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SEASONAL PHYTOPLANKTON SUCCESSION AS A FUNCTION OF SPECIES COMPETITION FOR PHOSPHORUS AND NITROGEN

Joseph V. DePinto, Victor J. Bierman, Jr., and Francis H. Verhoff[1]

INTRODUCTION

Excessive nutrient input and the resulting nuisance algal blooms in freshwater lakes have recently become a major topic of limnological investigation. From the viewpoint of lake management and/or restoration it is desirable to be able to predict *a priori* if a given set of environmental conditions will tend to favor a stable (nonblooming) or an unstable (frequent algal blooms) system. Furthermore, since cyanophyte blooms appear to be the most objectionable type, knowledge of the pattern of seasonal phytoplankton succession in a lake would be useful. It is well known that phytoplankton succession is affected by many factors including temperature, light, turbulence, inorganic nutrients, accessory organic materials, antibiotics, parasitism, predation, and all forms of competition (Hutchinson 1967). Attempts are being made to determine what variations in the above factors tend to bring about the dominance of unwanted blue-green algal blooms.

Among the earliest proponents of the theory that seasonal variations in chemical composition of lake water are to a large extent

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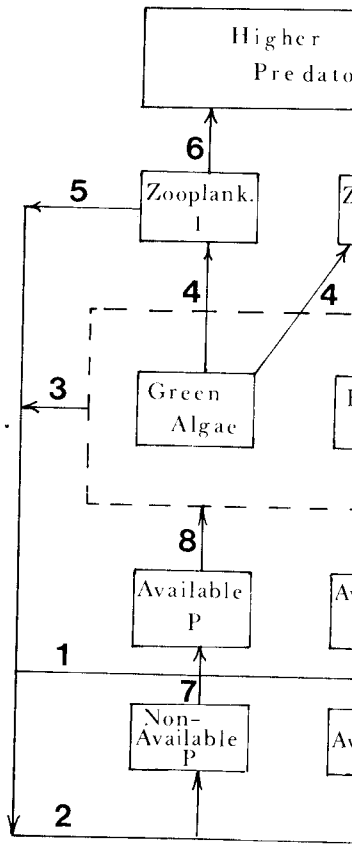
responsible for periodicity of phytoplankton was Pearsall (1932). In his studies of the net plankton of English lakes, he found that high nutrient levels in the spring caused a vernal diatom maximum that was often replaced by a chrysophycean when the silicate concentration fell and the nitrogen/phosphorus ratio rose. Later Hutchinson (1944) stressed that competitive interactions for nutrients between various species could be important factors in seasonal succession in lakes. As an example, he cited data from Linsley Pond, indicating that competition for phosphorus between *Fragilaria* and *Anabaena* was controlled by nitrate availability, with *Fragilaria* favored at high nitrate levels and *Anabaena* favored at low nitrogen levels.

More recently a number of authors (Bush and Welch 1972; Fitzgerald 1969; Shapiro 1973; and Stoermer 1973), have noted that variations in phosphorus and nitrogen levels, due to inputs and/or cycling, can have a causative effect on changes in species dominance. In this regard, a field study was undertaken to observe any correlations between nutrient levels and seasonal phytoplankton succession in a hypereutrophic lake (Stone Lake, Cassopolis, Michigan). The mechanisms behind the observed successional pattern can be qualitatively explained in terms of phosphorus and nitrogen levels in the epilimnion of the lake and a two-step process model of the kinetics of algal growth in eutrophic water bodies developed by Bierman, *et al.* (1973a, 1973b) and Verhoff, *et al.* (1972, 1973).

MODEL DESCRIPTION

The model utilizes separate nutrient transport and cell synthesis mechanisms to enable it to account for differences in nutrient uptake and storage and in intrinsic growth rate among phytoplankton species. Much experimental evidence (*e.g.*, Fuhs 1969, 1971; Droop 1973; Azad and Borchardt 1970; Caperon 1972, 1972b; and Eppley and Thomas 1969) indicates that the mechanisms of nutrient uptake and cell growth are quite distinct and that specific cell growth rates are dependent on intracellular levels of the limiting nutrients. This mechanism is in contrast to the classical Michaelis-Menten approach relating growth rates directly to medium nutrient concentrations.

The model components utilized in the application to Stone Lake are illustrated in Figure 6.1, which is a schematic of the nutrient compartments used in this case and the potential pathways of phosphorus and nitrogen between compartments. For the growth simulations employed herein, the epilimnion of Stone Lake during summer stratification was considered to be a completely mixed batch reactor (4 meters depth),



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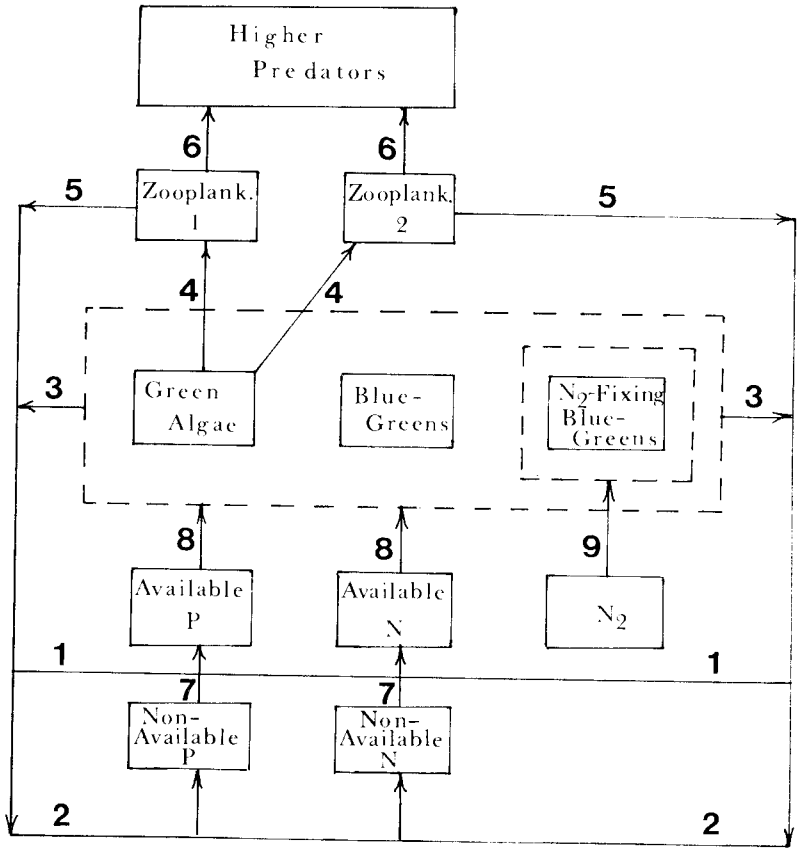

Figure 6.1 Schematic of the nutrient compartments used in the algal growth model for this study and the potential pathways of phosphorus and nitrogen between compartments.

with no external nutrient inputs and the only nutrient output being sinking of biomass into the hypolimnion. Note in Figure 6.1 that three important functional groups of phytoplankton are considered for this application: green algae and two blue-green algal groups, one of which can fix atmospheric nitrogen and the other of which must use dissolved, combined nitrogen. Different physiological input parameters and requirements (some based on species-specific data and others on estimations) have been assigned to the different groups, and along with other factors can explain the group successions.

The major working assumptions and specific coefficients used for the model applications in this paper are identical to those used by Bierman (1975) for Saginaw Bay, Lake Huron with the exception of those coefficients in Table 6.1. Since many of the coefficients in complex multiclass models must be estimated anyway, the different physical and hydrological characteristics between Stone Lake and Saginaw Bay naturally led to further ambiguities. Stone Lake has a very long hydraulic retention time (~6 years) and no significant external sources of nutrients, while Saginaw Bay has a retention time of only two months with heavy waste loadings from domestic as well as potentially inhibitory industrial sources. Also, it is unreasonable to assume that different algal species within a group would all have the same growth rate and sinking rate. Since the species list for Stone Lake is not the same as for Saginaw Bay, these parameters could easily vary from one application to another.

Table 6.1 Phytoplankton Parameters Unique to Stone Lake Application[a]

Parameter	Phytoplankton Group		
	Greens	Blue-Greens (non-N_2-fixing)	Blue-Greens (N_2-fixing)
Maximum growth rate (25°C) $(day)^{-1}$	1.6	1.1	1.1
Sinking rate (m/day)	0.3	0.1	0.1

[a]Remaining parameters used in this model application are detailed in Bierman (1975).

The model, of course, contains available phosphorus and nitrogen pools from which the algal groups can draw these nutrients. All other nutrients are considered to be in excess and never limiting. The box labeled N_2 indicates that when the concentration of available nitrogen falls below 300 μg N/l, the N_2-fixers gain a competitive advantage by fixing atmospheric nitrogen. This is a simplifying assumption based primarily on the work of Horne and Fogg (1970). For operation of the model, nitrogen fixation (pathway 9) is simulated by ignoring nitrogen transport from the medium by the N_2-fixers and arbitrarily setting the intracellular N at its maximum level. The specific growth rate as a function of nitrogen is therefore at its maximum level for the prevailing temperature and light attenuation conditions (Bierman 1975). This step has important repercussions on the nitrogen budget when these cells are lysed and decomposed with subsequent nutrient recycle.

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The model also includes nonavailable nutrient pools for phosphorus and nitrogen. Lines 1 and 7 represent inputs directly to the available pools, while line 2 represents the input to the nonavailable pools. Both pools are fed by the recycle of nutrients from the lysing and decomposition of algae (line 3) and from the excretion of zooplankton (line 5). Note that the zooplankton only graze the green algal group. The fraction of pathways 3 and 5, which goes into pathway 1, represents the recycle of excess phosphorus and nitrogen over the minimum cell stoichiometric requirements. DePinto (1975) found that *excess* intracellular phosphorus (present as inorganic phosphates) was rapidly released at the beginning of aerobic bacterial decomposition of laboratory cultures of *Chlorella vulgaris.* On the other hand, regeneration of organic cellular phosphorus was proportional to the degree of decomposition of the cellular organic matter. In line with this additional finding, the model places the minimum stoichiometric levels of phosphorus and nitrogen into the nonavailable pools (pathway 2). The resulting detrital material in these pools is then bacterially decomposed. In this way, phosphorus and nitrogen are slowly released back into the available pools via pathway 7.

The nutrient uptake step in this model involves a carrier-mediated transport of phosphorus and nitrogen using a reaction-diffusion mechanism presented by Verhoff, *et al.* (1973). The importance of this mechanism with respect to phytoplankton succession is that it allows the potential intermediate nutrient storage in excess of the cell's immediate metabolic needs, as well as species differences in nutrient uptake rates. In general, non-N_2-fixing blue-green algae appear to have the highest affinity for phosphorus (most efficient phosphorus transport system) followed by the N_2-fixing group, and finally green algae. With regard to nitrogen, all three groups are considered to have the same kinetics and stoichiometries and, therefore, compete on an equal basis for dissolved, combined nitrogen (except, of course, when N_2-fixation occurs). Due to the sparsity of data on nitrogen uptake, this assumption was necessary; however, the nitrogen uptake data of Fitzgerald (1968) seems to support this premise.

The second step in this model is cell synthesis, which operates independently of nutrient transport. Mass growth rate is related to the intracellular phosphorus levels according to the formalism of Fuhs (1969, 1971) and to the intracellular nitrogen levels according to the formalism of Caperon (1972). Whichever nutrient yields the lowest specific growth rate is considered to be limiting, and that limiting growth rate is the one used for the synthesis period under consideration. Temperature and light limitation are also considered in this model, where deviations from the optimum values cause reductions in specific growth rates as well as nutrient uptake rates (Bierman 1975). As far as algal group differences

in growth rates are concerned, green algae have intrinsically higher maximum phosphorus-dependent growth rates than blue-greens (Morton, *et al.* 1971; Payne 1973). Whether or not the specific growth rate of one algal group leads to its dominance over the others, however, depends on a great many factors other than its ability to grow under ideal conditions.

