

ALGAL BLOOM MANAGEMENT AND CONTROL

Ales Prokop, Nicholas L. Clesceri, and Sidney J. Curran

Nicholas L. Clesceri & Associates
Environmental Engineers and Consultants
Lake Shore Drive, Bolton Landing, NY-12814

Prepared for:

The Soap & Detergent Association
475 Park Avenue, South
New York, NY 10016

May 9, 1986

CONTENTS

	Page
LIST OF FIGURESiv
LIST OF TABLES	v
I. INTRODUCTION	1
II. REVIEW OF BASIC CONCEPTS IN FRESHWATER PHYTOPLANKTON ECOLOGY	2
A. ECOSYSTEM STRUCTURE	2
B. ALGAL CLASSIFICATION	3
C. FACTORS GOVERNING THE TEMPORAL AND SPATIAL STRUCTURE OF ECOSYSTEMS	5
Patterns of Seasonal Succession	5
Factors Causing Seasonal Succession	6
D. COMPETITIVE ADVANTAGES OF BLUE-GREEN ALGAE, GREEN ALGAE, AND DIATOMS	6
Competitive Advantages of Blue-Green Algae	6
Competitive Advantages of Green Algae and Diatoms	7
E. NUTRIENTS	8
Nutrient Limitation	8
Nutrient Uptake Kinetics	9
Uptake of Phosphorus	9
Carbon Dioxide10
Nitrogen and Nitrogen Fixation10
Silicon10
Other Nutrients11
F. OTHER FACTORS AFFECTING COMPETITION AMONG ALGAE11
Light11
pH Tolerance12
Growth Rates12
Resting Stages14
Buoyancy Control14
Nutrient Storage By Algae14
Patchiness14
Grazing15

	Parasitism15
	Allelopathy15
	Heterotrophy16
	Growth and Survival Strategies16
G.	ALGAL BLOOMS16
	Types of Algal Blooms16
	Causes For Algal Bloom Die-Offs17
	Nutrient Recycling After Algal Blooms18
H.	MODELING AND STATISTICAL TECHNIQUES18
	Statistical Analysis18
	Modeling and Simulation19
III.	NUTRIENT LOAD REDUCTIONS AND ALGAL BLOOMS: INTERNAL VERSUS EXTERNAL PHOSPHORUS LOADS21
	Internal Loads21
	External Loads22
IV.	PHYSICAL, MECHANICAL AND ENGINEERING APPROACHES TO BLOOM CONTROL23
A.	ARTIFICIAL CIRCULATION (DESTRATIFICATION) AND HYPOLIMNETIC AERATION23
	Artificial Circulation24
	Hypolimnetic Aeration26
B.	DIVERSION OF HYPOLIMNETIC WATER27
C.	SEDIMENT IMMOBILIZATION AND DREDGING28
D.	LAKE DILUTION/FLUSHING30
E.	ALGAE REMOVAL/HARVESTING30
F.	LIGHT MODIFICATION31
V.	CHEMICAL APPROACHES TO BLOOM CONTROL32
A.	NUTRIENT MANIPULATION32
	Nitrogen and Phosphorus32
B.	pH AND CO ₂ SHIFTS33
C.	IN-LAKE PHOSPHORUS REMOVAL34
D.	ALGICIDES35
E.	BACTERICIDES36
F.	METABOLIC INHIBITORS36

VI.	EXPERIMENTAL BIOLOGICAL APPROACHES OF BLOOM CONTROL37
	A. ALLELOPATHY37
	B. MACROPHYTES38
	C. PATHOGENS: VIRUSES38
	D. BACTERIA AND ACTINOMYCETES39
	E. GRAZING40
	F. GENERAL ECOSYSTEM MODELS43
	Ecosystem Structure43
	Addition and Removal of Trophic Levels46
	Fish (Top Predators)49
	Summary of Control With Top Predators50
VII.	CONCLUSIONS51
	LITERATURE CITED54

LIST OF TABLES

		Page
Table 1	Table 1: Common Algae in Freshwater Phytoplankton.	4
Table 2	Table 2: Trophic Levels Interaction.	41
Table 3	Table 3: Generalized Concept of Even/Odd Linked Systems and Their Effect on Ecosystem Composition	45
Table 4	Table 4: Trophic Levels Interaction.	48
Table 5	Table 5: Summary of Algal Bloom Management Strategies.	52

LIST OF FIGURES

		Page
Figure 1	Figure 1: Generalized Seasonal Succession of Phytoplankton	6
Figure 2	Figure 2: Branched Food Chains With Different Numbers of Trophic Levels.	46

I. INTRODUCTION

This report synthesizes the multitude of studies addressing the complex ecological factors contributing to the development of algal blooms in freshwater systems. The goal is to formulate a concise review of what is known about the factors causing algal blooms and to present the state of the art of bloom control and management. Emphasis is placed on blue-green algal blooms, as they are the blooms which produce the most objectionable or nuisance conditions. Algal control methods are thoroughly covered in order to provide a reference source from which possible solutions to a particular water quality problem can be selected. The review includes literature published prior to mid-1984, therefore, more recent research efforts and publications are not discussed.

II. REVIEW OF BASIC CONCEPTS IN FRESHWATER PHYTOPLANKTON ECOLOGY

A. ECOSYSTEM STRUCTURE

Simply stated, an ecosystem is a community of organisms and their physical environment interacting as an ecological unit. Odum (1971) provides a more complete definition:

"Any unit that includes all of the organisms (i.e., the 'community') in a given area interacting with the physical environment so that a flow of energy leads to clearly defined trophic structure, biotic diversity, and material cycles (i.e., exchange of materials between living and nonliving parts) within the system is an ecological system or ecosystem."

All components of an ecosystem interact through feedback loops which control the structure of the ecosystem. An example of this is the predator-prey relationship, in which the predator reduces the number of prey to the point the predators can no longer sustain themselves, at which point they decline in number, allowing the number of the prey to increase again. These feedback loops and mechanisms for interactions among ecosystem components, as well as within components, play a very important role in algal blooms, and at least a rudimentary understanding of them is necessary to perceive how best to control algal blooms.

