98	Cryptomonas	798
Chroococcus	90	Synedra	797
Tabellaria	86	Melosira	774
Dactylococcopsis	82	Dinobryon	594
Asterionella	74	Asterionella	491
Dinobryon	65	Tabellaria	455

Genus	N/P
Chroococcus	4.3
Lyngbya	4.6
Merismopedia	6.1
Dactylococcopsis	6.9
Anabaena	7.1
Aphanizomenon	7.5
Scenedesmus	8.5
Oscillatoria	9.0
Microcystis	9.7
Raphidiopsis	9.8
Nitzschia	10.4
Tabellaria	11.3
Cryptomonas	14.2
Melosira	14.4
Cyclotella	17.7
Stephanodiscus	17.8
Synedra	21.0
Asterionella	22.4
Fragilaria	22.9
Dinobryon	28.5

and *Ceratium,* were summer and fall forms, while *Dinobryon* and *Tabellaria* occurred equally through the seasons. The genera in this group remained tightly packed at the lower mean values for all of the nutrient series parameter except $NO_2 + NO_3$ where, as with the group at the high end, they generally scattered throughout the range. The association of *Asterionella* with particularly high $NO_2 + NO_3$ levels appears to be a consequence of its seasonal (spring) "preference."

Eleven blue-green algal genera were quite common in the study (Table 4). Nine of these were important dominants in that they achieved dominance in at least 10 samples (Table 5). All can be classified as summer and fall forms except *Dactylococcopsis* and *Oscillatoria*, which occurred equally in spring as well.

As a group, the blue-green algae were scattered throughout the upper and middle ranges of mean values for all the parameters (Table 4). Except for $NO_2 + NO_3$, they never appear at the extreme low end. The blue-green algae completely reversed their trend for $NO_2 + NO_3$, and most of the genera fell into the lower half of that list. This phenomenon cannot be readily explained on the basis of nitrogen fixation, since only one of five blue-green genera associated with the lowest mean $NO_2 + NO_3$ values is an acknowledged nitrogen fixer *(Anabaenopsis)*.

The three genera listed that have heterocysts and are known to contain species which fix nitrogen are *Anabaena, Aphanizomenon,* and *Anabaenopsis* (Fogg et al. 1973). Nitrogen fixation, an extremely important physiological process [in algae, associated uniquely with the blue-greens (Fogg et al. 1973)], would be expected to be associated with a naturally occurring group having similar environmental requirements. Our $NO_2 + NO_3$ data do not support that premise. In fact, scatter among the three genera was great, and mean values differed commonly by a factor of 2 (Table 4). Nor was there a clear

relationship with N/P ratio, since five nonheterocyctous genera had lower N/P ratio values than *Anabaena,* and seven showed lower values than *Aphanizomenon*. Similar N/P ratio trends were associated with dominant occurrences (Table 5).

In an attempt to determine the major constituents within phytoplankton communities, dominant occurrence status was attached to those genera which accounted for 10 percent or more of the numerical total cell count in a given sample. The 10 percent cutoff point is arbitrary and resulted in an average of about three genera exhibiting dominant occurrence in each sample. With this approach, every sample had members exhibiting dominant occurrence regardless of the total cell count.

In Table 5, each genus which achieved dominant occurrence at least 10 times was ranked by its frequency of dominant occurrence and the mean level of nutrients found associated with the dominant occurrence of that genus. The genera represented in Table 5 include nine blue-greens (Myxophyceae), eight diatoms (Chrysophyta), two flagellates (one Cryptophyta and one Chrysophyta), and one chlorococcalean (Chlorophyta). Obviously, blue-green and diatom genera numerically dominated a majority of samples. *Melosira* was by far the most common dominant genus, followed by *Oscillatoria* and *Lyngbya*. *Scenedesmus,* second only to *Melosira* in total occurrences, was considerably less important among dominant occurrence forms.

Asterionella appeared to exhibit dominant occurrence more frequently in spring, while *Stephanodiscus, Synedra,* and *Tabellaria* exhibited dominant occurrence more frequently in spring and summer and *Cryptomonas* and *Dinobryon* in spring and fall (Table 2). Dominant occurrence of *Fragilaria* occurred equally throughout the seasons. The remaining genera showed dominant occurrence more frequently in summer and fall.

As expected, the dominant occurrence category tended to narrow the ranges of associated nutrient conditions for most of the genera (Appendix A) by eliminating data associated with passive or chance occurrences of genera within a given sample, and by using data associated

with healthy populations. Note that a genus showing dominant occurrence at the time of sampling may have been in the growth, stationary, or decline phase. Naturally, nutrient requirements would vary accordingly. Therefore, there is no assurance that the conditions detected at the time of sampling were, in fact, optimal for growth of that genus.

DISCUSSION

Severe criticisms of limnological investigations conducted at the genus level have been directed primarily toward the variability in environmental requirements of the species comprising many genera. Weber (1971) provided a graphic illustration using *Cyclotella* as an example of a genus with individual species having requirements at all levels of the trophic scale. He concluded that it is pointless to discuss diatom populations at the genus level. Our data, for the most part, support this point of view, especially the data defining ranges of nutrient conditions associated with specific genus occurrence, whether it be dominant or not. The value of the criticism is not restricted to the diatoms, as we have shown similar results for most of the major groups occurring in freshwater plankton communities. There are, however, a number of genera which are either monospecific, have just a few species, or were represented only by a few species in the lakes sampled in the Southeast and East. Data associated with these genera would reflect monospecific requirements and would be useful on at least a regional basis.

The ranking schemes (Tables 4 and 5) used for comparing the differences between central tendencies of the various genera are important to illustrate trends with potential application in lake water quality assessment. Many of the genera followed consistent patterns in their ranking against many of the parameters. Shifts in conditions associated with dominant occurrence were often consistent in direction. *Scenedesmus,* one of the most common genera encountered, had mean values calculated from total occurrence data which consistently placed it mid-

way down the ranked lists (Table 4). Conditions associated with dominant occurrences of *Scenedesmus,* on the other hand, are characterized by extremely high mean values for total P, ortho P, and Kjeldahl nitrogen, reflecting highly enriched conditions during times of important growth (Table 5). If these relationships, particularly dominant occurrence trends, reflect conditions of competitive advantage for the genera, then the information may be used to evaluate or even predict water quality.

Of considerable interest is the consistent relationship noted between the occurrence of blue-green algae and low N/P ratios. The attainment of high relative importance (dominant occurrence) among the blue-green genera represented was invariably associated with very low N/P ratios. The competitive advantage of nitrogen-limiting (low N/P) conditions to a nitrogen-fixing blue-green algae seems obvious. What is far less clear is the similar affinity of the low N/P waters for the nonnitrogen fixers. Certainly these waters were, for the most part, highly enriched with phosphorus. The facility of some of the blue-greens for luxury uptake of phosphorus under such enriched conditions may provide a partial clue. It should be noted that low N/P ratios (Table 4) were invariably associated with higher Kjeldahl nitrogen values and with average or lower NH_3 values. *Anabaena* was a notable exception. Therefore organic nitrogen (KJEL minus NH_3) is high with low N/P ratios. A possible key to the nitrogen nutrition of the blue-greens (particularly the nonnitrogen fixers) may lie in the organic nitrogen component, either through direct assimilation by the blue-greens (see Williams 1975) or as a source for conversion by the bacteria often intimately associated with blue-green colonies and filaments.

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APPENDIX A

OCCURRENCE OF 57 PHYTOPLANKTON GENERA AS RELATED TO TOTAL PHOSPHORUS AND KJELDAHL NITROGEN LEVELS AND N/P RATIOS

This appendix was generated by computer. Because it was possible to use only upper case letters in the printout, all scientific names are printed in upper case letters and they are not italicized or underscored.

Using total phosphorus (Figure A-1) as an example, the various terms, symbols, and layout are defined as follows. The range, mean, and twice the standard deviation (STDV) are plotted against a logarithmic scale for dominant occurrence (DOM), nondominant occurrence (NONDOM), and nonoccurrence (NONOCC) categories. The plus symbol, +, following numerical scale values locates the proper position of each value. An "X" indicates the mean value for the respective occurrence categories, while "M" is the mean value for all occurrences of the genus. "S" gives the positions of two standard deviations on either side of the mean. Values of S below 1 were omitted. Occasionally S fell on the position of the vertical bar designating the range limit, in which case S replaced the bar.

Immediately following the genus name is the mean occurrence parameter value, M, in micrograms per liter. For the remaining categories, DOM, NONDOM, and NONOCC, the mean parameter value, X, in micrograms per liter is given and is followed in parentheses by the number of samples in which the genus was classified in each of the categories shown.