EXPERIMENTAL METHODS

The lake studied in this investigation is Stone Lake, located in the southern part of the State of Michigan (North 41° 45′, West 86°00). It is a dimictic, seepage lake with a surface area of approximately 61 hectares (150 acres). The maximum depth is 18.5 meters and the mean depth is 6 meters. Figure 6.2 is a hydrographic map of the lake charted by the University of Notre Dame (Tenney, *et al.* 1970).

Since Stone Lake is located immediately adjacent to the city of Cassopolis (population ~ 5000), beginning in 1939 it was used as the receiving water body for the wastewater effluent from the village. The lake received secondary effluent for approximately 27 years until, in 1965, a new wastewater treatment facility was built outside the drainage basin. Despite the almost complete curtailment of domestic pollution the lake has failed to show any significant improvement over the past 10 years. The continued hypereutrophic state of the lake is attributable to the 27 years of excessive inorganic nutrient inputs and a long hydraulic residence time (~ 6 years) which prevents flushing of these nutrients. Also, since the drainage basin of this lake (87 hectares or 215 acres) is relatively small in comparison with the surface area, the allochthonous nutrient inputs are quite small in comparison with the already high levels in the lake.

Based on rainfall data and analysis of total phosphorus concentrations in the runoff, it was estimated that the increase in total phosphorus concentration in the epilimnion over the six month period from mid-April to mid-October was approximately 17 μg P/l (Bierman 1973). This increase, due to external sources, amounts to less than 3% of the soluble orthophosphate concentration in the lake in January, 1973 (720 μg P/l). It is likely, therefore, that any fluctuations in nutrients in Stone Lake during summer stratification are due to internal cycling.

For this study, Stone Lake was monitored on a biweekly basis during the growing season of 1973. The following physical and chemical parameters were monitored: temperature, dissolved oxygen, pH, suspended solids, soluble orthophosphate, total phosphorus, soluble ammonia, nitrate and organic nitrogen. A quantitative and qualitative analysis of the phytoplankton community was made at the same time. All sampling was

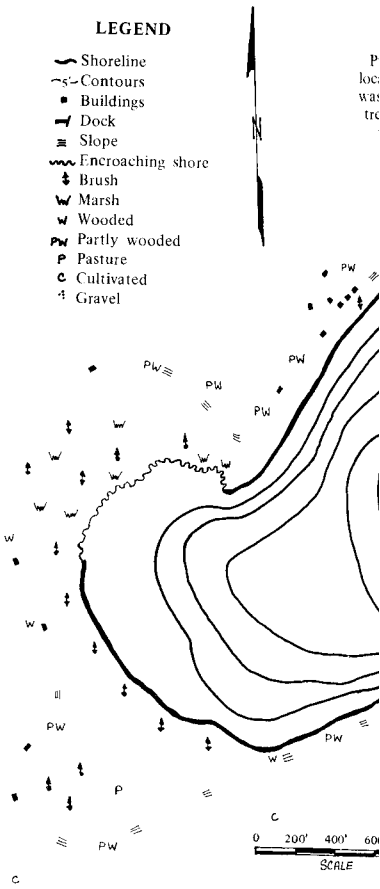

Figure 6.2 Hydrographic map at poi

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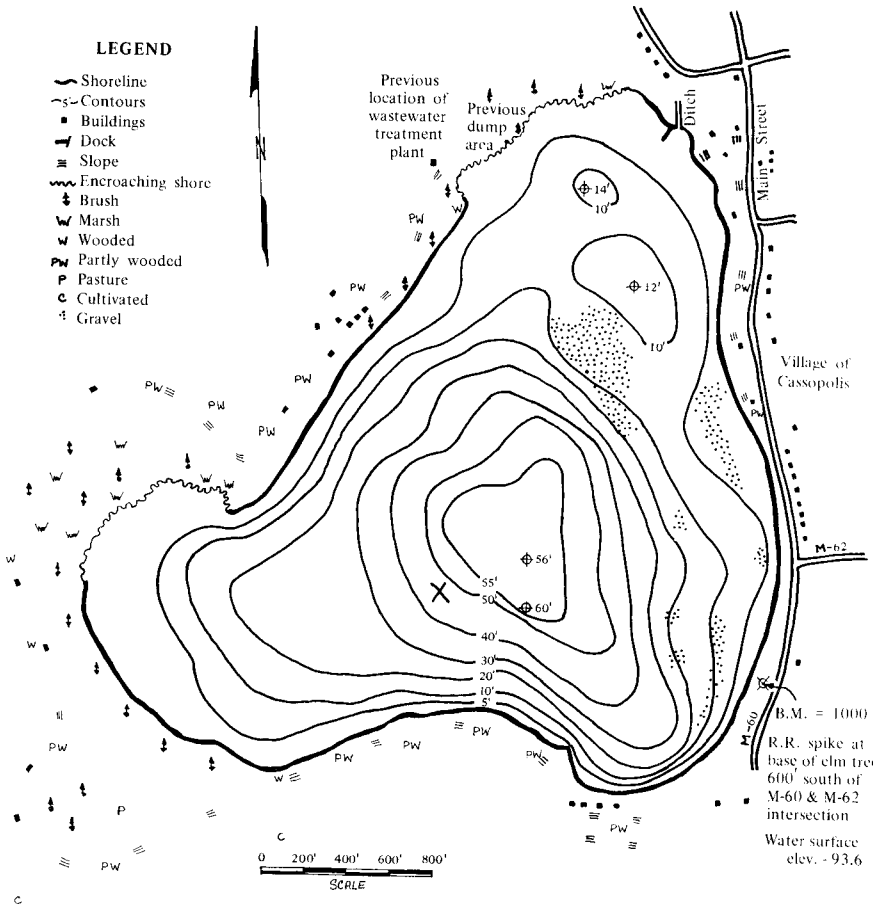

Figure 6.2 Hydrographic map of Stone Lake showing sampling station at point marked with X.

conducted at a sampling station located roughly in the center of the lake over the deepest point. The sampling station for this study, as indicated in Figure 6.2, was chosen to allow a study of the representative phytoplankton in the lake as well as a complete water column profile. A depth profile of all parameters was obtained by sampling at 1 meter intervals through the first 4 meters and then at 2 meter intervals from 6 through 14 meters.

Temperature and dissolved oxygen were measured in the field with an oxygen meter and probe. The remaining chemical parameters were determined by procedures described in *Standard Methods for the Examination of Water and Wastewater* (APHA 1971). Orthophosphate was determined by the stannous chloride method.

Phytoplankton samples were taken from the various depths in the lake with a plastic Kemmerer Sampler and preserved in formalin. Quantitative estimates were obtained by passing a suitable portion of the sample through a 1.2 μm membrane filter. The algae collected on the filter were stained with eosin Y and aniline blue (deNoyelles 1968), and the filters were dried and mounted in Permount to clear the filter for microscopic examination (McNabb 1960). Phytoplankton densities were obtained on the basis of the average number of cells (or groups of cells) per microscopic field (100x and 430x magnification) and the volume of water passing through the area of a given field.

Although the dominant phytoplankton found in the lake were keyed to the genus level, for the purpose of comparison of successional patterns with the model predictions the phytoplankton were categorized into three functional groups: (1) green algae, (2) non-N_2-fixing blue-green algae, and (3) N_2-fixing blue-green algae. A fourth group, diatoms, was not observed in significant numbers during the period of investigation (May-October, 1973). Cell counts were converted to dry weight biomass for the model application by applying the following conversion factors: 0.27×10^{-7} mg dry wt/cell (Barber 1968) for greens, 0.25×10^{-7} mg dry wt/cell for non-N_2-fixing blue-greens (AAP 1971), and 0.41×10^{-7} mg dry wt/cell for N_2-fixers (AAP 1971).

RESULTS OF LAKE MONITORING

For the purposes of this study we were interested in observing the nutrient-phytoplankton relationships in the epilimnion of a summer stratified lake. Figure 6.3 is a temperature isopleth for Stone Lake in which the two turnover periods and the thermal stratification period are graphically illustrated. The spring turnover occurred in late March with mixing conditions present until the middle of May. By the end of May a fairly stable thermal stratification had developed, lasting until the fall turnover at the end of October. Based on this temperature contour an average epilimnion depth of 4 meters was chosen for this study. Averages of the orthophosphate and inorganic nitrogen levels and phytoplankton biomass through the epilimnion for the stratification period from the end of May through the end of October are presented for analysis.

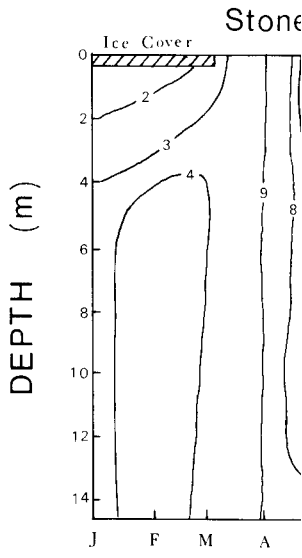

Figure 6.3 The temperature
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Phytoplankton Succession

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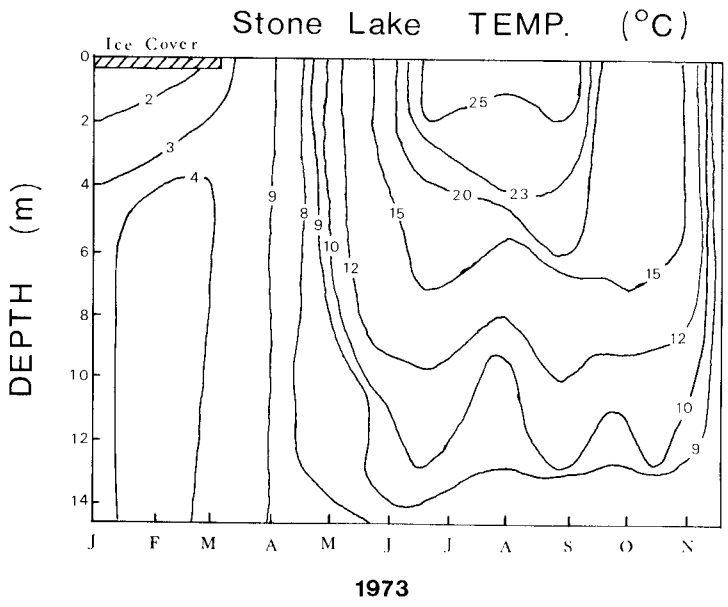

Figure 6.3 The temperature isopleth for Stone Lake (1973) indicates a fairly stable thermal stratification from the beginning of June through October.