One very general hierarchal classification of the levels of organization of an ecosystem includes the terms population and community. A population is simply a group of individuals of the same organism. A community includes all the populations occupying a given area. By combining the community and its interactions with the abiotic (nonliving) environment one describes an ecosystem.

A somewhat less general classification scheme breaks down the biotic (living) community into several general categories:

1. **Abiotic Environment:** Consists of all nonliving material in the ecosystem.
2. **Producers:** For the most part, these are green plants which utilize light in the process of photosynthesis to produce food from inorganic substances. Others, such as some bacteria, are chemosynthetic and use simple inorganic molecules as an energy source rather than light. These are all autotrophic organisms.
3. **Consumers:** Utilize the producers as a food source; these are heterotrophic organisms.
4. **Decomposers:** Decompose complex organic substances back into

simple inorganic molecules; these are also heterotrophic organisms.

Ecosystems can also be characterized by trophic levels, which are simply the sequence of steps in a food chain. Examples of trophic levels are:

1. Primary producers (e.g., macrophytes growing in the lake sediment; phytoplankton).
2. Herbivores (e.g., zooplankton which feed on aquatic plants).
3. Carnivores (e.g., carnivorous organisms such as many insect larvae and fish).

These trophic levels should not be confused with the trophic state of a lake (sometimes also called the trophic level of a lake) which refers to the quantity of utilizable nutrients and the resulting biotic community (e.g., oligotrophic, mesotrophic, or eutrophic).

B. ALGAL CLASSIFICATION

The nomenclature for freshwater phytoplankton is highly varied, particularly with respect to blue-green algae. The major taxonomical controversy is whether to classify the blue-green algae as algae, bacteria, or as a separate taxa altogether. This dilemma arises because, although they are photosynthetic organisms, their cellular structure is more similar to bacteria than plants (e.g., algae) In this report, the term blue-green algae will be used. However, at times the terms cyanobacteria, myxophyta, cyanochloronta, and others may be encountered in the literature; these all refer to what have traditionally been called the blue-green algae.

A general taxonomical listing of the major taxa represented in freshwater phytoplankton is provided in Table 1. For each, a few common genera are listed.

Table 1: Common Algae in Freshwater Phytoplankton.

I. Prokaryota.

A. Cyanophyta: Blue-greens.

<u>Anabaena</u>	<u>Coelosphaerium</u>	<u>Merismopedia</u>
<u>Aphanizomenon</u>	<u>Gloeocapsa</u>	<u>Microcystis</u>
<u>Aphanocapsa</u>	<u>Gloeotrichia</u>	<u>Oscillatoria</u>
<u>Aphanothece</u>	<u>Gomphosphaeria</u>	<u>Synechococcus</u>
<u>Chroococcus</u>	<u>Lyngbya</u>	

II. Eukaryota.

A. Chlorophyta: Green algae.

<u>Ankistrodesmus</u>	<u>Elakatothrix</u>	<u>Scenedesmus</u>
<u>Chlorella</u>	<u>Eudorina</u>	<u>Sphaerocystis</u>
<u>Closterium</u>	<u>Gemmellicystis</u>	<u>Staurastrum</u>
<u>Coelastrum</u>	<u>Oocystis</u>	<u>Staurodesmus</u>
<u>Coenococcus</u>	<u>Pandorina</u>	<u>Tetrastrum</u>
<u>Cosmarium</u>	<u>Pediastrum</u>	<u>Tribonema</u>
<u>Crucigenia</u>	<u>Radiococcus</u>	<u>Volvox</u>

B. Chrysophyta 1. Bacillariophyceae: Diatoms.

<u>Asterionella</u>	<u>Nitzschia</u>
<u>Cyclotella</u>	<u>Stephanodiscus</u>
<u>Diatoma</u>	<u>Synedra</u>
<u>Fragilaria</u>	<u>Tabellaria</u>
<u>Melosira</u>	

2. Chrysophyceae: Yellow-brown algae.

<u>Ankyra</u>	<u>Mallomonas</u>
<u>Chromulina</u>	<u>Monodus</u>
<u>Dinobryon</u>	<u>Synura</u>
<u>Erkenia</u>	<u>Uroglena</u>

C. Cryptophyta

<u>Chroomonas</u>	<u>Cryptomonas</u>	<u>Rhodomonas</u>
-------------------	--------------------	-------------------

D. Pyrrophyta: Dinoflagellates.

<u>Ceratium</u>	<u>Peridinium</u>
-----------------	-------------------

C. FACTORS GOVERNING THE TEMPORAL AND SPATIAL STRUCTURE OF ECOSYSTEMS

The structure of an ecosystem changes through processes called succession and periodicity. Many authors treat these terms as synonyms, and others give distinct definitions to each. To avoid the semantic issue and the confusion it generates, the term seasonal succession will be used to refer to the changes in an ecosystem's structure which occur in a similar pattern every year. Figure 1 provides a generalized view of the pattern of freshwater phytoplankton seasonal succession. These are month to month, or season to season, shifts in the composition of the biota (flora and fauna) which are similar from year to year as long as no major perturbations occur, such as major climatic changes. The term succession, without a modifier, will be used to describe the grander changes which occur over time, such as the natural aging of a lake from oligotrophy to mesotrophy to eutrophy, and finally, to a terrestrial system. Succession is caused primarily by external large scale factors (e.g., climatic changes and nutrient loads).

Patterns of Seasonal Succession

In an oligotrophic lake, the seasonal succession pattern is usually composed of many overlapping population growth curves whose magnitudes (peaks) are relatively small. This results in a very complex and highly stable progression of organisms with time. With increasing trophy, the pattern gradually changes from the many distinct, small peaks to a few nearly single organism peaks (e.g., a single diatom or blue-green alga species dominant at any given time) which is representative of eutrophic lakes. Highly eutrophic systems, which are characterized by low diversity and few trophic levels, are less stable systems than oligotrophic systems, which are characterized by high diversity and at least several trophic levels. Eutrophic systems typically exhibit dramatic, rapid changes in structure, whereas shifts in the structure of an oligotrophic lake generally occur more slowly and smoothly.