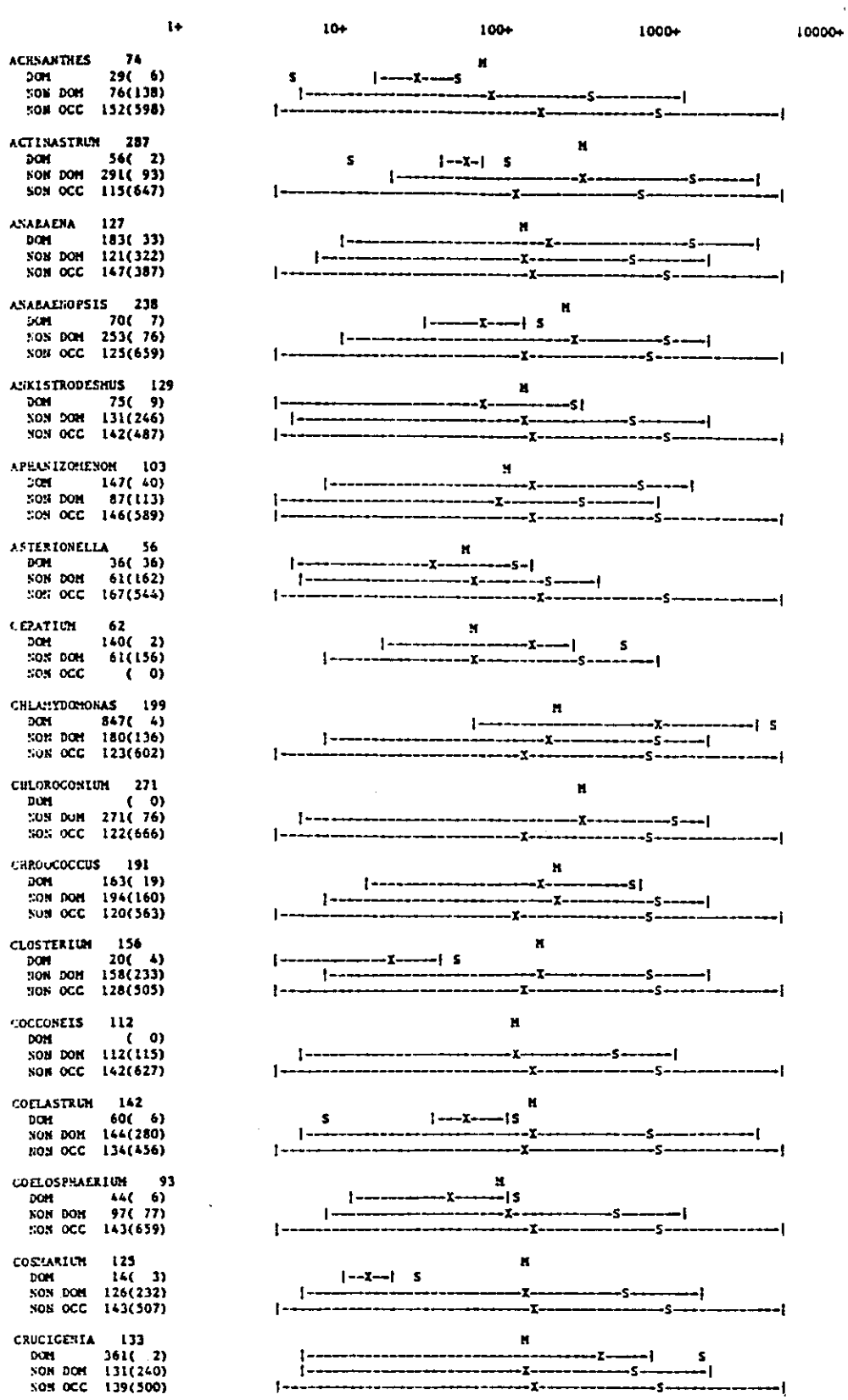
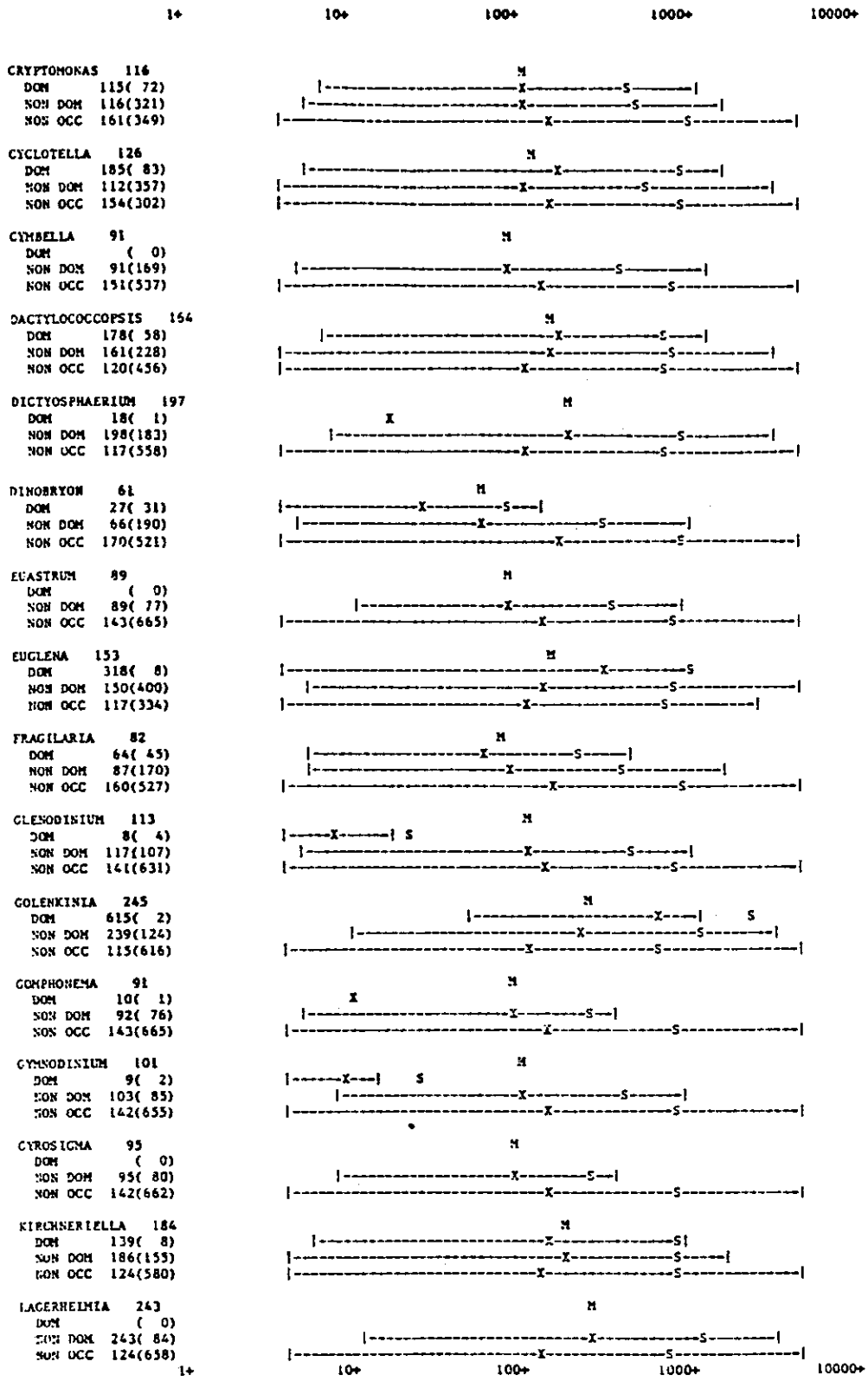


FIGURE A-1. Occurrence of 57 phytoplankton genera as related to total phosphorus levels.