Phytoplankton Succession

Like many eutrophic lakes, Stone Lake is a highly unstable system, and its phytoplankton assemblage is, therefore, prone to domination by only one or two species at any given time. This tendency is illustrated by noting the composition of the major blooms occurring in the lake. The relative magnitude and timing of the blooms are shown in Figure 6.4, which is a plot of the average phytoplankton biomass (dry weight) in the upper 4 meters of Stone Lake during the summer stratification. The graph illustrates the variation not only of the total crop but also of the three functional groups discussed above. The total crop exhibited two prominent peaks, one in late July and the other in October. The first peak was composed of two somewhat overlapping blooms, first a N_2-fixing bloom of *Aphonizomenon* and *Anabaena* followed closely by a non-nitrogen-fixing bloom consisting primarily of *Microcystis*. Although the green algae group had been represented by a small but diverse population throughout the summer, it was not until late September that this group attained any appreciable biomass. This second major peak in the

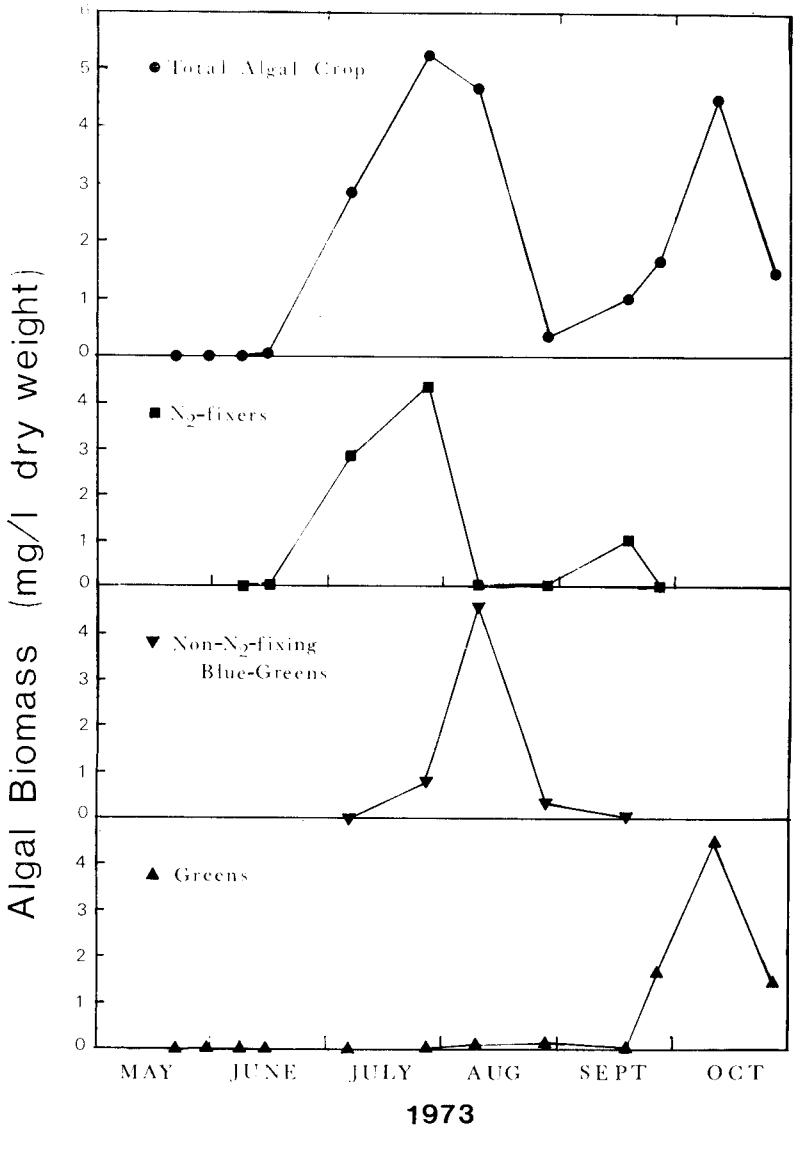

Figure 6.4 The average phytoplankton biomass (dry weight) in the upper four meters of Stone Lake during the summer stratification illustrates the unstable nature of the system.

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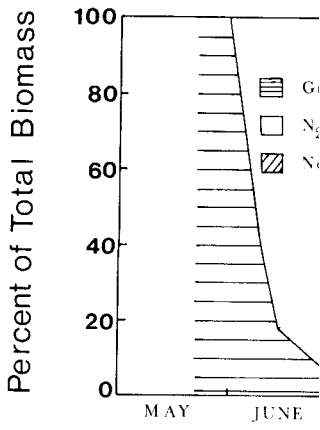

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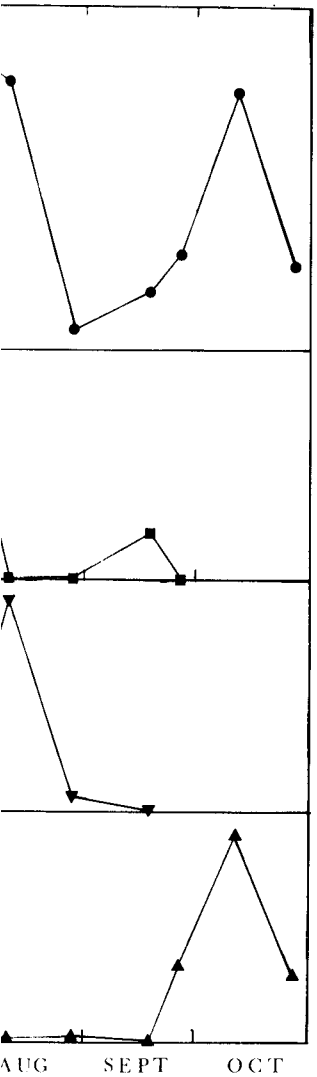

ıass (dry weight) in the upper
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total crop can be attributed mainly to the bloom-forming green algae *Microspora*, although other green algae contributed to the production during this period.

It should be mentioned at this point that the authors are aware that perhaps two weeks between sampling dates (see Figure 6.4) is probably too long for a phytoplankton successional study. There is no question that more frequent sampling would have provided a better curve and maximum biomass for the algal blooms; nevertheless, it can be stated that phytoplankton concentrations are probably changing at least as fast as indicated in Figure 6.4. Also, the rapid increase and decrease of algae blooms has been evident in suspended solids data throughout the previous seven years of observation of Stone Lake (Theis, *et al.* 1975). It is believed, therefore, that these data are sufficient for the purposes of this study.

The successional pattern of the three phytoplankton groups is more easily visualized in Figure 6.5, which is a graphic illustration of the percentage of the total phytoplankton biomass occupied by each group.

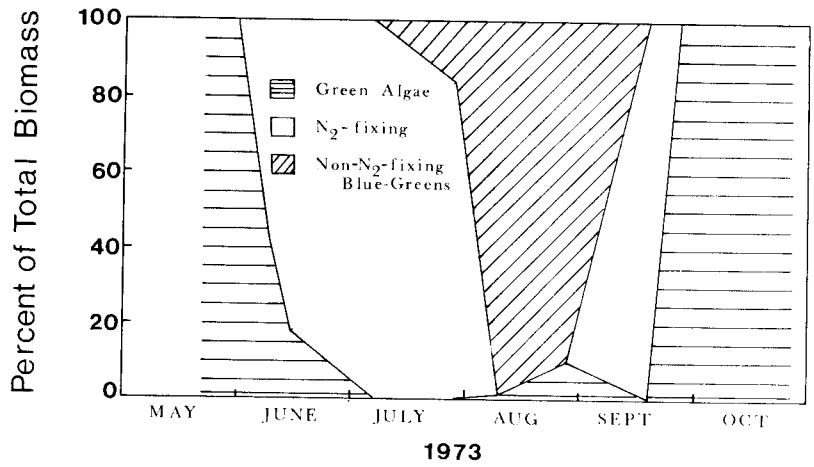

Figure 6.5 The phytoplankton succession in Stone Lake during the summer of 1973 is summarized as a cyclic pattern from non-N_2-fixing algae to N_2-fixing algae and back again, a cycle that is repeated twice during this time period.

The rapid and almost complete shifts in group dominance can be fully appreciated with this type of figure. In the early stages of stratification a small (less than 1 mg/l dry weight) but relatively diverse group of green algae were the only phytoplankton present. By the beginning of July, however, the N_2-fixing group accounted for virtually 100% of the algal

biomass. The next shift came towards the end of July and favored the non-N_2-fixing blue-green *Microcystis* in combination with some greens. This bloom preceded another N_2-fixing peak (exclusively *Anabaena*) in September. Finally, towards the end of summer stratification, the green algae group regained the majority of the total biomass. The phytoplankton succession in Stone Lake during the summer of 1973 can therefore be summarized as a cyclic pattern from non-N_2-fixing algae (greens and non-N_2-fixing blue-greens) to N_2-fixing blue-greens and back again. This cycle repeated itself twice from May through October.

Nutrient Variations

As indicated earlier Stone Lake has an extremely high level of phosphorus throughout the year (Figure 6.6). At no point in time or depth did the soluble orthophosphate concentration go below 1.0 mg/l as PO_4 (326 μg P/l). This concentration is extremely high even in comparison with other eutrophic lakes. For example, the soluble reactive phosphorus at 5-meter depth in Lake Erie varies from 1 to 11 μg P/l, and the total phosphorus at the same depth ranges from 15 to 50 μg P/l (Great Lakes Water Quality Board 1973). It is therefore highly unlikely that phosphorus is limiting at any time in Stone Lake.

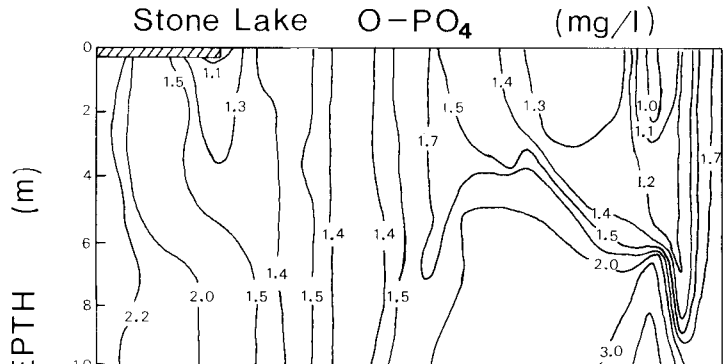

Figure 6.6 The soluble orthophosphate isopleth for Stone Lake (1973) graphically points out the constant high levels of this nutrient during the period of study.

A plot of the average soluble or
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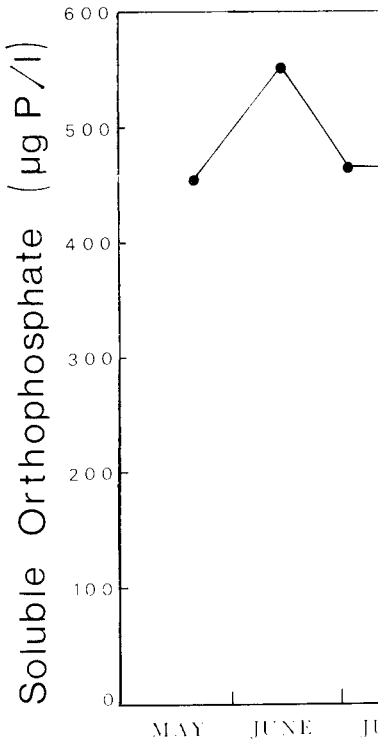

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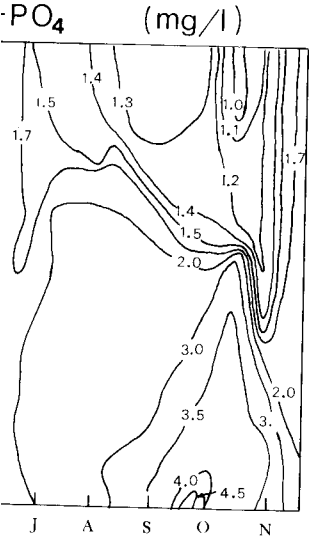

isopleth for Stone Lake (1973)
high levels of this nutrient
of study.