Figure 1: Generalized Seasonal Succession of Phytoplankton.

Diatoms	Green Algae/ Chrysophytes	Blue-Greens	Diatoms
Spring/ Early Summer	Late Spring/ Early Summer	Late Summer/ Autumn	Late Autumn

Factors Causing Seasonal Succession

The causative factors for seasonal succession can be categorized as allogenic (external to the organism or community), such as water chemistry, turbulence due to wind, floods, light periodicity, and temperature, or, as autogenic (internal) of phytoplankton, such as species physiological and life history characteristics, competition, grazing by herbivores, parasitism, allelopathy (the chemical inhibition of one organism by another), and other factors under biological control. As will be shown in later sections, these factors form the basis for algal bloom management strategies.

D. COMPETITIVE ADVANTAGES OF BLUE-GREEN ALGAE, GREEN ALGAE, AND DIATOMS

Competitive Advantages of Blue-Green Algae

It is useful to enumerate the different competitive capabilities of blue-green algae versus green algae and diatoms. These explain why blue-green algal blooms have been so difficult to eliminate or control. The competitive strategies form the basis for many bloom management techniques, including nitrogen and phosphorus enrichments, pH and CO₂ manipulations, and mixing/destratification. The conditions and factors contributing to the competitive advantage of blue-green algae include:

1. Resistance to grazing pressure (mainly attributable to the relatively large size of the colonies).
2. Ability to minimize sedimentation losses via buoyancy.

3. Low energy expenditure (respiration) in the dark.
4. Nitrogen fixation by some species at low N:P ratios.
5. Rapid nutrient recycling/regeneration after the die-off of blue-green algal blooms, thereby providing a nutrient supply for subsequent bloom species.
6. Resting stages highly resistant to unfavorable conditions.
7. Specially developed nitrogen storage system; phosphorus storage equally as efficient as that of green algae; access to hypolimnion nutrients via buoyancy control.
8. Higher affinity for CO_2 than green algae or diatoms.
9. Diverse nutritional metabolism, such as bicarbonate utilization in absence of CO_2 , and heterotrophy.
10. Ability to utilize low levels of some nutrients through chelation (the combination of a substance with a metal ion, thereby keeping it in solution).

Competitive Advantages of Green Algae and Diatoms

The competitive advantages and strategies of green algae/diatoms are:

1. Ability to respond to high light fluxes (high tolerance to light inhibition phenomena).
2. High affinity for phosphorus uptake (low saturation constant for phosphorus uptake).
3. Broad pH tolerance.
4. High growth (reproduction) rates.
5. Low sinking rate for green algae; however, diatoms have a high sinking rate.
6. Some protection from grazing available for diatoms and small flagellates via patchiness.

E. NUTRIENTS

Nutrient Limitation

There has been considerable experimental documentation of the importance of nutrient limitation as a factor which determines the algal species composition of lakes. Important aspects of the limiting nutrient concept include:

1. The population level is determined by the resource in lowest supply (e.g., nutrients). This is Liebig's "Law of the Minimum", or the concept of limiting factors.
2. The reaction of a population to any resource is typically in a threshold manner. This means that below a certain resource level there is no growth of a given species, while above the threshold level, growth can occur.
3. An interaction of several nutrients is possible in a synergistic way.

Theories of nutrient limited growth and competition for resources are well documented in general microbiological and limnological literature (e.g., Paerl, 1982; Tilman et al., 1982).

It must be stressed that knowledge concerning resources (e.g. nutrients) must be acquired before any management technique can be applied. Methods which are available to determine the factors which limit primary productivity in freshwaters are:

1. Bioassay (nutrient enrichment) experiments which use either a test organism or natural communities in laboratory or in situ experiments (Schanz et al., 1979; Paerl, 1982; U.S. EPA, 1971).
2. Phosphorus turnover experiments based on the fact that, under conditions of phosphorus limitation, the phosphorus turnover time is short due to rapid phosphorus uptake (Prepas, 1983; Chow-Fraser and Duthie, 1983).
3. Alkaline phosphatase activity experiments using the observation that the alkaline phosphatase activity increases as cells become starved by phosphorus. As a result, it is inversely related to the nutritional status of the water body and can serve as an indicator of phosphorus limitation (Cembella et al., 1984a; Rueter, 1983).

4. The ratio of the nitrogen concentration to the phosphorus concentration (N:P ratio) is often used as a general indicator.

Nutrient Uptake Kinetics

A vast amount of literature is available concerning nutrient uptake and the competitive advantages of individual algal species and groups, especially with respect to phosphorus, silica, and nitrogen. Nutrient uptake is usually related to nutrient concentrations within the algal cell (intracellular concentration). A point worth mentioning is that nutrient uptake occurs against a concentration gradient, and is an aerobic process that requires consumption of energy. Energy must be expended in moving a substance from a region of lower concentration (lake water) to one of higher concentration (the algal cell).

Uptake of Phosphorus

The inverse relationship between internal and external phosphorus levels is of ecological importance. It represents one of the most efficient mechanisms for phosphorus removal present in nature. Phosphorus is taken up by algae in the epilimnion under aerobic conditions, and becomes stored as polyphosphate bodies within the cell. Phosphorus is released by a somewhat faster process under anaerobic conditions which may prevail in the hypolimnion and in sediments. The fundamentals of phosphorus uptake and release are discussed by Jensen et al. (1976), Nyholm (1978), Falkner et al. (1984); and Cembella et al. (1984a,b).

Algal growth rates are not readily described in terms of external phosphorus concentration because of the internal accumulation of phosphorus in the form of polyphosphate bodies. Instead, the growth rate can be related to the cell concentration of the limiting nutrient (phosphorus). Rhee and Gotham (1980) and Shuter (1978) list some minimal cell nitrogen and phosphorus quotas, beneath which an algal cell can not function.