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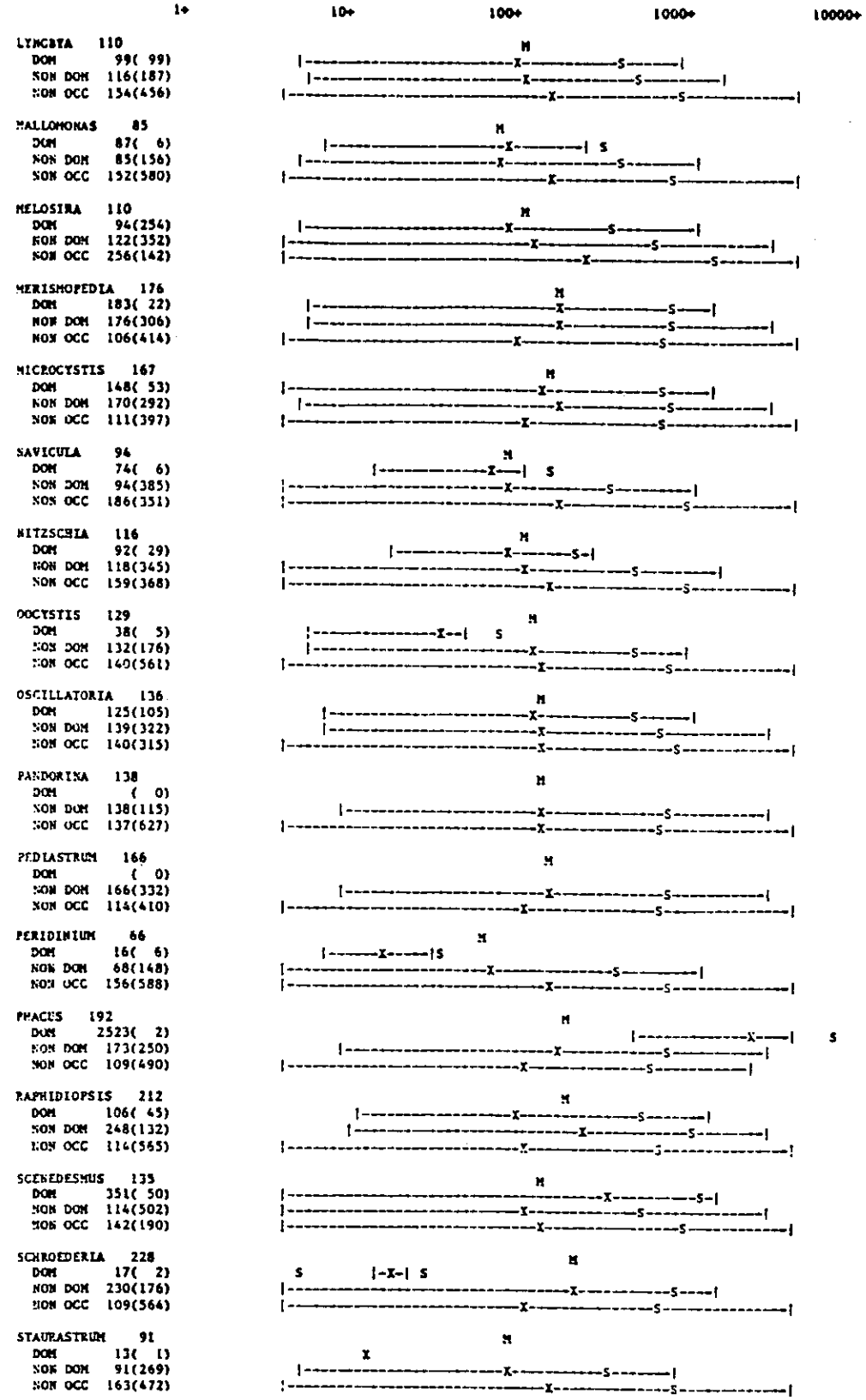

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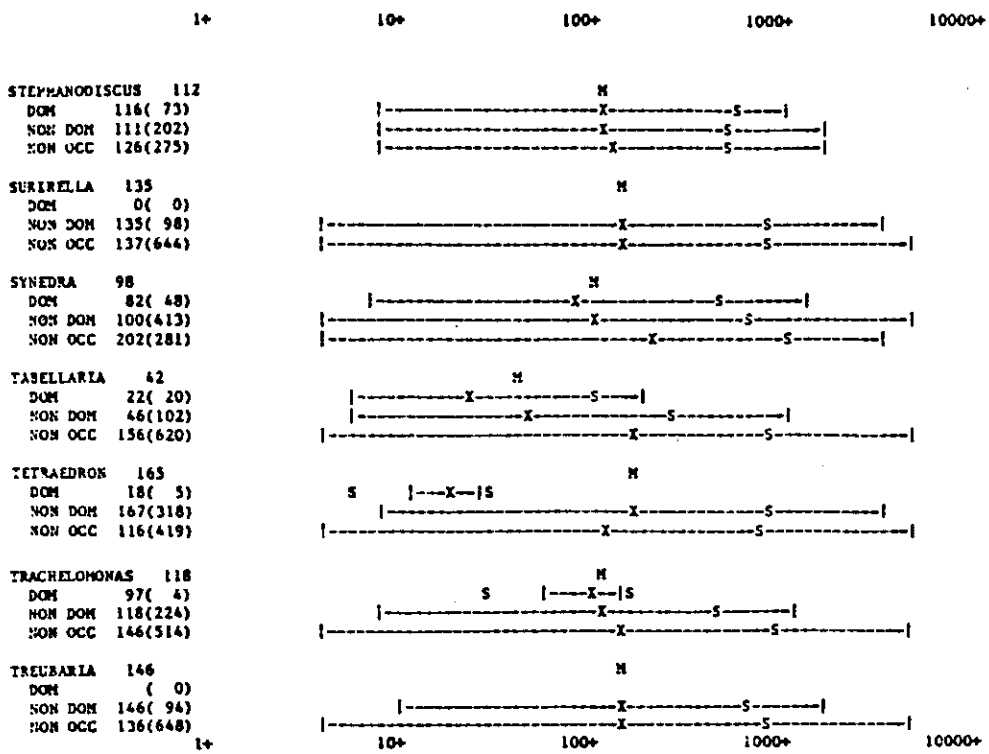

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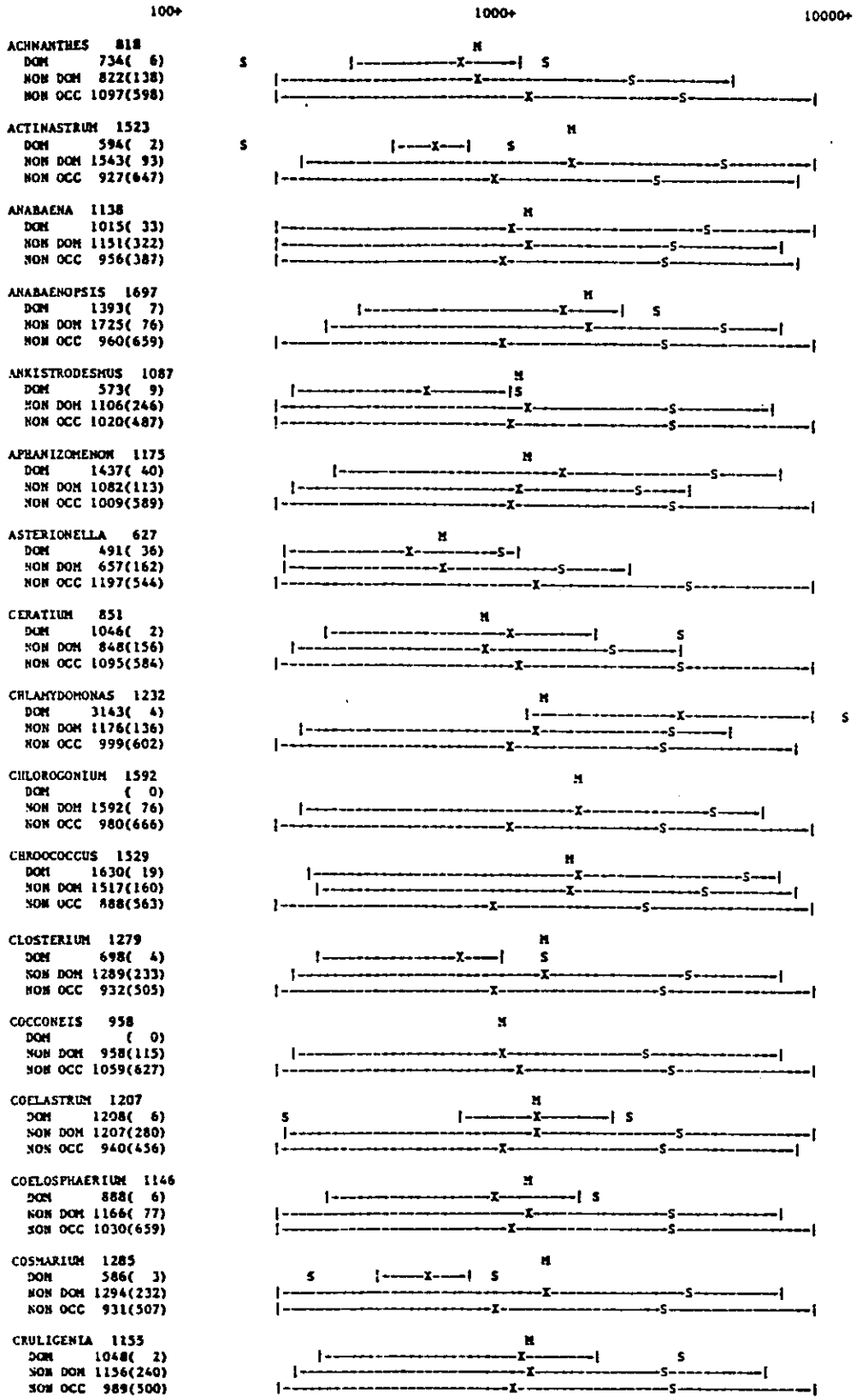
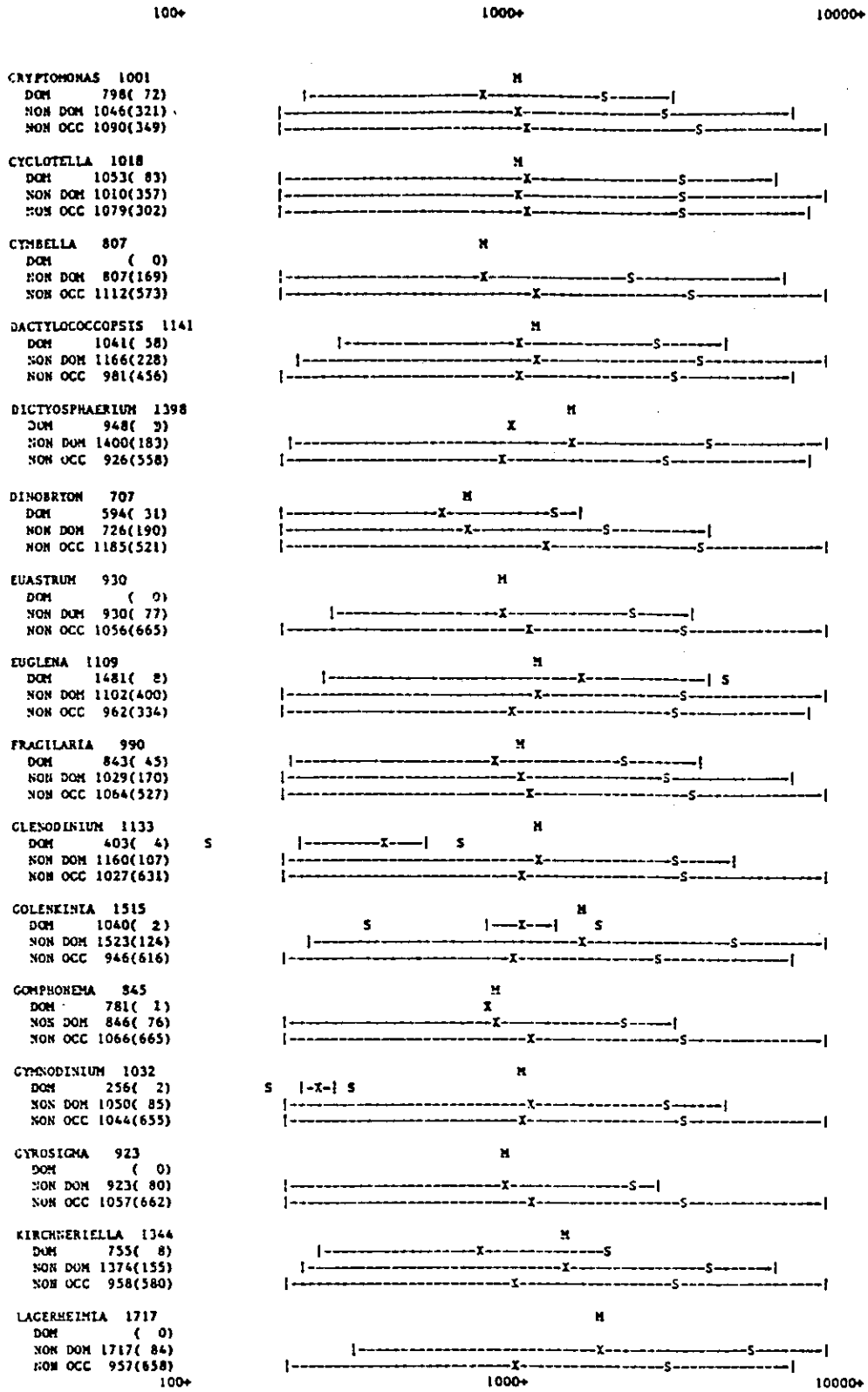