A plot of the average soluble orthophosphate concentration in the epilimnion through the summer stratification period is presented in Figure 6.7. With the exception of a sharp rise in early June and a sharp decline in mid-October, the phosphorus level in the epilimnion remains relatively

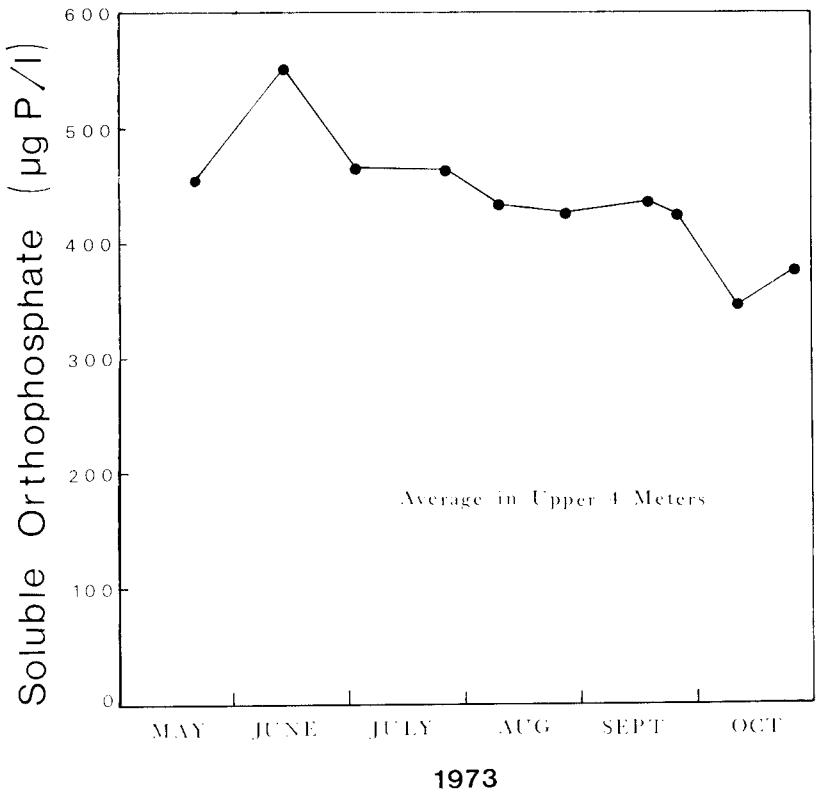

Figure 6.7 A relatively small percentage of the available phosphorus in the epilimnion of Stone Lake was utilized for algal growth.

unchanged. It is worthy of note that the 100 μg P/l increase from May 21 through June 14 coincided with the die-off of a large-rooted macrophyte growth that covered approximately one-third of the lake bottom. The subsequent decrease in phosphorus back to the previous level coincides with the onset of the large nitrogen-fixing cyanophyte bloom in the last half of June. Subsequent algal growth did little to further reduce the phosphate until the large green algae bloom in October apparently

caused about an 80 μg P/l decrease in soluble orthophosphate. This apparent additional phosphorus requirement may be explained by the fact that some green algae that tend to develop in hypereutrophic environments have higher minimum intracellular phosphorus requirements than blue-greens (Soeder, *et al.* 1971; Uhlmann 1971).

It is obvious from the above discussion that some physical or chemical parameter besides phosphorus is limiting the size of the algal community in Stone Lake. On the other hand, combined inorganic nitrogen appears to be an important factor in regulating the seasonal succession of the three phytoplankton groups in question. In contrast to phosphorus, the nitrogen levels in the epilimnion of Stone Lake at the beginning of this study are quite low for a eutrophic system (Figures 6.8 and 6.9). A plot of the combined inorganic nitrogen in the epilimnion of the lake reveals that the average nitrogen level was about 100 μg N/l at the onset of stratification (Figure 6.10). These low nitrogen levels coincided with the onset of the nitrogen-fixing blue-green bloom (*Aphanizomenon* and *Anabaena*) in the last two weeks of June. It is also noteworthy that the apparent high rate of nitrogen fixation during late June and early July corresponded to a rather dramatic increase in the soluble inorganic nitrogen in the euphotic zone. Although N_2-fixation itself was never actually measured (*e.g.*, acetylene reduction), heterocysts were observed during this bloom. Also, the model simulations suggest that it is not likely that this rise in the inorganic nitrogen concentration was entirely due to external inputs.

A decrease in nitrogen through August was closely correlated with the *Microcystis* bloom during that month. Again, immediately following the nitrogen dip, a bloom of N_2-fixing *Anabaena* became predominant. Inorganic nitrogen levels rose sharply in the lake through October. Based on the magnitude of this increase (Figure 6.10), it is highly unlikely that this rise in nitrogen levels was due entirely to nitrogen regeneration in the upper waters of the lake. Based on Figures 6.8 and 6.9, it is apparent that the majority of the combined nitrogen increase in the lake was the result of ammonia increase. The gradual build-up of ammonia in the hypolimnion of the lake (probably due to decomposition of falling plankton and deamination of organic nitrogen compounds in the sediments) through the summer (Figure 6.8) and the decreased thermal stability undoubtedly contributed to the rise in surface values through a vertical transport mechanism. Regardless of its source, this large increase in inorganic nitrogen may well have been the stimulus for the substantial green algae bloom in October.

One could characterize the nitrogen-phytoplankton relationship in this particular lake by saying that given the high available phosphorus levels,

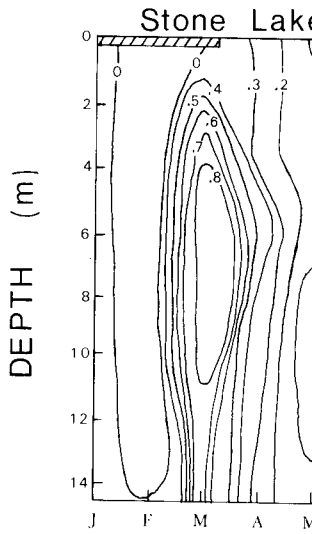

Figure 6.8 Very low NH_3-N levels w
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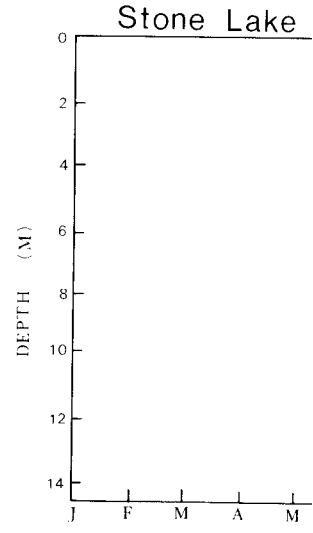

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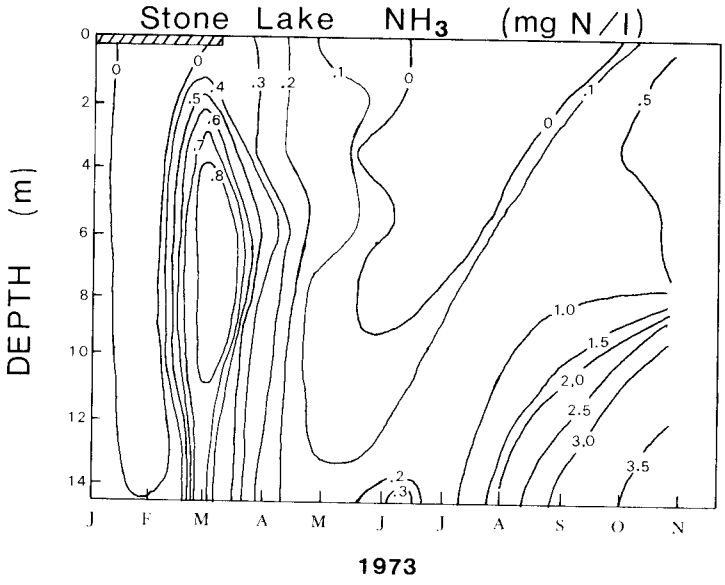

Figure 6.8 Very low NH_3-N levels were noted in the surface waters of Stone Lake until the concentrations began to build up in the hypolimnion and the thermal stratification began to break down.

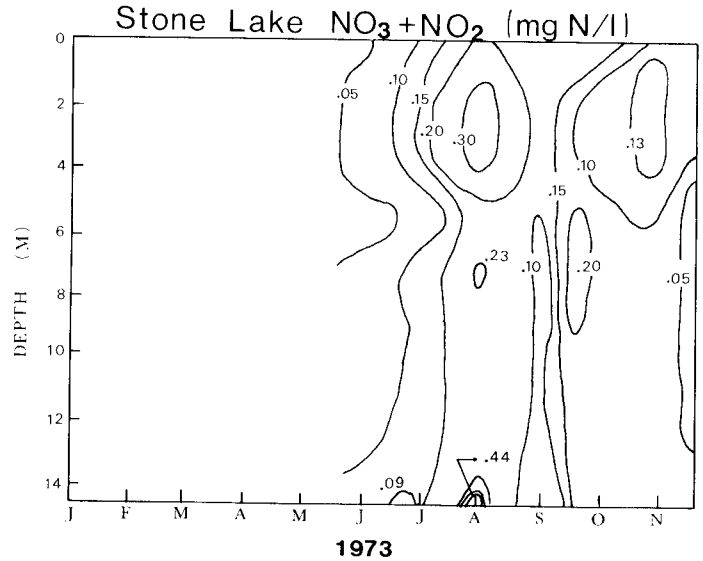

Figure 6.9 Nitrate regeneration occurs through July, during the period of N_2-fixing blue-green algae dominance.

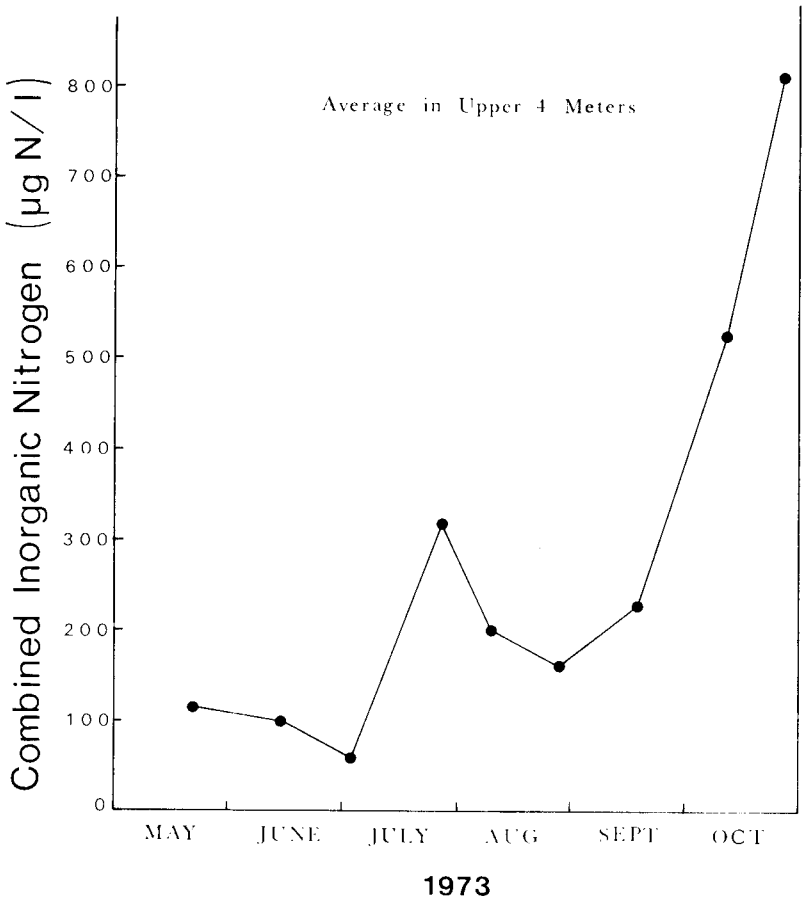

Figure 6.10 At minimum values of combined inorganic nitrogen in the upper four meters of Stone Lake, the N_2-fixing algae were dominant. Their activity apparently recharged the surface waters with available nitrogen.

the system favors a succession towards N_2-fixing blue-green algae when combined inorganic nitrogen concentrations in the euphotic zone drop below about 200 µg N/l. This tendency for nitrogen-deficient conditions to provide a competitive advantage to N_2-fixing algae has been observed by others (Ogawa and Carr 1969; Vanderhoef, *et al.* 1974).