Substrate (e.g., nutrient) uptake rates are cell size related because the uptake of substrate occurs through diffusion and diffusion is dependent on the cell's surface area. Small cells have a larger surface area to volume ratio than large cells, therefore, smaller cells are superior in uptake rate when compared to large ones. Reynolds (1984a), Smith and Kalff (1982; 1983), and Banse (1976) related different physiological responses to the ones.

Phosphorus uptake is not only mediated by algae, but also by the bacteria present in the lake water. Phosphorus dynamics in freshwater aquatic ecosystems is extremely complex and can not be

covered adequately here. Numerous recent articles cover the topic well (e.g., Lean and White, 1983; Currie and Kalff, 1984a,; Cole, 1982; Norman and Sager, 1978; Paerl and Downes, 1978; Peters, 1978, 1979; Lean, 1973a,b; Dorich et al., 1980; Williams et al., 1980).

Carbon Dioxide

Carbon dioxide (CO₂) is a nutrient which blue-green algae have a superior ability to take up, as compared to other algal types. Blue-green algae have a lower saturation constant and, therefore, a higher affinity for CO₂ than green algae (Olofsson and Woodard, 1977). Blue-greens can also utilize more forms of inorganic carbon compared to greens because they possess the enzyme carbonic anhydrase, enabling them to utilize the bicarbonate ion (King, 1970; Paerl, 1982). Bicarbonate utilization may become especially important at higher pH levels at which the dissolved CO₂ concentration is low and the bicarbonate concentration is high. Thus, it is possible for dissolved inorganic carbon to limit the productivity in lakes having an excess of phosphorus and nitrogen.

Nitrogen and Nitrogen Fixation

The forms of nitrogen most algae preferentially utilize are the inorganic nitrate and ammonia ions. Nitrate and ammonia uptake kinetics are summarized in Carpenter and Guillard (1971) and Berman et al. (1984). The nitrogen fixation of some blue-green algae represents another adaptive feature providing them with a competitive advantage. Nitrogen fixation is nearly restricted to blue-greens possessing heterocysts, including the genera Anabaena, Oscillatoria, and Aphanizomenon (Stewart, 1973). Members of the order Nostocales are the blue-greens most likely to exhibit nitrogen fixation capabilities. Thus, under nitrogen limiting conditions, when most algae are starved for nitrogen, some bloom forming blue-greens are able to obtain their nitrogen through the process of nitrogen fixation.

Silicon

Unlike other algae, diatoms require large amounts of silicon, which they incorporate into their cell walls (frustules). Silicon limitation is one of the major factors which is responsible for the decline of vernal diatom blooms. Thus, silicon limitation is an important factor, dictating both algal community composition and the primary productivity in lakes

supporting periodic diatom blooms (Paerl, 1982; Tilman, 1977; 1981).

Other Nutrients

Phytoplankton have requirements for a variety of minor elements, such as iron, manganese, copper, zinc, molybdenum, and boron (Paerl, 1982). Iron, for example, can cause a shift in the dominant organism from green to blue-green algae (i.e., Oscillatoria) (Gibson and Smith, 1983). On the other hand, the manganese concentration can inhibit blue-green algae more than it inhibits either green algae or diatoms.

F. OTHER FACTORS AFFECTING COMPETITION AMONG ALGAE

Some algae, notably blue-greens, excrete compounds called hydroxamates (e.g., siderochromes and catechols). The function of these compounds is to:

1. Selectively chelate ferric ions and aid in their transport across the cell membrane. This provides blue-green algae a competitive advantage.
2. Siderochromes are toxic to many competing algal species and can limit their growth (Murphy et al., 1976).

The ability of blue-green algae to sequester iron with hydroxamate chelators helps them to utilize levels of iron which are normally not available to other algae. These levels are usually unavailable due to coprecipitation with phosphates and carbonates (Paerl, 1982). The sequestering capability is especially important for nitrogen-fixing blue-green algae (e.g., Anabaena, Aphanizomenon, and Oscillatoria) in which nitrogen uptake (fixation) coincides with the rapid uptake of other ions (Murphy et al., 1976). Due to these complexing agents, blue-greens are more tolerant to an excess of heavy metals than are green algae. The complexing agents chelate the metals, thereby protecting the blue-green algae from the toxic effects of heavy metals (Spencer and Greene, 1981).

Light

Photosynthetic rates in relation to light are generally higher in algae having a low surface area:volume ratio (e.g., green algae and diatoms). These algae out compete blue-greens under conditions of low light availability. High

fluxes (intensities) of light are preferred by most green algae, and also by some dinoflagellates. This explains why they usually reside at the uppermost layer of the water column and are inhibitory to blue-greens by reducing the light intensity. Low light fluxes are favored by diatoms, flagellates and the rest of the dinoflagellates, and therefore, they are usually located at a greater depth in the water column (Wall and Briand, 1979; Reynolds, 1984a). Blue-green algae compensate for light levels with their ability to adjust their position in the water column through buoyancy control. Thus, they obtain the optimal light (or nutrient) conditions.

pH Tolerance

There is a striking difference in the pH tolerance among algae. Generally, green algae have a wide tolerance, while blue-greens are tolerant only at higher pH values. Specifically, a pH lower than 7.4 is favorable to green algae, and this fact is used in some lake manipulation/control strategies (Brock, 1973).

Growth Rates

Under natural field conditions, the specific growth rate of a population is the difference between specific rates of production and loss:

$$\text{spec. growth rate} = \text{spec. production rate} - \text{spec. loss rate}$$

Losses occur due to respiration, sinking (sedimentation), death, excretion, parasitism, and grazing, among others. Of these, sinking and grazing are the primary factors affecting the loss rate. Some growth constants for algae (maximum growth rate, saturation constant) are provided in Tilman et al. (1982).

Respiration Rates

Respirational losses are related to the area:volume ratio. Respirational losses (in the absence of light) are greatest for nanoplankton because they are small cells which contribute to accelerated catabolism, death, and sinking. Respirational losses lessen for larger cells (Reynolds, 1984a).