Figure A-2. Occurrence of 57 phytoplankton genera as related to total Kjeldahl nitrogen levels.



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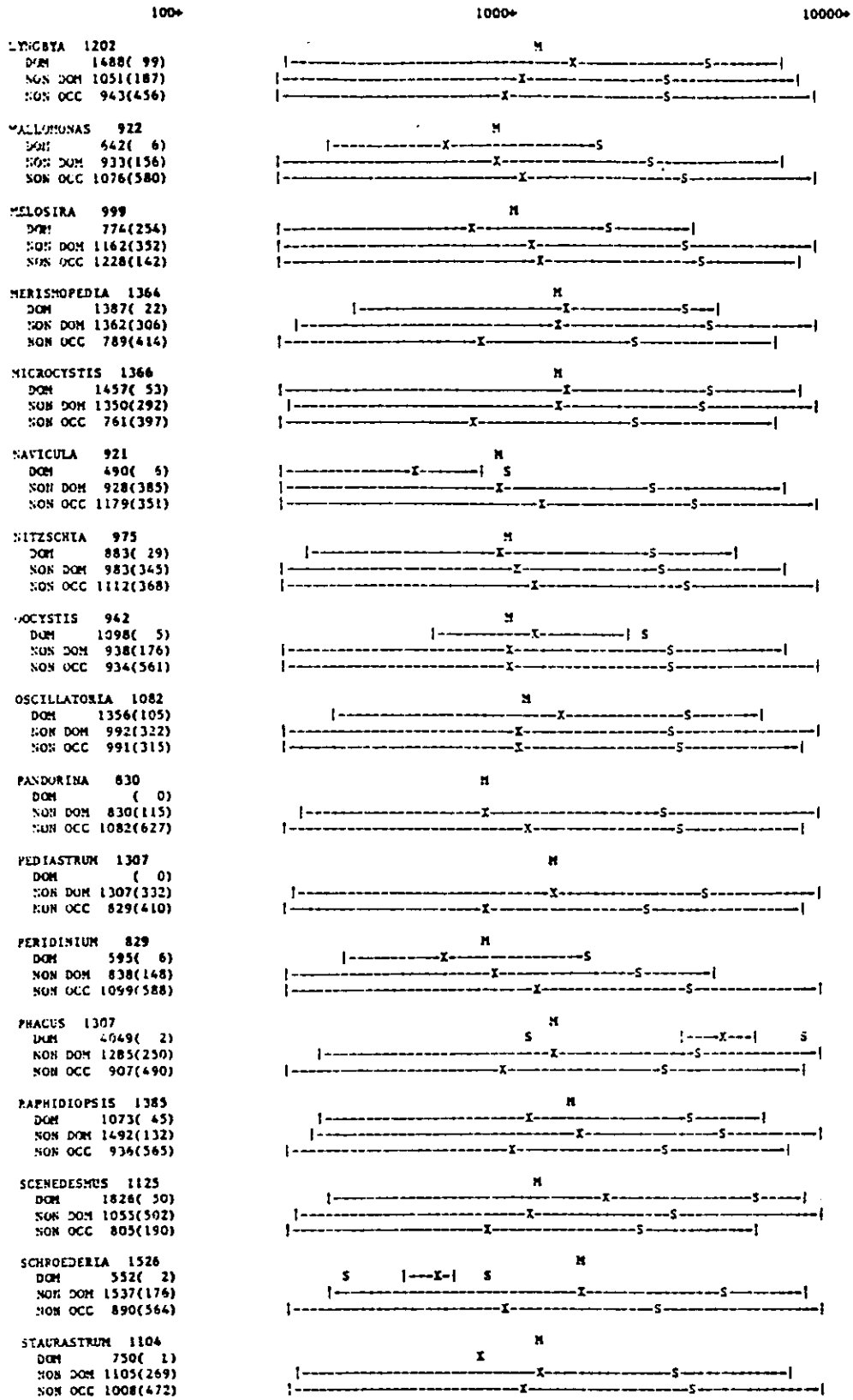

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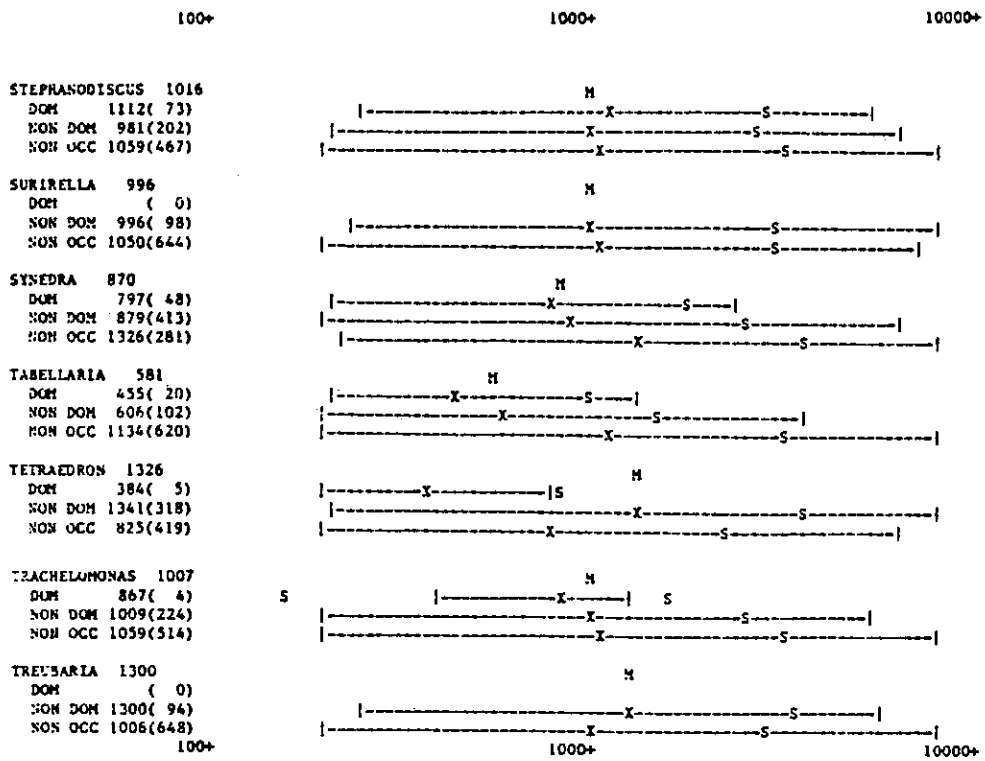