COMPARISON WITH MODEL SI

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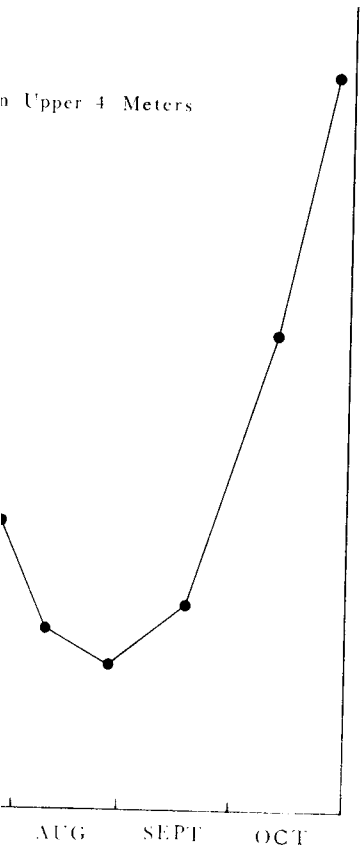

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COMPARISON WITH MODEL SIMULATIONS

The application of the algal growth model to the Stone Lake data reveals some very interesting insights into the mechanisms involved in phytoplankton growth and succession. Since phosphorus is present in vast excess it appears that the nitrogen dynamics, in particular, N_2-fixation and nitrogen recycle, play a large role in determining phytoplankton group dominance. Also of significance is the means with which the model handles the death rate (decay rate) of the algal blooms. It will become obvious that some death mechanism other than nutrient or light limitation must be important; from the studies of DePinto (1975) the mechanism appears to be heterotrophic activity. The following model simulations will concentrate on illustrating the importance of the mechanisms of N_2-fixation, nitrogen regeneration, and algal death rates in regulating the Stone Lake phytoplankton periodicity. It should be understood that these simulations are not predictive in nature but are only attempts to describe a given data set and to ask research questions.

The best model simulation of the Stone Lake data was obtained when atmospheric nitrogen was allowed as a source of available nitrogen for the N_2-fixing group (providing an unlimited supply of available nitrogen), nitrogen regeneration from all three algal groups contributed to the available nitrogen pool, and a stringent mechanism for the decline of algal group blooms was applied (Figure 6.11). Of these three mechanisms the most difficult one to include in this model was the decay of the phytoplankton blooms. Since the data of DePinto (1975) indicates that most of the nutrients contained within the algae can be released within 30 days of microbial degradation in the dark, the algal decay mechanism must reflect this finding. To model this phenomenon properly, however, a component of heterotrophic microbes containing various degradation stoichiometries should be included. But the interest of this report was to examine the effect of differences in algal groups, and hence, insufficient information on the heterotrophic activity made it impossible to incorporate this component on anything but an arbitrary basis.

A simple description of the decay process might clarify it. As the algal crop increases, more carbonaceous materials become available for microbiological decay; the microbe population then also increases but with some lag behind the algae. Because of the intrinsically more rapid growth rate of the heterotrophic bacteria, however, their ability to degrade the algae eventually surpasses the rate of algal growth. As a result a rapid decrease in the algal population ensues and is then followed by a decline in heterotrophic activity.

There are several ways in which this phenomenon of microbial decay can arbitrarily be included in the model. Generally we can say that this

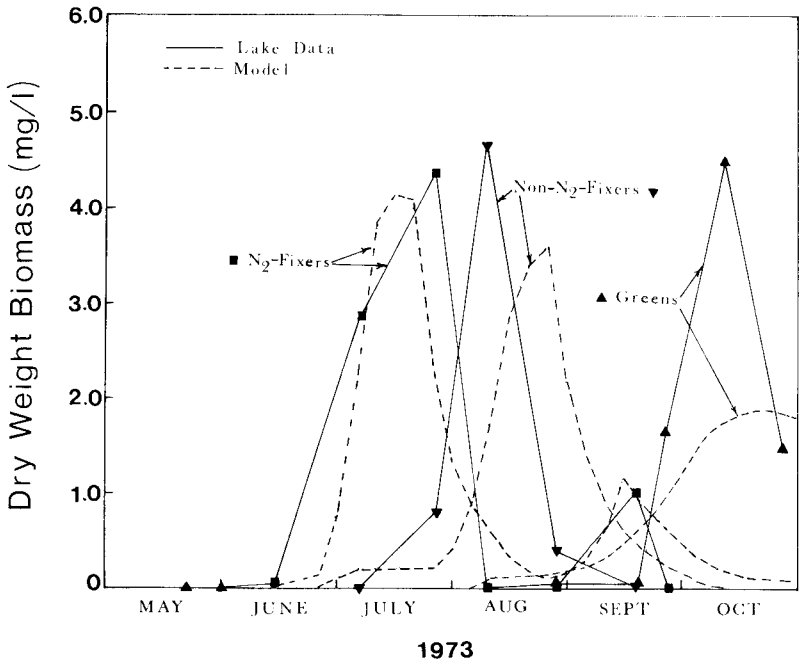


Figure 6.11 The best model simulation was obtained by allowing nitrogen fixation and regeneration and by employing a second-order decay term for each algal group based on its biomass and the biomass of the total crop. In addition the specific growth rate of each group was constrained to zero as that particular group reached its peak.

decay rate not only depends upon the algal concentration at a given instant but also upon the previous 30 days. One way of including this factor is to employ, as a variable, the average algal concentration over some previous period or possibly the integral of the concentration minus some steady-state value. The easiest way, however, is to adjust the growth and decay rates as algal concentrations get high. This is essentially the procedure used here. For each algal group the death mechanism includes a second order algal decay term that is proportional to the product of the dry weight biomass of the group in question and the biomass of the entire phytoplankton assemblage. This term represents an algal death (or lysing) rate, which is at its largest during the peak of any bloom but which also depends on the abundance of other algal groups, representing a competitive inhibition. This decay term takes the form

r_i

where

k = decay constant [day · °C ·

T = water temperature [°C]

r_i = change in biomass of i^{th} al

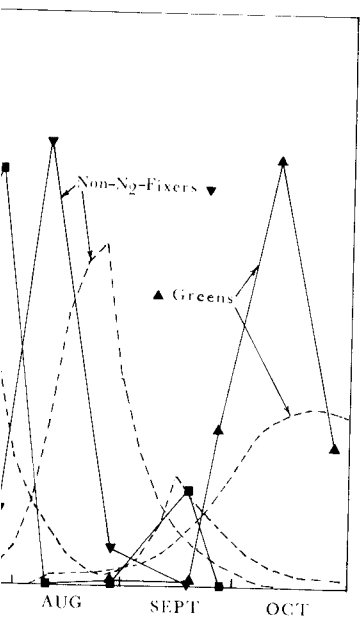
A_i = biomass of i^{th} algal group

A_t = biomass of total algal crop

It can be used to adjust the biomas over any given time period. The tion is 0.0015 (day · °C · mg/l)$^{-1}$ experiments on aerobic decomposi (1971) and DePinto (1975).

This decay term is not sufficie algal blooms observed in Stone La high heterotrophic activity. Thus, on the individual algal groups dur growth rate, which is the only po determining equation, was arbitrar mental data indicated that an indi Likewise, when the experimental group had reached its minimum, t removed. While a zero growth rat the simplest method of simulating algae.

A close inspection of Figure 6. the above elements compares quite the exact timing and maximum bi the important thing to notice is th simulated and their timing and bio only drastic difference between the be in the rather low model predict October. This variation can be eas model as applied here considers on external inputs and, therefore, does addition of nitrogen to the availab plankton decomposition and zoopla bloom, which the model predicts, the October combined inorganic ni high due to probable input of amm discrepancy is graphically illustrate



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$$r_i = -k \cdot T \cdot A_i \cdot A_t$$

where

k = decay constant [day · °C · mg/l]$^{-1}$
T = water temperature [°C]
r_i = change in biomass of i^{th} algal group due to lysing [mg/l · day]
A_i = biomass of i^{th} algal group [mg/l]
A_t = biomass of total algal crop [mg/l]

It can be used to adjust the biomass obtained from the growth rate term over any given time period. The value for k used in this model application is 0.0015 (day · °C · mg/l)$^{-1}$, which is consistent with the laboratory experiments on aerobic decomposition of algae by Jewell and McCarty (1971) and DePinto (1975).

This decay term is not sufficient to explain the rapid declines of the algal blooms observed in Stone Lake and, as might be expected, from high heterotrophic activity. Thus, an additional constraint was placed on the individual algal groups during their domination. The specific growth rate, which is the only positive term in the phytoplankter biomass-determining equation, was arbitrarily set equal to zero when the experimental data indicated that an individual algal group was on the decline. Likewise, when the experimental data indicated that a particular algal group had reached its minimum, the zero growth rate constraint was removed. While a zero growth rate is unlikely, this constraint is about the simplest method of simulating the effect of microbial degradation of algae.

A close inspection of Figure 6.11 reveals that the model incorporating the above elements compares quite favorably with the lake data. Although the exact timing and maximum biomass of each bloom is not reproduced, the important thing to notice is that the relative succession of groups is simulated and their timing and biomass are qualitatively represented. The only drastic difference between the model and the lake data appears to be in the rather low model prediction for the green algal bloom in October. This variation can be easily explained by realizing that the model as applied here considers only the epilimnion of the lake with no external inputs and, therefore, does not contain a mechanism for the addition of nitrogen to the available pool other than recycle from phytoplankton decomposition and zooplankton excretion. As a result, the green bloom, which the model predicts, becomes nitrogen-limited while in reality the October combined inorganic nitrogen levels in upper waters are quite high due to probable input of ammonia from the hypolimnion. This discrepancy is graphically illustrated in Figure 6.12. Note that the model

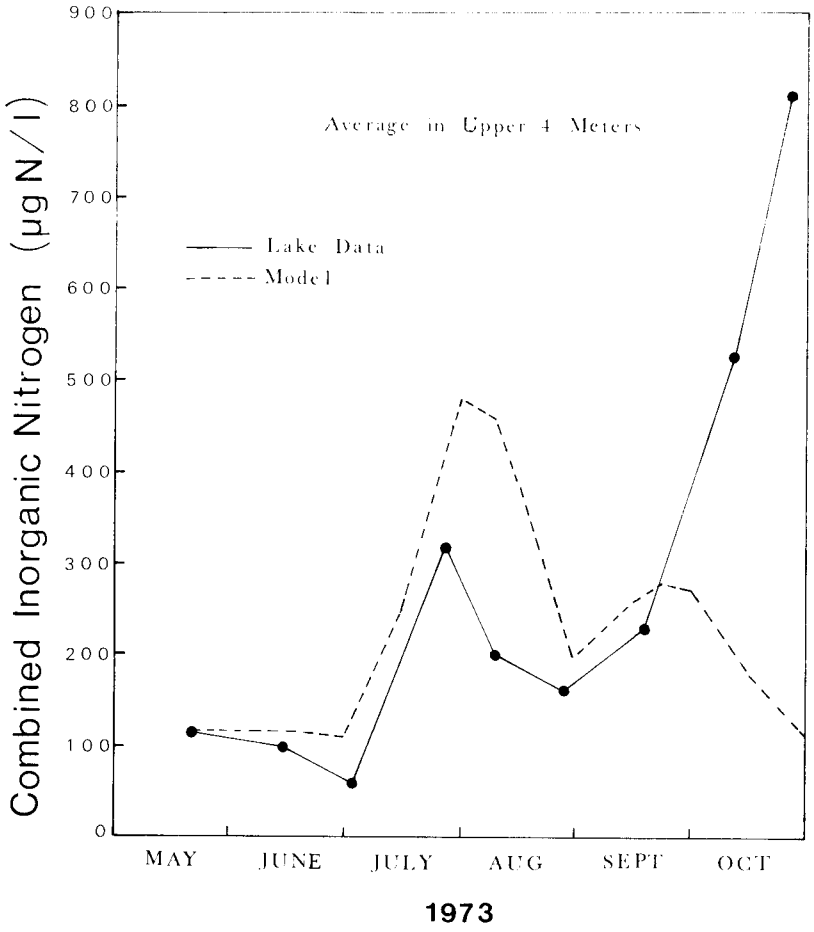
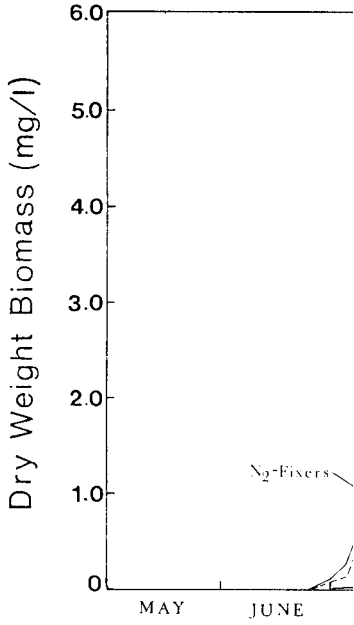