Sinking Rates

Reynolds (1984a) and Jorgensen (1980) summarized differences in sinking rates among different algal groups. Diatoms are highly prone to sedimentation due to their high silica content and resulting weight. Cell size is the other important factor involved in sinking rates. The higher sinking rates of larger cells are often counteracted by other mechanisms, including motility (flagellates, dinoflagellates, some colonial green algae) and buoyancy (some blue-greens).

Growth Rates

Growth rates of phytoplankton are usually estimated by measuring rates of photosynthesis, biomass accumulation, or nutrient uptake. However, nutrient uptake is not always parallel to growth due to the intracellular accumulation of nutrients in the form of reserve materials (luxury uptake). Reynolds (1984a) divided phytoplankton into three groups on the basis of cell or colony shape and size. In the following, the highest growth rates are found in the first group, and the lowest rates in the third:

1. Vernal or early summer opportunistic group: Composed of nanoplankton, which are small and have a simple shape.
2. Well mixed vernal or late summer periods: Composed primarily of diatoms.
3. Summer dominants: Typically form large units with a low surface area to volume ratio (colonial greens, followed by blue-greens, which are followed by dinoflagellates).

This classification of algal groups is closely related to the seasonal succession of phytoplankton, as they usually appear sequentially during the growing season.

Grazing Rates

Although the grazing of phytoplankton by zooplankton is an important aspect of community ecology, our understanding of it is limited by the relatively sparse information available on the feeding habits of herbivorous zooplankton and the availability of laboratory procedures with which to accurately quantify the effects and selectivity of grazing. Presently, it is thought that the major factor governing grazing is cell or colony size. Reynolds (1984b) discusses the subject in greater detail.

Resting Stages

Blue-green algae are better able to survive in winter or other unsuitable conditions than are other algae. They form a highly resistant resting stage which provides a special survival mechanism with which they can survive such unfavorable conditions (Reynolds, 1984a).

Buoyancy Control

Buoyancy due to the formation of gas vacuoles is a way for algae to prevent sinking. Buoyancy control is well developed in most blue-green algae, including the common bloom forming algae Aphanizomenon, Anabaena, and Microcystis. The primary factor controlling buoyancy is light intensity; when light is low, upward migration prevails. The ability of blue-green algae to move in and out of a eutrophic euphotic zone enables them to successfully exploit light availability and avoid nutrient depleted areas of the euphotic zone (Konopka et al., 1978; Ganf and Oliver, 1982). Buoyancy control also allows blue-green algae to migrate to the water surface during periods of high pH in thermally stratified water columns, and to use CO₂ at the interface to maintain high photosynthetic rates (Paerl and Ustach, 1982; Paerl, 1983).

Nutrient Storage By Algae

The ability to store nutrients is common among all algal types. The uptake and storage of nutrients in excess of the cell's immediate needs is called 'luxury uptake'. By having storage capabilities, microorganisms can survive and grow during periods of severe nutrient depletion in the surrounding water. Most algae can accumulate and store phosphorus in the form of polyphosphate bodies. In certain blue-green algae, nitrogen is stored in the form of granules of cyanophycin and in the proteinaceous matter of eukaryotic phytoplankton (Paerl, 1982). Other storage materials include sulfur in granules or drops, and organic carbon in polyhydroxybutyrate bodies, lipids, or starch.

Patchiness

Spatial organization is important in the dynamics of biological communities. The phytoplankton population is often found in clumps or patches for a variety of reasons:

1. Variations in nutrient supply.

2. Limited dispersal after reproduction.
3. Protection from grazing.

Mixing represents an intervening factor in aquatic environments. When mixing is incomplete, considerable spatial segregation exists.

George and Heaney (1978) recognize that daily mean wind speeds above 100 km/day are sufficient to break down patches of phytoplankton through mixing, while velocities less than 50 km/day allow for the formation of dense, small-scale, near-surface aggregations of dinoflagellates.

Grazing

Although knowledge is incomplete concerning food selection by zooplankton, it appears to be based exclusively on the size of algae, with the maximum dimension of ingested food particles being related to the zooplankton body size (Reynolds, 1984a). Different grazing mechanisms (raptorial, selective and nonselective filtering) are briefly discussed in Canale et al. (1976). In terms of algal competitive advantages, small algal cells or colonies having a maximum dimension of about 40 μm are those most frequently grazed by zooplankton. This results in the differential mortality of phytoplankton, with blue-green algae not being consumed to the extent of most other algal types.

Parasitism

Only some algal species are known to be sensitive to lysis by algoviruses and lytic bacteria. Due to the limited data available, no conclusions can be drawn concerning the competitive advantage parasitism might provide to algae.

Allelopathy

Allelopathy is the chemical inhibition of one organism by another. Certain extracellular metabolites of blue-green algae can inhibit the growth of diatoms in laboratory cultures and in natural systems. The chemical nature of these metabolites has not yet been identified (Keating, 1976; 1977; 1978).

Heterotrophy

Some blue-green algae are capable of utilizing organic compounds in the presence (photoheterotrophy) or absence (chemoheterotrophy) of light. This permits prolonged survival with little or no light (Ellis and Stanford, 1982).

Growth and Survival Strategies

A theory based on a combination of survival (reproduction), loss, and growth capabilities of a group of organisms led to the establishment of the theory of two survival strategies: r- and K-selection (Pianka, 1970). The prefix r- refers to the maximal intrinsic rate of growth, while K- refers to the carrying capacity (resource control of populations such as by the food or nutrient supply). The strategy of r-selection favors fast growing, opportunistic species, which are prone to loss processes (e.g., grazing). K-selection favors slower growing species (i.e., those less vulnerable to loss processes). Typically, seasonal succession proceeds from a green algae/diatom bloom to a blue-green bloom. Thus, it follows that to arrest succession and prevent formation of a blue-green bloom, conditions for the elimination of K-selection are necessary. One approach used is nutrient manipulation to remove resource control (K-selection) of the algal community and encourage predator control (r-selection).