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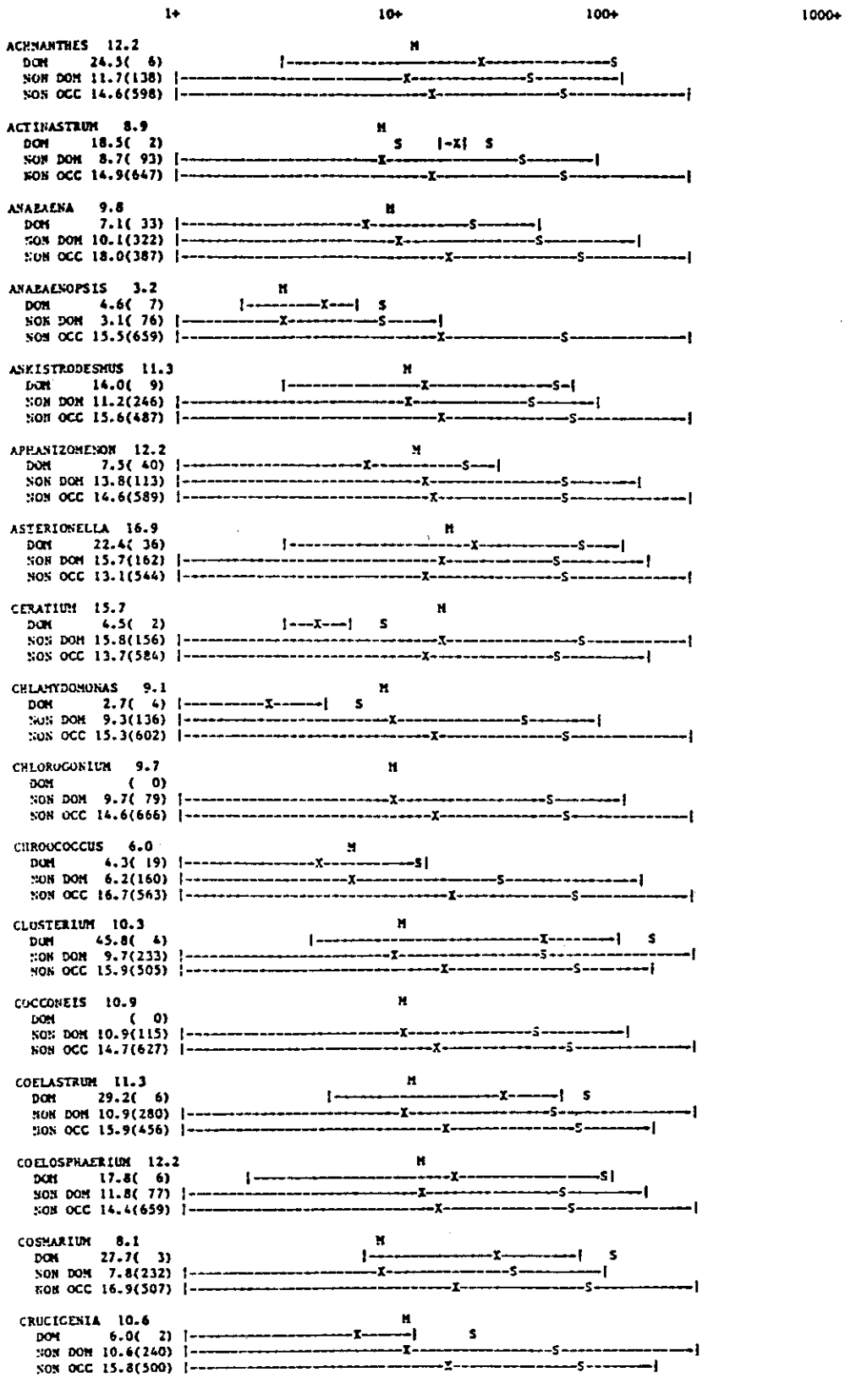
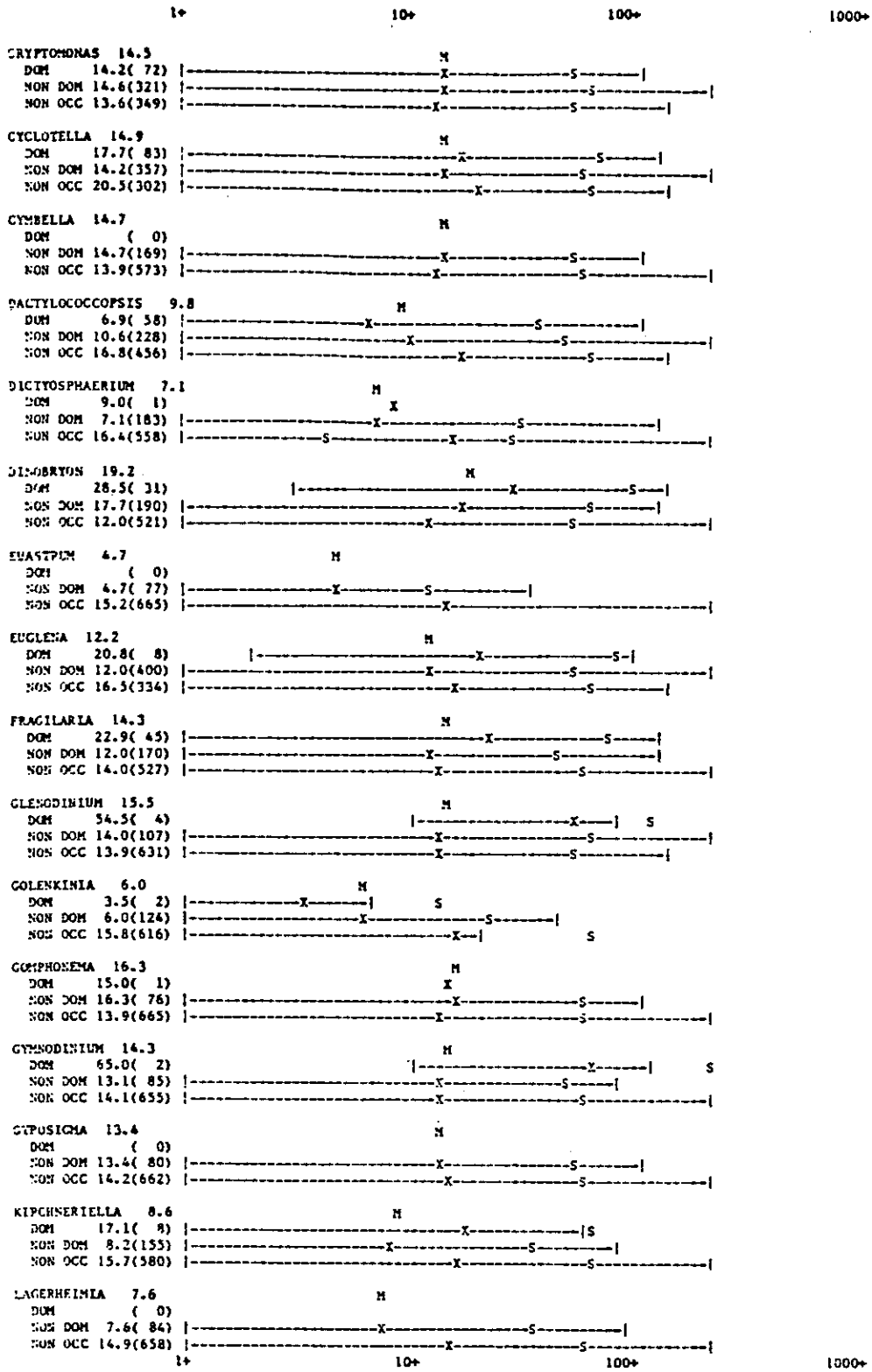


Figure A-3. Occurrence of 57 phytoplankton genera as related to N/P ratio values.