Figure 6.12 Much of the large increase in combined inorganic nitrogen in the surface waters during October is due to factors for which the model cannot account.

predicts the large nitrogen regeneration from the July N_2-fixing bloom. According to the model, however, the green algae rapidly reduce the a available nitrogen level to the point where it becomes limiting.

In order to best see the effect of the nitrogen dynamics and algal death mechanism, it is appropriate to examine model simulations with each of the factors discussed above individually "turned off." Figure 6.13 demonstrates the importance of N_2-fixation in this particular system. It represents the model output of the phytoplankton growth curves when



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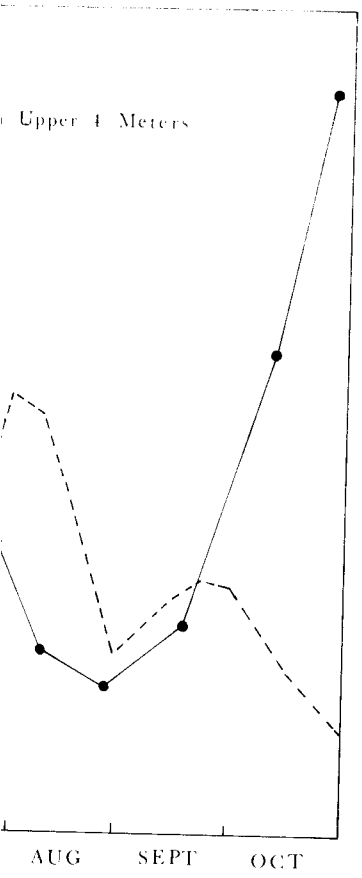

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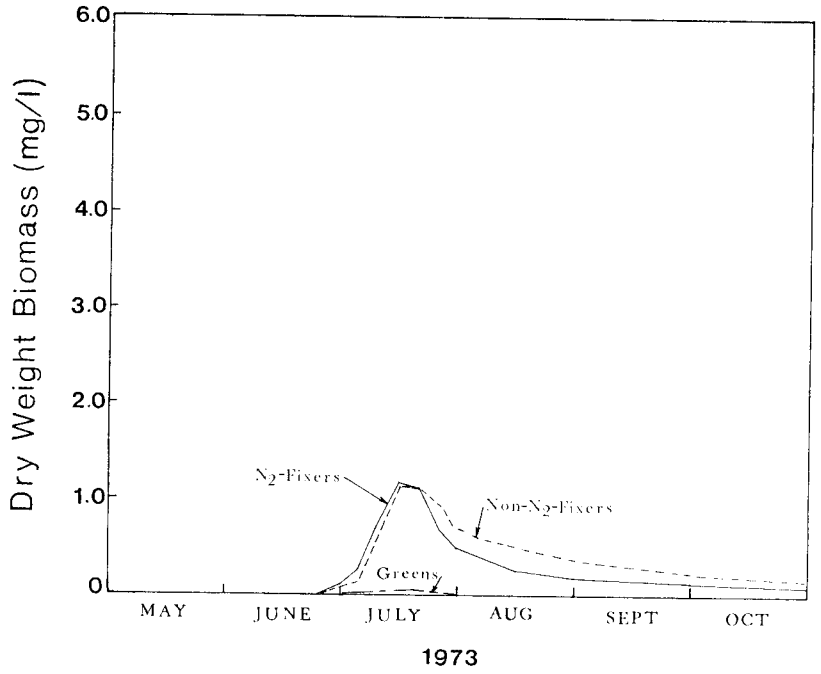

Figure 6.13 The model simulation with N_2-fixation turned off graphically illustrates the importance of this nutrient source in Stone Lake.

the only change in the model is that the N_2-fixing group is *not* allowed to have an unlimited nitrogen source via the atmosphere. From this graph it is obvious that it is nitrogen fixation and the subsequent recycle of this fixed nitrogen that allows the development of the large blooms observed in Stone Lake. Although not shown here, the model predicts that the combined inorganic nitrogen level in the epilimnion of the lake drops to essentially zero by the middle of July. Thus the system becomes severely nitrogen-limited without N_2-fixation as a source.

To see the importance of the regeneration of the fixed nitrogen in this system, the model was run allowing N_2-fixation but with all nitrogen recycle turned off. The only remaining potential source of nitrogen to the available pool was the possible leakage of intracellular nitrogen back to solution under conditions when the external medium concentrations became quite low and the intracellular concentrations of a particular group (most likely the N_2-fixing blue-greens) greatly exceeded the minimum stoichiometric amounts. The model simulation of the algal system

under these circumstances is shown in Figure 6.14. Note that the absence of nitrogen recycle has little effect on the N_2-fixing blue-greens. Comparison of Figure 6.14 with Figure 6.11, however, reveals that the key effect of excluding nitrogen recycle is to induce nitrogen limitation on the two algal groups that require NH_3-N or NO_3-N as their nitrogen source. There is a small *Microcystis* bloom in August that develops from the small amount of available nitrogen present in the system at the start of the season. This non-N_2-fixing blue-green peak, however, is only one-third the size of the actual *Microcystis* bloom that occurred in the lake. It nevertheless uses practically the whole available nitrogen pool, thus preventing the development of a green algae group. Some nitrogen does leak back into the medium ($\sim$ 50 μg N/l) during the second N_2-fixing bloom, but the amount is too small to aid in the development of a green bloom.

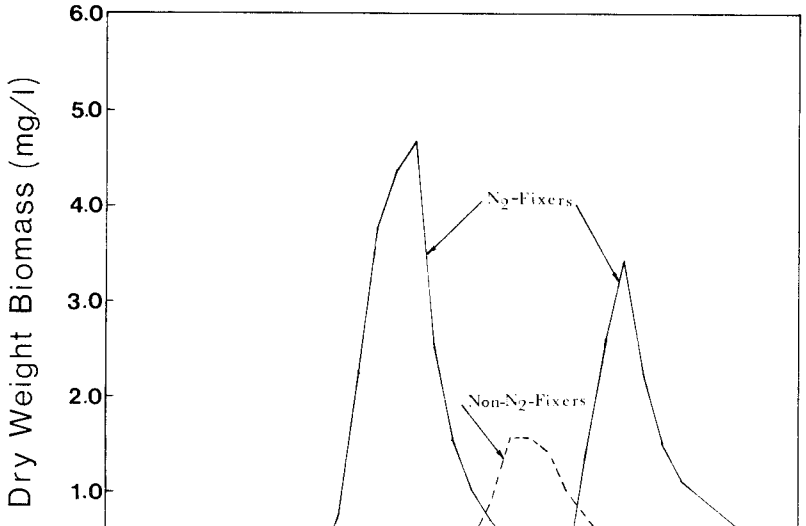

Figure 6.14 Without nitrogen recycle the model predicts that non-N_2-fixing algae never attain significant levels, while the nitrogen recycle has little effect on the algae capable of fixing nitrogen from the atmosphere.

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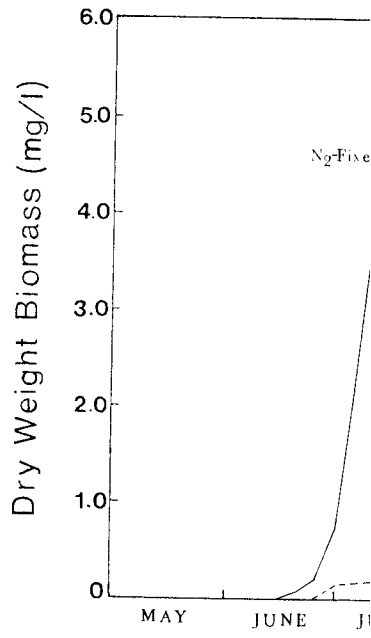

Figure 6.15 This model simulation ill
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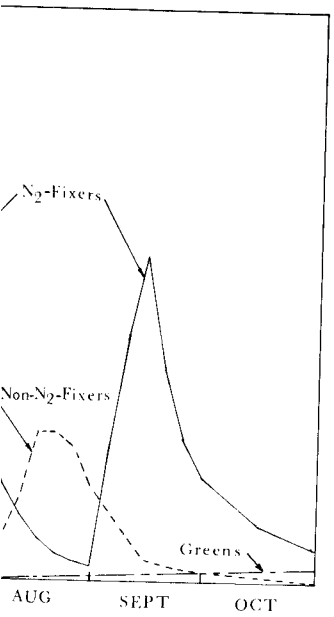


el predicts that non-N_2-fixing algae
rogen recycle has little effect
from the atmosphere.

The remainder of the model simulations are intended to demonstrate the importance of a death mechanism in the timing of phytoplankton succession. With this intent the model was run without the specific growth rate constraint previously employed but with the second order decay term. The results of this simulation are shown in Figure 6.15.

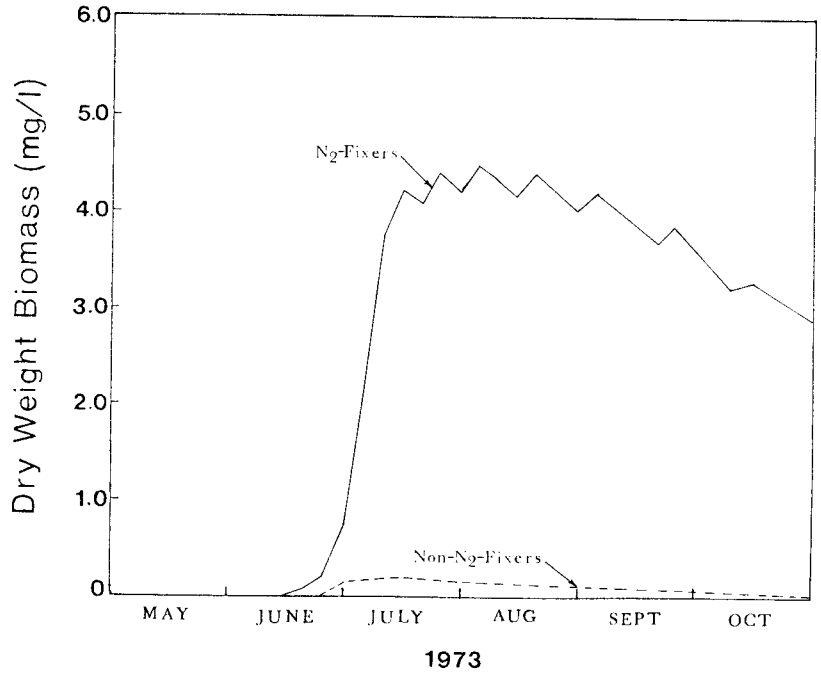


Figure 6.15 This model simulation illustrates that a second order algal decay term alone is not enough to simulate algal bloom declines and the relative timing of succession.