G. ALGAL BLOOMS

Types of Algal Blooms

The following four types of algal blooms are those commonly encountered in freshwater systems (Kalff and Knoechel, 1978):

1. Blue-green: Typically composed of large filamentous or colonial species with low growth rates, and low loss rates due to buoyancy control which minimizes the loss of cells through sinking. Anabaena, Aphanizomenon, and Microcystis are probably the most common blue-green genera found in these noxious blooms, and are often accompanied by large dinoflagellates such as Ceratium. However, other blue-greens also form blooms (Kalff and Knoechel, 1978; Reynolds et al., 1981, 1984a; Reynolds and Walsby, 1975; Round, 1981): Anabaenopsis, Coelosphaerium, Gloeotrichia, Gomphosphaeria, Oscillatoria, Spirulina, and Trichodesmium.
2. Diatom: These most often occur in the spring (vernal bloom) as the first major growth observed. However, in lakes having

a deep mixed zone, or in shallow, well-mixed lakes, a diatom bloom may persist throughout the growing season. High losses attributable to sinking due to the high silica content of the diatoms' cell wall (frustule) and silicon nutrient limitation are the major factors restricting diatom blooms. A few of the common genera are: Asterionella, Cyclotella, Fragilaria, Melosira, Stephanodiscus, and Synedra.

3. Nanoplankton: Composed of small, single celled or colonial algae (up to 50 μm in diameter) with high production rates. These may represent nearly 100 percent of the biomass in oligotrophic lakes. Examples of nanoplankton include: Aphanocapsa and Aphanotheca (blue-greens); Chlorella (green); Cryptomonas and Rhodomonas (Cryptophytes); Chromulina and Mallomonas (chrysophytes); and Cyclotella (centric diatom).
4. Dinoflagellates: A dinoflagellate bloom usually follows a blue-green bloom as the final seasonal succession stage. Representatives of this group include Ceratium and Peridinium.

Of the above, the blue-green bloom is the one which is most often considered objectionable and a nuisance. Blue-green blooms are highly undesirable because:

1. They form mats and scums on the lake surface which are unsightly, can produce noxious odors, and interfere with water sports and fishing.
2. Some of the algae are toxic to fish and mammals (including humans).

Causes For Algal Bloom Die-Offs

The sudden collapse (crash, die-off) of an algal bloom is not clearly understood. The explanations for die-off are numerous, but largely speculative in nature. Some key factors are probably:

1. Bacterial decomposition and further autolysis.
2. Acute nutrient deficiency due to overpopulation.
3. Emergence of algal parasites (pathogens), such as algoviruses, fungi, and lytic bacteria.
4. Autodestruction by growth-inhibiting substances excreted by algae.
5. Reduction of light due to periods of heavy overcast or to the interactive effects of light intensity and temperature (e.g.,

changes in pigment concentrations due to shading [Collins and Boylen, 1982]). For example, even 1 or 2 days of dark incubation leads to a rapid loss in the photosynthetic ability of the blue-green alga Anabaena.

6. Washout of the bloom population by water outflow.
7. High sinking rate of bloom population through either a change in the physiological state (diatoms) or buoyancy (blue-greens).
8. Consumption by herbivores.
9. Photooxidative losses of the upper layer of bloom.

Among the above explanations, the most important are probably grazing, decomposition/autolysis, and sedimentation losses.

Nutrient Recycling After Algal Blooms

There appear to be basic differences between blue-greens and diatoms in relation to the release of nutrients upon the death of an algal cell. When a diatom bloom subsides, senescent cells sink into the hypolimnion, carrying their nutrient content out of the epilimnetic photic zone. These nutrients are essentially unavailable for further algal growth until the fall turnover when mixing of the entire water column occurs. On the other hand, when a blue-green cell dies, it rapidly lyses and releases most of its protoplasm, including soluble nitrogen and phosphorus compounds, directly into the epilimnion. These nutrients are immediately recycled by other algae or bacteria and can stimulate their growth (Fallon and Brock, 1979; 1980).

H. MODELING AND STATISTICAL TECHNIQUES

Extensive literature exists concerning the statistical analysis of algal populations and communities. Therefore, only a brief overview of some of the available approaches will be presented.

Statistical Analysis

Factor or multivariate analysis is useful in analyzing data sets with large numbers of observations on many variables. Multivariate analysis provides a tool with which one can gain an

understanding of phytoplankton periodicity and the ecological strategies of various algal groups. Cluster and principal components analysis is another alternative. Some applications of the above techniques to algal data are presented in Haertel (1976), Baybutt and Makarewics (1981), Gordon et al. (1981), Toetz (1983), and Paloheimo and Zimmerman (1983).

Gates et al. (1983) state that principal components analysis provides a way of allocating biomass among planktonic compartments in relation to lake chemistry/physics. Zimmerman et al. (1983) list some examples of composite variables derived from principal component analysis.

There is no question about the usefulness of performing some kind of statistical analysis on the data. However, as Kalff and Knoechel (1978) state, a note of caution is warranted:

"The algal data obtained are most frequently subjected to correlation analysis and the assumed casual relationships may be spurious... The succession from a diatom to a blue-green dominant community could, through correlation analysis, have been attributed to species specific temperature optima for growth whereas it was instead the result of a minimal blue-green loss rate rather than a superior growth rate".

Modeling and Simulation

Modeling and simulation presents another approach to data analysis. It must be stressed that models, to have some use, should have sufficient complexity and structure to represent the natural community. However, a model must also be simple enough for practical application, and must use readily obtainable data. The benefits of models include:

1. They can serve as a basis for generating hypotheses of ecosystem behavior and can lead to their subsequent testing.
2. They can estimate rates that are not amenable to direct measurement (e.g.: recycling of nutrients, particularly nutrients released by zooplankton, macrophytes, etc.).
3. They contribute significantly to the understanding of ecosystem behavior, nutrient recycling, algal bloom die-offs, and other dynamic natural processes.
4. They provide for a sensitive analysis of parameters, and can serve to assess possible control measures in terms of their overall effect.
5. They can serve as a management tool for decision making by incorporating economic factors of bloom control.