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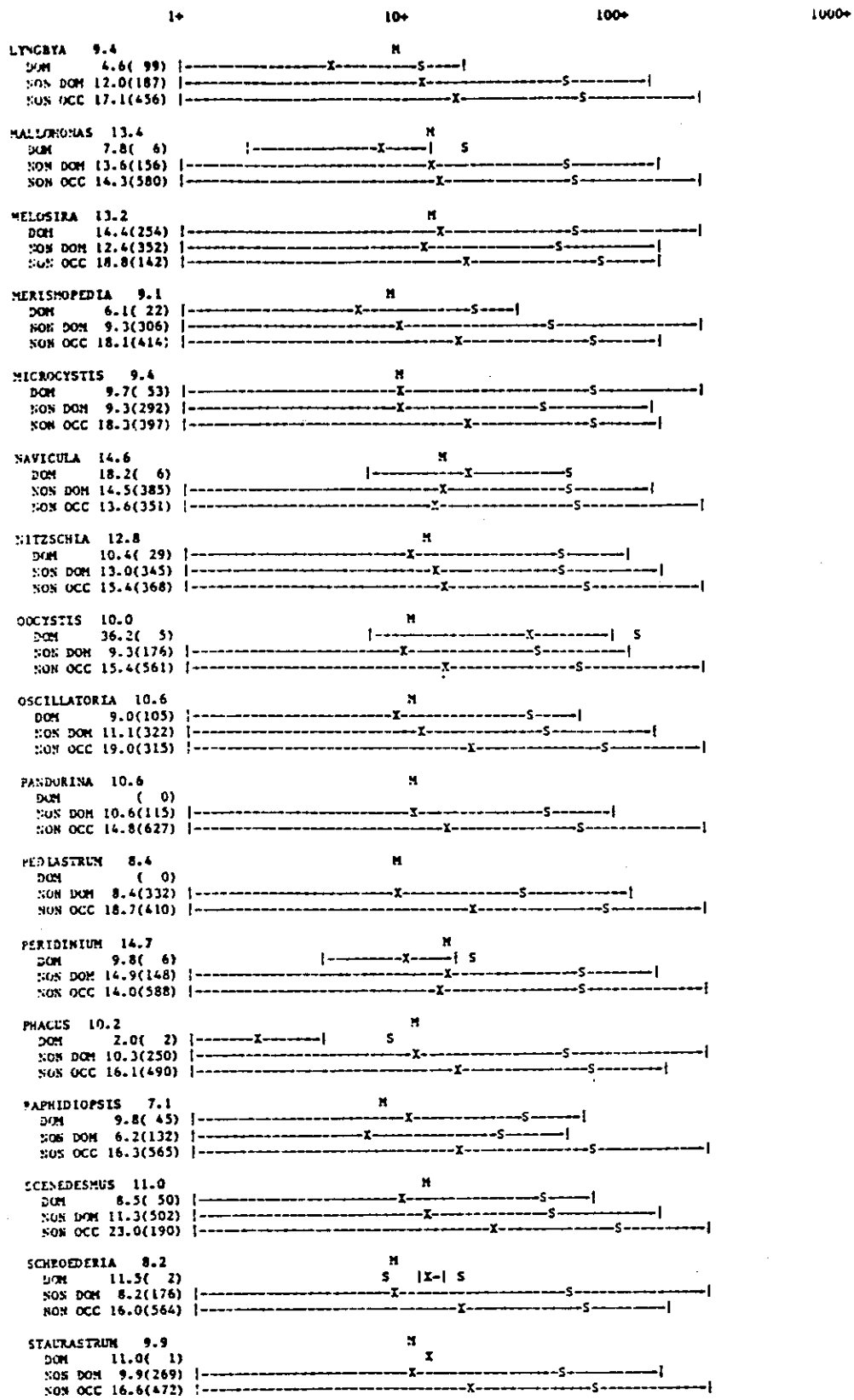

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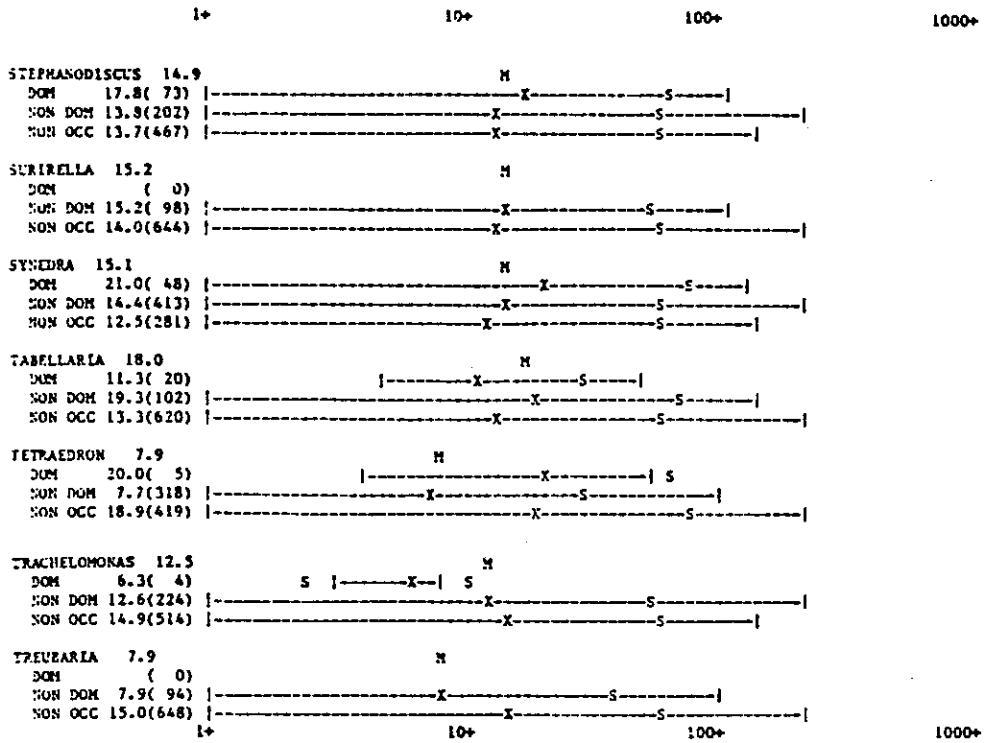

Figure A-3 (continued)

THE EFFECT OF LIGHT ATTENUATION ON THE RELATIONSHIP OF PHYTOPLANKTON BIOMASS TO PHOSPHORUS LEVELS

by

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INTRODUCTION

Phosphorus supply is considered to be the primary determinant of algal community biomass and production in most temperate zone lakes (Schindler 1974, Williams et al. 1977, Lambou et al. 1976, Dillon and Rigler 1974, Bachmann and Jones 1974, Edmondson 1970). Kalff and Knoechel (1978) state that the strong relationship between total phosphorus and phytoplankton biomass as measured by chlorophyll a concentrations has been clearly confirmed. They further state that what is presently needed, in order to predict algal biomass for management decisions on individual lakes, is a quantitative understanding of the orders-of-magnitude range in biomass (chlorophyll a per unit of phosphorus).

Solar radiation is required for photosynthesis and heat maintenance in the environment. The transparency of natural waters varies widely; it depends upon both the type and quantity of dissolved substances and suspended particles present, and the angle and intensity of the entering light. In general, approximately 53 percent of the total incident light is transformed into heat and is extinguished in the first meter of water (Reid 1961). Light and temperature are important in regulating many chemical, physical, and biological processes.

During the spring, summer, and fall of 1972 through 1975, approximately 800 lakes and reservoirs were sampled throughout the 48 contiguous United States. About 2-1/2 million physical, chemical, and biological measurements were made. The purpose of this paper is to examine the effects of light attenuation upon the production of chlorophyll a per unit of total phosphorus in the lakes sampled.

MATERIALS AND METHODS

Each water body was normally sampled once during spring, summer, and fall. The methods employed for sampling, analysis, and data

storage and manipulation in this paper are similar to those described by Lambou et al. (1979) at this workshop and U.S. EPA (1975). However, mean total phosphorus values for a given lake were determined by utilizing data collected from the entire water column instead of the photic zone as described by Lambou et al. (1979). In addition, only one integrated chlorophyll a measurement (surface to the compensation point) and one Secchi depth measurement were made at any individual sampling station. The sampling periods for each season are given by sampling year in Table 1.

Table 1. Seasonal sampling periods for 1972 through 1975.

Sampling Year	No. of Lakes	Season		
		Spring	Summer	Fall
1972	222	5/20-7/19	7/20-9/24	9/15-11/16
1973	241	3/7-7/11	7/5-9/18	9/19-11/4
1974	145	3/4-5/12	5/13-9/5	9/11-11/14
1975	149	2/21-6/10	6/11-9/3	9/4-12/11

RESULTS AND DISCUSSION

A strong relationship between chlorophyll a and total phosphorus has been described by Jones and Bachmann (1976), Dillon and Rigler (1974), Sakamoto (1966), and Carlson (1977). The reported log-log product moment correlation coefficients calculated from raw data ranged from 0.85 to 0.98 (Table 2). The implication of these findings is that phosphorus is the element which controls algal biomass; however, the lakes utilized by the above authors in deriving their relationships are largely phosphorus-limited lakes.

The slopes of the regression lines from the four sources cited above are all greater than 1.4 (Table 2) which indicates that proportional increases in algal chlorophyll a accrue at a faster rate than increases in total phosphorus concentrations, i.e., the response ratio (chlorophyll a per unit of total phosphorus) is greater at high concentrations of total phosphorus than at low concentrations.

However, the log-log regression equations derived from the lakes we sampled (Table 2) suggest that chlorophyll a produced per unit of total phosphorus decreases as total phosphorus increases. The mean response ratios for our lakes are compared on a seasonal basis (Table 3). Since lake management decisions to control or manipulate phytoplankton biomass are usually based on summer data and we observed the greatest potential response of the phytoplankton community to available nutrients during summer (Table 3), only summer data are used throughout the remainder of this report.

Table 2. Reported relationships between chlorophyll a and total phosphorus.