In this run the rise of the N_2-fixing bloom is as before; however, the decay term alone is not enough to induce the rapid decline of this bloom. As a result the N_2-fixers dominate the assemblage throughout the growing season, even though sufficient nitrogen has been introduced into the medium by recycle to stimulate blooms in the other two groups. No such blooms occur, however, primarily because the decay term, the magnitude of which is a function of the total crop, is too large to allow their development. Although interspecies competition and inhibition certainly may exist, they rarely operate to the extent that once a species is dominant it remains so to the exclusion of all others.

Since the above simulation proved to be unrealistic, it was thought that perhaps the decay term should be group specific rather than depending also on the total crop. Therefore, a simulation was made with unconstrained specific growth rates and second order algal decay term proportional to the square of the given algal group biomass to which it is applied ($r_i = - k \cdot T \cdot A_i^2$). In this case (Figure 6.16) all three groups develop a bloom, but the individual decay terms alone are insufficient to simulate the biomass declines. The blooms gradually wane, primarily because of light limitation, but without a specific growth rate constraint these decay mechanisms are not large enough to counteract the phytoplankton growth term.

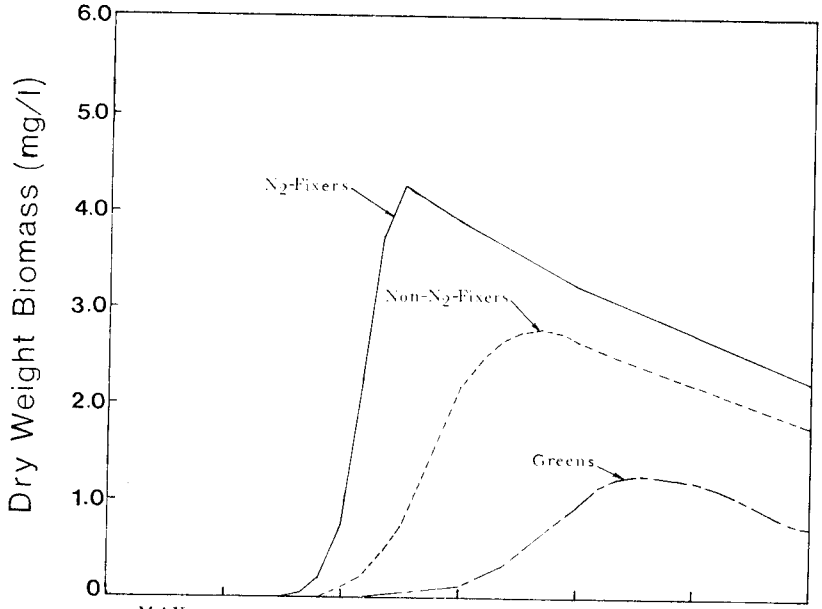
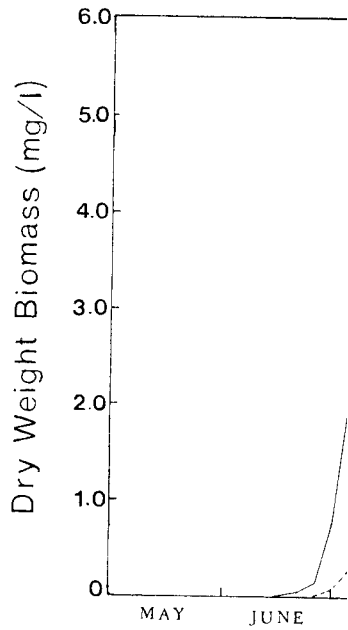


Figure 6.16 An algal group-specific second-order decay term without the growth rate constraint also failed to simulate phytoplankton periodicity.

A better comparison between the two decay terms used is afforded by comparing Figure 6.17 (group-specific decay term) with Figure 6.11. The run that produced Figure 6.17 is identical with the run for Figure 6.11 except that the second-order decay term is a function of the square of the individual group biomass. This simulation is quite reasonable in



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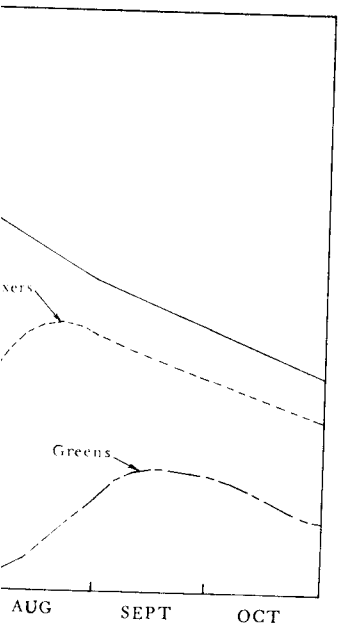

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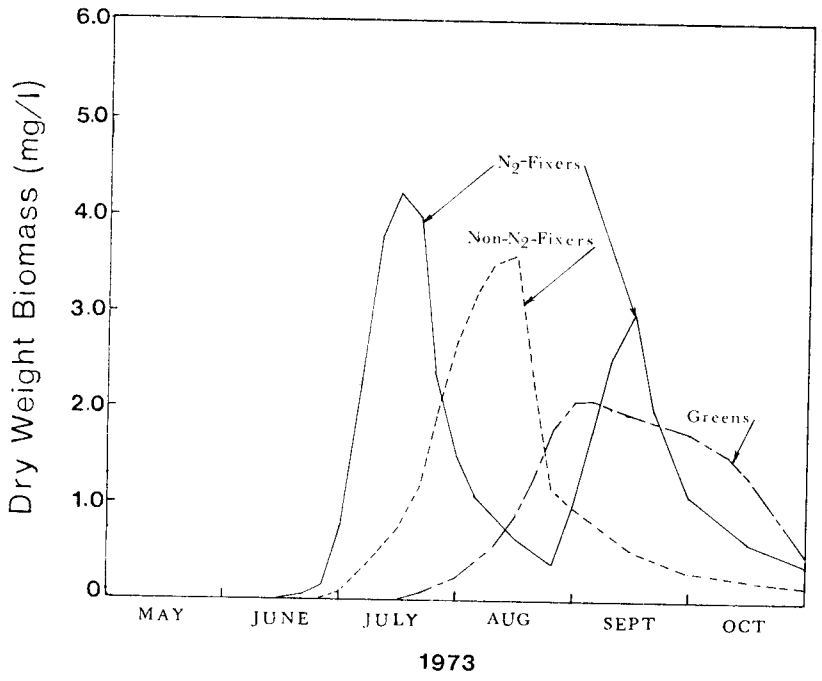

Figure 6.17 This simulation is identical with that shown in Figure 6.11 except that the decay term is group-specific. Note that the green algae develop much sooner and the second N_2-fixer bloom attains roughly three times the biomass.

that it more accurately predicts the development of the first two blooms; however, it also allows the green algae to develop much sooner than in the first run because their decay term is not affected by the total crop at that time. While one might say that Figure 6.11 is a slightly better representation of the lake data, in reality a mixture of the two conditions would probably be best.

The comparison of Figures 6.11 and 6.17 points out a fundamental question that can only be answered by further experimental research: Why can one algal group apparently grow exponentially in the presence of a bacteria community that is destroying another algal group? A definitive answer to this question is not within the scope of this study; however, some possibilities include: different bacterial species degrade different algal species, the bacterial community has become adapted to the original bloom and a lag time is required before the bacteria can

affect the new algal group, or other environmental conditions favor the growth of the new algal group to the extent that bacterial decay is a small perturbation on their large growth rate.

DISCUSSION AND CONCLUSIONS

The application of the two-step algal growth model employed in this study brought to light three basic observations about the seasonal phytoplankton succession in Stone Lake (an example of a hypereutrophic lake). The first obvious conclusion, based solely on the data, is that the constant excess of available phosphorus allows all phytoplankton species to pursue their control strategies regardless of any phosphorus stoichiometric differences. It should also be pointed out that the same situation very likely exists for carbon since the average alkalinity of the lake is 120-140 mg/l as $CaCO_3$ and the pH is typically 8 to 9 in the surface waters.

The second observation is that nitrogen fixation and its subsequent recycle is probably the primary reason for the large blooms occurring in Stone Lake. The relatively rapid regeneration of fixed nitrogen appears to play an important role in aquatic systems with low flushing rates. On the other hand, Verhoff, *et al.* (1975) have shown that nutrient recycle does not significantly affect systems with very short retention times (fast moving rivers, for example). Stone Lake, however, has a relatively long hydraulic retention time. In this case the Stone Lake example showed first that the activity of nitrogen-fixing blue-green algae can recharge the upper waters of a lake system with sufficient combined inorganic nitrogen to promote the resurgence of non-N_2-fixer blooms. It also confirmed that the model's output was consistent with the hypothesis that a substantial portion of the nutrients taken up by the plankton in the epilimnion of a stratified lake can be returned to the soluble inorganic state for reuse during the same growing season.

Finally, it should be stressed that our first attempts to describe the Stone Lake data with a relatively sophisticated multiclass model based strictly on phosphorus and nitrogen dynamics [with temperature, light, and zooplankton grazing factors (Biermann 1975)] failed to completely explain the successional pattern. It was obvious that something, unaccounted for by the model, was occurring in the lake and that this interaction was instrumental in the rapid decline of the algal blooms. Controlled laboratory investigations (DePinto 1975) indicated that the magnitude of the heterotrophic bacterial population could be a significant factor in causing the crash of algal blooms and the subsequent nutrient regeneration. In this study it was noted that 53-95% decomposition (as measured by percent reduction in particulate COD) occurred in bacterial-inoculated *Chlorella vulgaris* cultures in less than a two-month,

dark incubation period, about on
The fact that bacteria-free *Chlore*
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REFERENCES

Algal Assay Procedure–Bottle Tes
Program, Environmental Protec
Azad, H. S. and J. A. Borchardt.
Algae," *Environ. Sci. Technol.*
Barber, J. "The Influx of Potassi
Biophys. Acta **163**, 141 (1968)
Bierman, V. J., Jr. Internal Repo
Bierman, V. J., Jr., F. H. Verhoff
"Multi-Nutrient Dynamic Mode
tition in Eutrophic Lakes," *Mo*
Proceeding of a Workshop, Sep
Water Research Laboratory and
Logan, Utah (1973a), pp. 89-1
Bierman, V. J., Jr. "Dynamic Ma
Eutrophic Freshwater Lakes,"
Notre Dame, Indiana (1973b).
Bierman, V. J., Jr. "Mathematica
of Blue-Green Algae by Nutrie
the Division of Environmental
Philadelphia, Pa., April 6-11, 1
Bush, R. M. and E. B. Welch. "I
tors in a Hypereutrophic Lake,
(1972).
Caperon, J. and J. Meyer. "Nitro
plankton. I. Changes in Popul
Growth Rate," *Deep Sea Res.*

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dark incubation period, about one-third of which was a bacterial lag time. The fact that bacteria-free *Chlorella* cultures remained viable in the dark for over 70 days substantiated the contention that the bacteria were the causative agents. Further evidence in support of this hypothesis has recently been reported by Gunnison and Alexander (1975), particularly for cyanophytes. The second-order decay terms and the growth rate constraint were built into the model in an attempt to point out the need for an algal death mechanism. Using the model as a research tool by running comparative simulations without the various death mechanisms emphasized this need.