Examples of the application of modeling to phytoplankton behavior are provided in Bierman et al. (1976), Canale et al. (1976), Cordeiro et al. (1977), and Huff et al. (1977).

III. NUTRIENT LOAD REDUCTIONS AND ALGAL BLOOMS: INTERNAL VERSUS EXTERNAL PHOSPHORUS LOADS

External loads are associated with nutrient inflows via surface and ground water, and precipitation, while internal loads originate in the lake's hypolimnion, the interstitial water of the sediments, and the sediment water interface. Reductions in the external nutrient load are generally a prerequisite to, or a corequisite, to the lake restoration techniques discussed in the following sections.

Internal Loads

Internal nutrient recycling (load) depends on the following set of processes (Stauffer and Lee, 1977; Stauffer and Armstrong, 1984):

1. Mineralization of sediments and release of nutrients, particularly when the overlaying water is anoxic, with subsequent transport of nutrients to the epilimnion. This transport occurs via slow diffusion through the interstitial water of sediments into the hypolimnion, followed by faster turbulent diffusion through the thermocline (although eddy diffusion coefficients in the thermocline of many small and medium-sized lakes are rather small). This process depends heavily on temperature.
2. Resuspension of lake sediments during mixing, with subsequent mineralization of dissolved and particulate materials within the epilimnion.
3. Release of nutrients from bacteria, zooplankton and macrophytes. Phosphorus from zooplankton is considered to be a major part of the total balance.

French (1984) found the internal phosphorus load to be related to several factors:

1. Dissolved oxygen.
2. pH.
3. Temperature.
4. Mixing.
5. Biological effects (invertebrates, grazers, bacteria).

The magnitude of the internal phosphorus load is related to lake depth due to the importance of mixing. The contribution of internal phosphorus to the lake's total phosphorus budget can be appreciable, particularly in shallow lakes (Ahlgren, 1977;

Armstrong and Stauffer, 1980; Larsen and Malueg, 1981; Larsen et al., 1975, 1979; Porcella et al., 1980). Thus, some investigators have constructed models utilizing these parameters (Fee, 1979).

Another way of estimating the phosphorus internal load from the anoxic hypolimnion is via phosphorus retention (Nurnberg, 1984). Retention is the difference between lake input and output and is easily determined from the mass balance.

External Loads

The sources of external nutrient loads to a lake can be classified as either natural or anthropogenic (man-made), and as point or non-point.

Examples of point sources are:

1. Municipal wastewater treatment plant discharges.
2. Industrial wastewater discharges.

Examples of non-point sources are:

1. Agricultural runoff.
2. Urban runoff.
3. Ground water.
4. Atmosphere.

Comprehensive discussions of external nutrient loads and control strategies for improving water quality are readily available in the literature (Chapra and Reckhow, 1983; Maki et al., 1984; Porcella et al., 1974; Reckhow and Chapra, 1983; Smith and Shapiro, 1981; U.S. EPA, 1976; U.S. EPA, 1975; Uttormark and Hutchins, 1980; Woolheiser et al., 1975).

IV. PHYSICAL, MECHANICAL AND ENGINEERING APPROACHES TO BLOOM CONTROL

Methods Discussed In This Section

- A. Aeration and/or circulation of lake water.
 - 1. Artificial circulation (destratification).
 - a. Before stratification is established.
 - b. After epilimnion and hypolimnion are clearly defined.
 - 1. Hypolimnetic aeration.
 - a. Pumping of hypolimnetic water to the surface.
 - b. Aeration of the hypolimnion/sediment.
 - B. Diversion of hypolimnion water.
 - C. Removal/immobilization of sediment.
 - D. Lake dilution/flushing.
 - E. Algae removal/harvesting.
 - F. Light modification.
-

A. ARTIFICIAL CIRCULATION (DESTRATIFICATION) AND HYPOLIMNETIC AERATION

Aeration/circulation is an inexpensive restoration alternative which may be effective in removing the symptoms, but not necessarily the cause, of eutrophication. It is particularly attractive when other remedial actions are considered to be too expensive or are not technically feasible.

Techniques included in this category can be separated into two classes, hypolimnetic aeration and artificial circulation. Both utilize a combination of mixing and aeration to achieve the oxygenation of either the lake's hypolimnion or the entire lake. The major distinction between the methods is that hypolimnetic aeration maintains the integrity of thermal stratification and simply aerates the hypolimnion, whereas artificial circulation (destratification) mixes the entire contents of the lake. Artificial circulation has been used more frequently than hypolimnetic aeration.

Although hypolimnetic aeration has no known adverse effects, there is no evidence, at the present time, that hypolimnetic aeration will control algal blooms (Pastorok et al., 1981). According to Pastorok:

"When a cold water supply is needed, and control of algal blooms is not critical, hypolimnetic aeration is recommended. On the other hand, artificial circulation is preferred whenever limitation of algal biomass is desirable, oxygenation of the metalimnion is required, or loss of cool water is acceptable ... Either aeration/circulation method [artificial circulation or hypolimnetic aeration] is recommended for use by water supply managers seeking to alleviate 'taste and odor' problems resulting from high concentrations of iron, manganese, hydrogen sulfide, and other chemicals which accumulate in the anoxic hypolimnion."

Thus, although hypolimnetic aeration is a valuable restoration technique for some water quality problems, it presently has little merit in the control of algal blooms.

Artificial Circulation

Artificial circulation and the equipment required to perform it have been fully discussed by a number of investigators (Kothandaraman and Evans, 1981; Pastorok et al., 1981; Reynolds, 1984b). The three basic approaches to artificial circulation are:

1. Aeration of the lake beginning in the spring prior to stratification.
2. Artificial destratification in which mixing and aeration are used to break down thermal stratification after the formation of the hypolimnion and epilimnion.
3. Intermittent artificial destratification in which mixing and aeration are used to destratify the lake on an intermittent basis (e.g., every 3 to 4 weeks).