Source	Regression Equation Chlorophyll a (CHLA) and Total Phosphorus (TP) (µg/liter)	No. of Lakes	Log-Log Product Moment Correlation Coefficients
Jones and Bachmann (1976)	Log CHLA = -1.09 + 1.46 Log TP	143	r = 0.95
Dillon and Rigler (1974)	Log CHLA = -1.136 + 1.45 Log TP	46	r = 0.95
Sakamoto (1966) (as calculated by Dillon and Rigler)	Log CHLA = -1.13 + 1.58 Log TP	28	r = 0.98
Carlson (1977)	Log CHLA = -1.06 + 1.45 Log TP	43	r = 0.85
This study	Log CHLA = -0.11 + 0.64 Log TP	771	r = 0.60

A histogram of the summer response ratio (chlorophyll a/total phosphorus) for 771 lakes and reservoirs located in the contiguous United States is presented in Figure 1. The response ratio varied from 0.002 to 2.26 with a mean of 0.29 (Table 3). The concentration of chlorophyll a per unit of total phosphorus varied between lakes as can be seen from Figure 1 and Table 3.

Table 3. Response ratio by season.

Parameter	Season*		
	Spring	Summer	Fall
Mean response ratio	0.24	0.29	0.24
Standard deviation	0.27	0.29	0.21
Minimum response ratio	0.001	0.002	0.001
Maximum response ratio	2.81	2.26	1.60
Number of lakes	785	771	777

*A one-way ANOVA and Student Newman Keuls multiple range test indicated a significant difference between summer value and fall and spring values at the 0.05 level.

The relationship between Secchi disk transparency and chlorophyll a concentrations has been described by a number of investigators (Edmondson 1970; Bachmann and Jones 1974; Carlson 1977). After analyzing data from 147 lakes, Carlson (1977) described a strong relationship ($r = 0.93$) between chlorophyll a (μg/ℓ) and Secchi depth (m):

$$\ln(\text{Secchi depth}) = 2.04 - 0.68 \ln(\text{chlorophyll } a) \qquad (1)$$

The lakes Carlson utilized were relatively free of nonchlorophyll-related particles. The strength of the relationship Carlson described indicates that light attenuation from any source other than chlorophyll a-related particles was homogeneous in the population of lakes represented in his study.

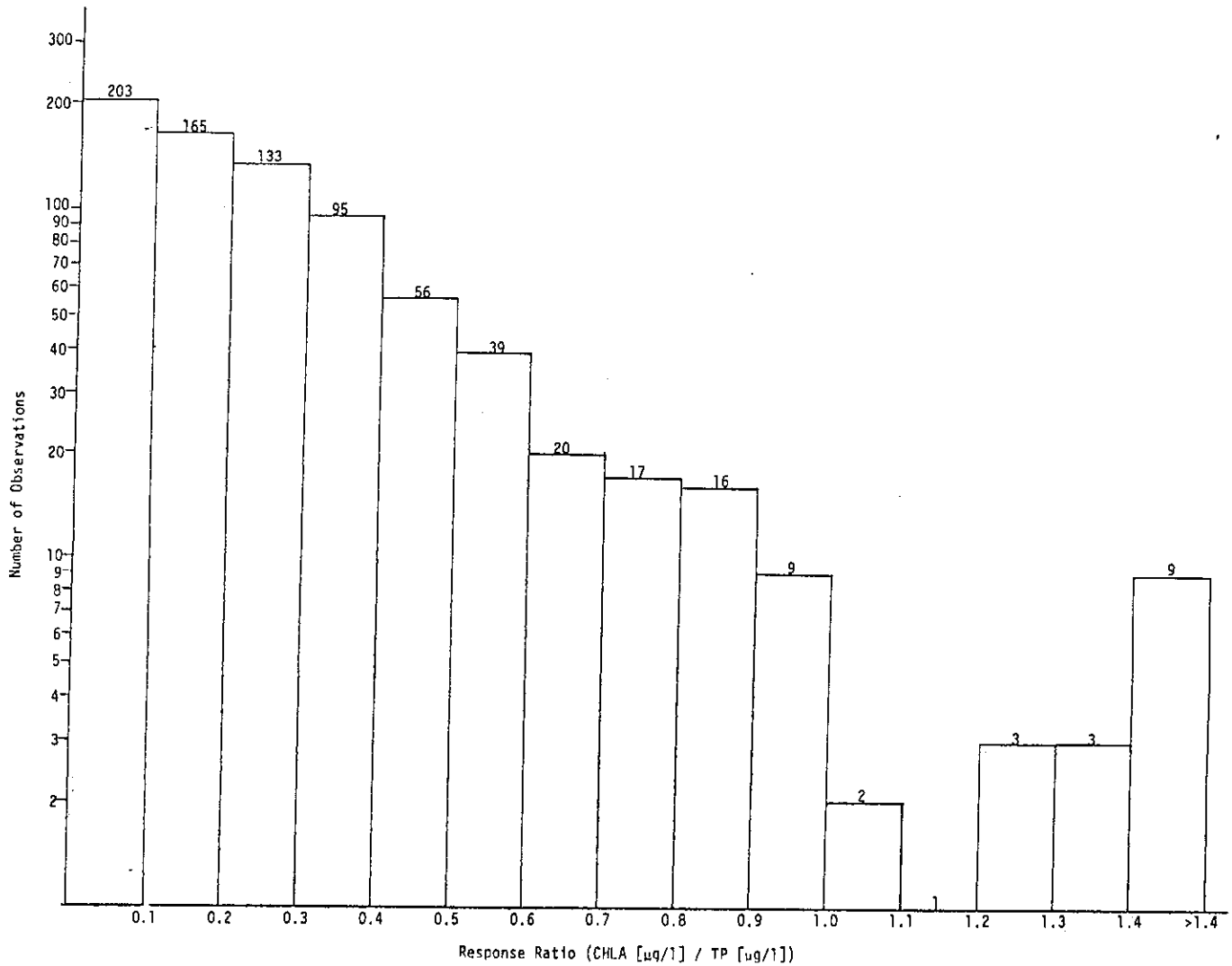

FIGURE 1. Response ratio in 757 United States lakes and reservoirs.

A natural log transformation of our summer chlorophyll a and Secchi depth resulted in a correlation coefficient of only 0.56 (Figure 2). This indicates that light attenuation due to nonchlorophyll a-related suspensoids or dissolved color must be important factors in a number of lakes and reservoirs sampled in our study.

If Carlson's regression equation accurately describes the relationship between chlorophyll a and Secchi depth in water bodies relatively free of nonchlorophyll a-related particles or dissolved color interferences, it can be utilized in conjunction with observed chlorophyll a concentrations and Secchi depth measurements to estimate light attenuation due to nonchlorophyll a-related particles or dissolved color. We did this in the following manner.

$$RS = PS - OS \qquad (2)$$

where RS = residual Secchi, an index of nonchlorophyll a-related light attenuation

PS = predicted Secchi, determined by substituting our mean ambient summer chlorophyll a value for a given lake into Carlson's regression equation

OS = the observed mean ambient summer Secchi depth value for the same lake

If the residual Secchi value is positive, we expect nonchlorophyll a-related suspensoids or color interferences. As residual Secchi values increase, light attenuation due to the nonchlorophyll a-related factors increases. If the residual Secchi value is equal to zero, then we assume the light attenuation is mainly caused by chlorophyll a-related particles.

We calculated a residual Secchi value for each of our lakes by the method presented above and plotted them against the response ratio to examine the effects of light interference upon the relationship of chlorophyll a to total phosphorus (Figure 3).