This study has by no means eliminated alternate possibilities for the decline of algal blooms in Stone Lake, such as trace nutrient limitations, fungi, algal parasites, and toxic materials. It merely points out that the highly unstable, hypereutrophic lakes might better be modeled if the heterotrophic bacterial concentrations in these systems were also modeled. Instead of the two second-order mechanisms used in this study, the decomposition of phytoplankton groups might then be expressed by a function that considers bacteria-phytoplankton interactions explicitly.

REFERENCES

Algal Assay Procedure–Bottle Test. National Eutrophication Research Program, Environmental Protection Agency, Corvallis, Oregon (1971).

Azad, H. S. and J. A. Borchardt. "Variation in Phosphorus Uptake by Algae," *Environ. Sci. Technol.* **4**, 737 (1970).

Barber, J. "The Influx of Potassium into *Chlorella Pyrenoidosa*," *Biochim. Biophys. Acta* **163**, 141 (1968).

Bierman, V. J., Jr. Internal Report, University of Notre Dame (1973).

Bierman, V. J., Jr., F. H. Verhoff, T. L. Poulsen, and M. W. Tenney. "Multi-Nutrient Dynamic Models of Algal Growth and Species Competition in Eutrophic Lakes," *Modeling the Eutrophication Process*, Proceeding of a Workshop, September 5-7, 1973, sponsored by Utah Water Research Laboratory and Environmental Protection Agency, Logan, Utah (1973a), pp. 89-109.

Bierman, V. J., Jr. "Dynamic Mathematical Model of Algae Growth in Eutrophic Freshwater Lakes," Ph.D. thesis, University of Notre Dame, Notre Dame, Indiana (1973b).

Bierman, V. J., Jr. "Mathematical Model of the Selective Enhancement of Blue-Green Algae by Nutrient Enrichment," paper presented before the Division of Environmental Chemistry, American Chemical Society, Philadelphia, Pa., April 6-11, 1975.

Bush, R. M. and E. B. Welch. "Plankton Associations and Related Factors in a Hypereutrophic Lake," *Water Air Soil Pollution* **1**, 257 (1972).

Caperon, J. and J. Meyer. "Nitrogen-Limited Growth of Marine Phytoplankton. I. Changes in Population Characteristics with Steady-State Growth Rate," *Deep Sea Res.* **19**, 601 (1972).

Caperon, J. and J. Meyer. "Nitrogen-Limited Growth of Marine Phytoplankton. II. Uptake Kinetics and Their Role in Nutrient-Limited Growth of Phytoplankton," *Deep Sea Res.* **19**, 619 (1972a).

deNoyelles, F., Jr. "A Stained Organism Filter Technique for Concentration of Phytoplankton," *Limnol. Oceanogr.* **13**, 562 (1968).

DePinto, J. V. "Studies on Phosphorus and Nitrogen Regeneration: The Effect of Aerobic Bacteria on Phytoplankton Decomposition and Succession in Freshwater Lakes," Ph.D. thesis, University of Notre Dame, Notre Dame, Indiana (1975).

Droop, M. R. "Some Thoughts on Nutrient Limitation in Algae," *J. Phycol.* **9**, 264 (1973).

Eppley, R. W. and W. H. Thomas. "Comparison of Half-Saturation Constants for Growth and Nitrate Uptake of Marine Phytoplankton," *J. Phycol.* **5**, 375 (1969).

Fitzgerald, G. P. "Detection of Limiting or Surplus Nitrogen in Algae and Aquatic Weeds," *J. Phycol.* **4**, 121 (1968).

Fitzgerald, G. P. "Some Factors in the Competition or Antagonism Among Bacteria, Algae, and Aquatic Weeds," *J. Phycol.* **5**, 351 (1969).

Fuhs, G. W. "Phosphorus Content and Rate of Growth in the Diatoms *Cyclotella nana* and *Thalassiosira fluviatilis*," *J. Phycol.* **5**, 312 (1969).

Fuhs, G. W., S. D. Demmerle, E. Canelli, and M. Chen. "Characterization of Phosphorus-Limited Planktonic Algae," in *Nutrients and Eutrophication: The Limiting Nutrient Controversy*, Proceedings of a Symposium, American Society of Limnology and Oceanography (1971), pp. 113-132.

Great Lakes Water Quality Board. *Great Lakes Water Quality*, Annual Report to the International Joint Commission (April 1973).

Gunnison, D. and M. Alexander. "Resistance and Susceptibility of Algae to Decomposition by Natural Microbial Communities," *Limnol. Oceanogr.* **20**(1), 64 (1975).

Horne, A. J. and G. E. Fogg. "Nitrogen Fixation in Some English Lakes," *Proc. Royal Society*, London, Series B **175**, 351 (1970).

Hutchinson, G. E. "Limnological Studies in Connecticut. VII. A Critical Examination of the Supposed Relationship Between Phytoplankton Periodicity and Chemical Changes in Lake Waters," *Ecology* **25**, 3 (1944).

Hutchinson, G. E. *A Treatise on Limnology*, Vol. 2 (New York: John Wiley and Sons, Inc., 1967).

Jewell, W. J. and P. L. McCarty. "Aerobic Decomposition of Algae," *Environ. Sci. Technol.* **5**(10), 1023 (1971).

McNabb, A. D. "Enumeration of Freshwater Phytoplankton Concentrated on the Membrane Filter," *Limnol. Oceanogr.* **5**, 57 (1960).

Morton, S. D., P. H. Derse, and R. C. Sernan. "The Carbon Dioxide System and Eutrophication," Office of Research and Monitoring, Environmental Protection Agency (1971).

Ogawa, R. E. and J. F. Carr. "The Influence of Nitrogen on Heterocyst Production in Blue-Green Algae," *Limnol. Oceanogr.* **14**, 342 (1969).

Payne, A. G. "Responses of the Three Test Algae of the Algae Assay Procedure: Bottle Test," paper presented at the Thirty-Sixth Annual Meeting of the American Society of Limnology and Oceanography, Salt Lake City, Utah, June 12, 1973.

Peasall, W. H. "Phytoplankton i
of the Phytoplankton in Relat
20, 241 (1932).

Shapiro, J. "Blue-Green Algae:
179, 382 (1973).

Soeder, D. J., H. Muller, H. D. P
of Planktonic Algae: Some C
national Association of Theore
(1971).

Standard Methods for the Examir
ed. (Washington, D. C.: Ame

Stoermer, E. F. "Analysis of Phy
During IFYGL," First Annual
EPA 660/3-73-021 (December,

Tenney, M. W., W. F. Echelberger
Domestic Pollution Abatement
on FWQA grant WPD-126, Dep
Notre Dame (1970).

Theis, T. and J. V. DePinto. "St
Final Report on Grant No. R-8
tion Agency, Pacific Northwest
Corvallis, Oregon (in press).

Uhlmann, D. "Influence of Dilut
plankton Populations of Hyper
Internat. Assoc. Theoret. Appl.

Vanderhoef, L. N., C. Huang, R.
Fixation (Acetylene Reduction)
Michigan, in Relation to Nutrie
19(1), 119 (1974).

Verhoff, F. H., K. R. Sundareson,
Microbial Growth," *Biotechnol.*

Verhoff, F. H., J. B. Carberry, V.
"Mass Transport of Metabolites,
Amer. Inst. Chem. Engin. Symp

Verhoff, F. H., M. Sandoval, T. H
Nutrient Cycling in Rivers," Pa
Environmental Chemistry, Amer
Pa., April 6-11, 1975.

-Limited Growth of Marine Phyto-
Their Role in Nutrient-Limited
Sea Res. **19**, 619 (1972a).
ism Filter Technique for Concen-
. Oceanogr. **13**, 562 (1968).
us and Nitrogen Regeneration: The
oplankton Decomposition and
Ph.D. thesis, University of Notre
).
utrient Limitation in Algae," *J. Phycol.*

Comparison of Half-Saturation Con-
ke of Marine Phytoplankton," *J.*

ing or Surplus Nitrogen in Algae
121 (1968).
ie Competition or Antagonism
: Weeds," *J. Phycol.* **5**, 351 (1969).
d Rate of Growth in the Diatoms
viatilis," *J. Phycol.* **5**, 312 (1969).
lli, and M. Chen. "Characteriza-
nic Algae," in *Nutrients and*
ent Controversy, Proceedings of a
imnology and Oceanography

at Lakes Water Quality, Annual
ommission (April 1973).
istance and Susceptibility of Algae
ial Communities," *Limnol. Oceanogr.*

en Fixation in Some English Lakes,"
B **175**, 351 (1970).
ies in Connecticut. VII. A Critical
onship Between Phytoplankton
Lake Waters," *Ecology* **25**, 3

ology, Vol. 2 (New York: John

obic Decomposition of Algae,"
1971).
water Phytoplankton Concentrated
ceanogr. **5**, 57 (1960).
Sernan. "The Carbon Dioxide
of Research and Monitoring,
71).
luence of Nitrogen on Heterocyst
nol. Oceanogr. **14**, 342 (1969).
Test Algae of the Algae Assay
nted at the Thirty-Sixth Annual
Limnology and Oceanography,

Peasall, W. H. "Phytoplankton in the English Lakes. II. The Composition of the Phytoplankton in Relation to Dissolved Substances," *J. Ecol.* **20**, 241 (1932).

Shapiro, J. "Blue-Green Algae: Why They Become Dominant," *Science* **179**, 382 (1973).

Soeder, D. J., H. Muller, H. D. Payer, and N. Schulle. "Mineral Nutrition of Planktonic Algae: Some Considerations, Some Experiments," *International Association of Theoretical and Applied Limnology* **19**, 39 (1971).

Standard Methods for the Examination of Water and Wastewater, 13th ed. (Washington, D. C.: American Public Health Association, 1971).

Stoermer, E. F. "Analysis of Phytoplankton Composition and Abundance During IFYGL," First Annual Reports of the EPA IFYGL Projects, EPA 660/3-73-021 (December, 1973), p. 90.

Tenney, M. W., W. F. Echelberger, and T. C. Griffing. "Effects of Domestic Pollution Abatement on an Eutrophic Lake," Partial report on FWQA grant WPD-126, Department of Civil Eng., University of Notre Dame (1970).

Theis, T. and J. V. DePinto. "Studies on the Reclamation of Stone Lake," Final Report on Grant No. R-801245 from the Environmental Protection Agency, Pacific Northwest Environmental Research Laboratory, Corvallis, Oregon (in press).

Uhlmann, D. "Influence of Dilution, Sinking, and Grazing Rate on Phytoplankton Populations of Hyperfertilized Ponds and Micro-Ecosystems," *Internat. Assoc. Theoret. Appl. Limnol.* **19**, 100 (1971).

Vanderhoef, L. N., C. Huang, R. Musil, and J. Williams. "Nitrogen Fixation (Acetylene Reduction) by Phytoplankton in Green Bay, Lake Michigan, in Relation to Nutrient Concentration," *Limnol. Oceanogr.* **19**(1), 119 (1974).

Verhoff, F. H., K. R. Sundareson, and M. W. Tenney. "A Mechanism of Microbial Growth," *Biotechnol. Bioengin.* **14**, 411 (1972).

Verhoff, F. H., J. B. Carberry, V. J. Bierman, Jr., and M. W. Tenney. "Mass Transport of Metabolites, Especially Phosphorus in Cells," *Amer. Inst. Chem. Engin. Symp. Series 129*, **69**, 227 (1973).

Verhoff, F. H., M. Sandoval, T. H. Cahill. "Mathematical Modeling of Nutrient Cycling in Rivers," Paper presented before the Division of Environmental Chemistry, American Chemical Society, Philadelphia, Pa., April 6-11, 1975.