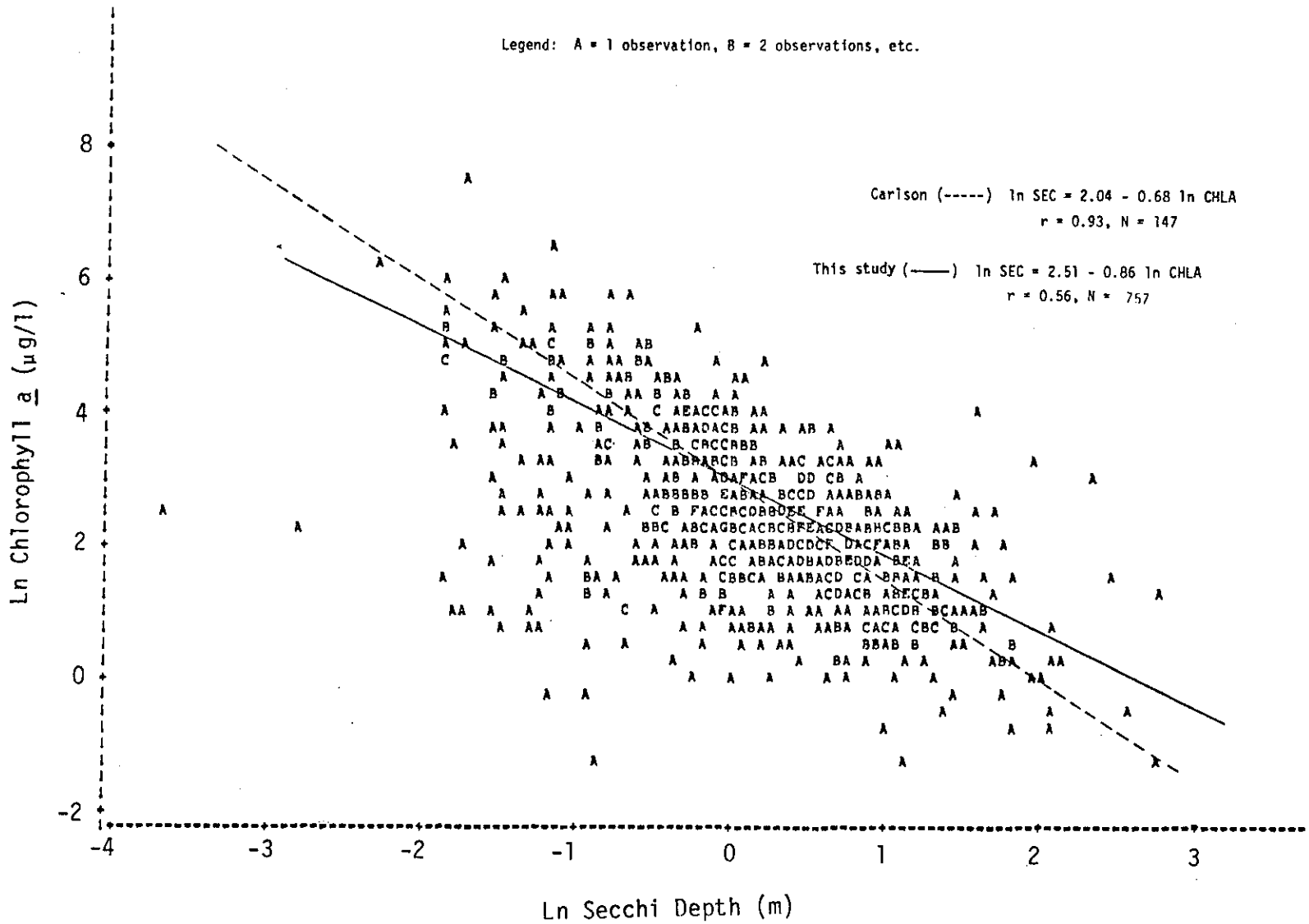

FIGURE 2. Relationship of chlorophyll a to Secchi depth for United States lakes and reservoirs [Carlson's (1977) regression line is presented for comparison].

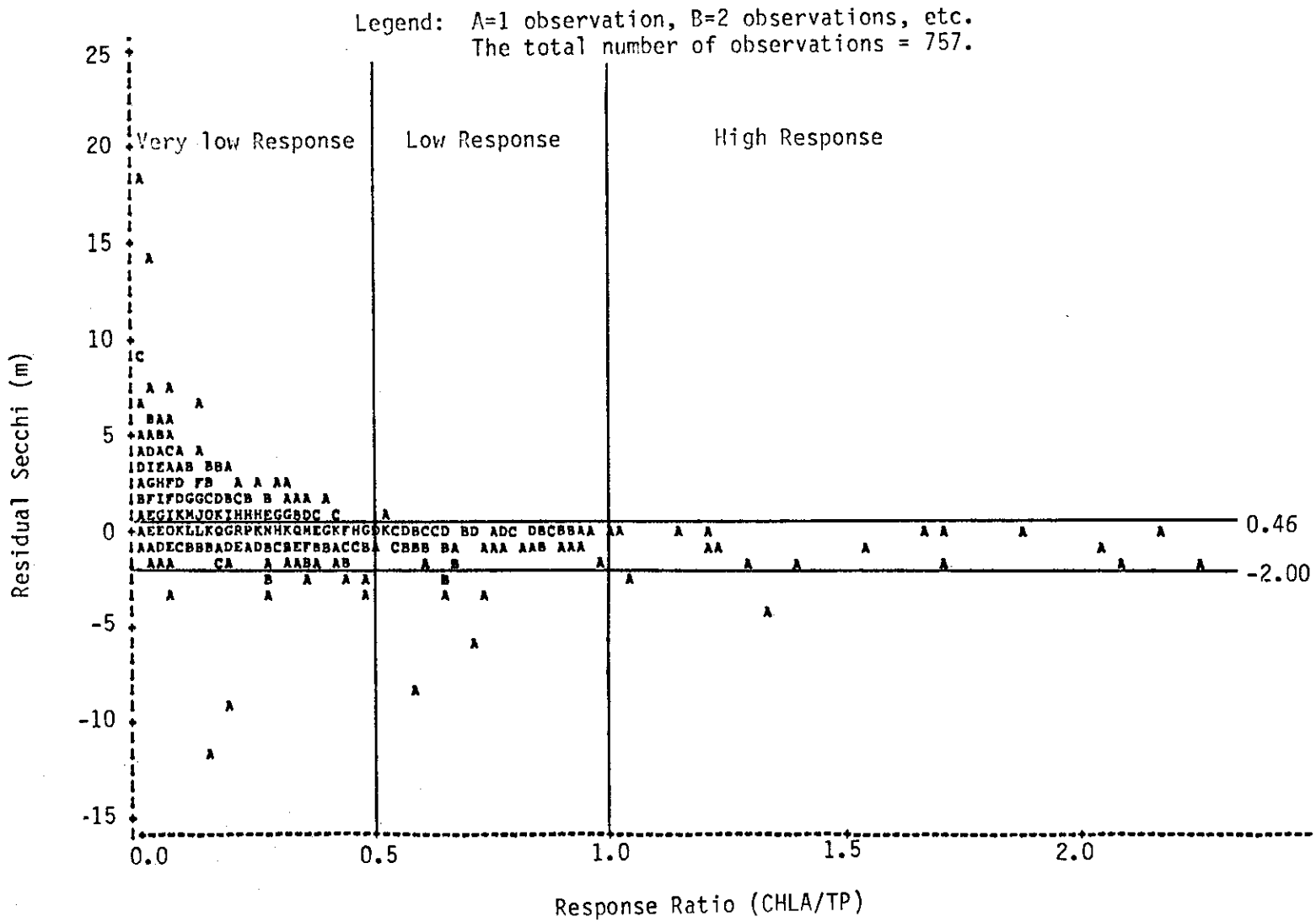

FIGURE 3. The relationship of light attenuation to response ratio.

Theoretically, if all of the light attenuation was caused solely by chlorophyll a-related particles in Carlson's equation, no lakes or reservoirs would have residual Secchi values below zero. Obviously, all lakes have some light attenuation due to nonchlorophyll-related particles and color interferences. Therefore, the true zero line (where virtually all light interferences are due solely to chlorophyll a-related particles) is less than a residual Secchi value of zero. The true zero line should contain lakes and reservoirs that extend over the full range of response, because many lakes are relatively free of nonchlorophyll a-related particles. Examination of Figure 3 and a consideration of experimental error led us to the conclusion that the population of lakes that extend over the full range of response ratios and lie between residual Secchi values of 0.46 to -2.00 encompasses the true zero line. Since Secchi values less than the true zero line are theoretically impossible, we believe the residual Secchi values less than -2.00 in Figure 4 are due to experimental error.

We divided the response ratio into three groups; "very-low" response (0.00 to <0.50), "low" response (0.50 to <1.0), and "high" response (≥1.0). Our rationale for the breakdown presented is that with a response of approximately 1.0 or above, all the total phosphorus in the system is "theoretically" associated with cellular chlorophyll a (Strickland 1960). Therefore, at a response ratio of 1 or greater, the algae are utilizing all available phosphorus and incorporating it into cellular material. At a response ratio of 0.5, half of the total phosphorus is theoretically tied up in phytoplankton cells, while the other half of the total phosphorus pool is extracellular. These divisions are somewhat arbitrary, as the relationship between cellular phosphorus and chlorophyll a can dramatically change, depending upon environment conditions and phytoplankton community composition; e.g., luxury uptake by selected phytoplankton forms and increased chlorophyll a production per unit of biomass under low-light conditions can occur. Even though the divisions of the response ratio are somewhat arbitrary, they provide a useful mechanism to compare major response groups.

Two groups are defined by residual Secchi values in Figure 3. One group is defined as having residual Secchi values of >0.46 (high nonchlorophyll light interference) while the other group has residual Secchi values between 0.46 and -2.00 (low nonchlorophyll light interference).

Only 1 of 104 water bodies was detected in the low or high response groups that had a residual Secchi of >0.46 (m) while 307 of 632 (49%) of the water bodies with a very low response had a residual Secchi of >0.46 (m). Therefore, we believe that light, or a combination of light and other factors, was responsible for the inefficient utilization of total phosphorus in the low response group.

It is concluded that in many U.S. lakes and reservoirs, light attenuation from other than chlorophyll-related particles can dramatically affect the quantity of phytoplankton biomass present. The use of models to predict phytoplankton biomass from actual or potential phosphorus concentrations in individual water bodies could lead to faulty management decisions if the effect of light attenuation from other than chlorophyll-related particles is not taken into consideration.

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Final report.
Bibliography: p. 376-377.

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