Regardless of which approach is used, artificial circulation involves the pumping of cold water from near the lake bottom to the surface where it is mixed with the warmer surface water. Intermittent destratification, however, includes an additional factor. The theory is that, by periodically disturbing the algal community, no species will have sufficient time to reach its peak biomass. Generally, a combination of mechanical mixing (pumping) and aeration using compressed air or oxygen is used.

Destratification often leads to a number of changes (Kothandaraman and Evans, 1981; Pastorok et al., 1981):

1. Decreases the internal load of nutrients from lake sediments (particularly of phosphorus, ammonia, and silica). This

occurs via the rise of the redox potential of the lake bottom.

2. Increases the mixed depth of phytoplankton and improves the transparency of the lake.
3. Decreases the algal standing crop.
4. A shift in algal species toward dominance of green algae/diatoms due to the elimination of the competitive advantage of buoyancy control in blue-greens.
5. Increases the grazing pressure on phytoplankton by shifting the community toward more edible forms and by increasing the abundance of large zooplankton.
6. Lowers the pH through higher concentration of CO₂.
7. Reduces or eliminates taste and odor problems.

The results of destratification are not quite as conclusive as they appear above. Pastorok et al. (1981) found that in 13 of 23 lakes where mixing (destratification) was complete, the effect on phytoplankton was favorable, and a decrease in algal biomass or density was observed. However, no change was observed in three lakes, and in seven algal biomass increased or the results were unclear. With incomplete mixing, algal density either did not change or increased.

A careful evaluation of the effect of destratification resulted in the following guidelines, which reflect differences in the trophic state and physical-chemical characteristics of lakes (Pastorok et al., 1981):

1. Reductions in the standing crop of phytoplankton are expected in lakes which are light-limited. Destratification increases the depth of mixing leading to algae spending more time in regions with less light.
2. Destratification will lead to increased green:blue-green algae ratios only under light-limited conditions. Destratification is recommended when the problem species are known to be sensitive to a disruption of their vertical positioning in the water column (e.g., blue-green algae).
3. A slight increase in the standing crop will occur in lakes limited by nutrients. This occurs because of a slight increase of nutrients via increased mixing.
4. A decrease in pH will accompany an increase in the green:blue-green ratio, and vice versa.
5. Little change is expected in lakes with relatively low

phytoplankton standing crops (e.g., oligotrophic lakes).

6. Destratification (and also hypolimnetic aeration) should be considered only in cases where internal loading is high relative to external loading, that is, in shallow lakes. Otherwise, nutrient concentrations in the photic zone could be appreciably increased through augmentation by hypolimnetic phosphorus.

Major problems which must be considered prior to the use of artificial destratification include:

1. It may eliminate the cold water habitat at midwater or near the bottom leading to the disappearance of the coldwater fishery.
2. Pastorok et al. (1981) warn: "In some instances, treatment has aggravated already existing problems, or caused new problems to arise, but these results can usually be attributed to faulty design of the aeration device, improper application of the technique, or inadequate understanding of the biological community and its response mechanisms."

The results of intermittent destratification experiments reported by Reynolds (1984b) indicated a significantly reduced phytoplankton standing crop was achieved, high algal peaks were depressed, and high populations of blue-green algae were avoided. Phytoplankton were divided into the following groups according to their reactions to the mixing effects:

1. Species favored by mixing: Asterionella, Fragilaria, Staurostrum, and Oscillatoria.
2. Species whose growth was arrested by mixing: Anabaena, Ceratium, Volvox, and Microcystis.
3. Species favoring stability (no mixing) and reduced optical depth (high light flux): unicellular green algae.

Hypolimnetic Aeration

Aeration of the hypolimnion has been used less frequently than artificial aeration. There are two major variations of hypolimnetic aeration (Jorgensen, 1980):

1. Pumping of hypolimnetic water to the surface, where it is aerated by contact with the atmosphere and transported back to the hypolimnion. No mixing with the epilimnetic water takes place and thermal stratification is not destroyed.

2. Aeration directly into the hypolimnion, again without mixing with the epilimnion water.

Typically, the following benefits are achieved from this method (Ashley, 1983; Fast and Lorenzen, 1978):

1. Although a disturbance of the thermocline is avoided, increased circulation in the hypolimnion causes an increase in the vertical exchange of nutrients across the thermocline. This is not a concern in lakes whose photic zone is already receiving high internal nutrient loads (e.g., many shallow lakes).
2. The oxygen concentration of the hypolimnion is increased.
3. Internal phosphorus loading is reduced, and should reverse eutrophication in lakes characterized by excessive internal loading.
4. CO₂ from the hypolimnion is vented out thereby increasing the pH.
5. Calcium, magnesium, bicarbonate, and phosphate contents are decreased via calcium carbonate-phosphate coprecipitation.
6. A significant increase in large zooplankton is noted, accompanied by a decrease in phytoplankton abundance.

Carefully controlled field tests are needed to fully evaluate this method and establish its cost effectiveness.

B. DIVERSION OF HYPOLIMNETIC WATER

By discharging hypolimnetic rather than epilimnetic water, the nutrient and oxygen balance of the lake should improve. However, the heat balance is also changed because the hypolimnetic water is cooler than epilimnetic water, and mineralization and internal loading are accelerated. The thermocline is lowered, but total destratification does not take place. Bottom discharge will also remove nutrient rich hypolimnetic water from the system. Although this may decrease the algal standing crop, the discharge water may increase the algal population downstream. Thus, subsurface outflow will store heat and dissipate nutrients; on the other hand, surface outflow will dissipate heat and accumulate nutrients (Jorgensen, 1980). This measure is not likely to be widely adopted because it is likely to create problems somewhere downstream.

C. SEDIMENT IMMOBILIZATION AND DREDGING

It is well known that the release of phosphorus from sediments in heavily polluted water bodies can be responsible for a significant internal phosphorus load. The internal load can counteract, or cause a significant delay, in a lake's response to any restoration attempts (Ahlgren, 1977; Armstrong and Stauffer, 1980; Larsen and Malueg, 1981; Larsen et al., 1975; 1979; 1980). This is especially true when the internal load represents a significant portion of the total load, and in shallow lakes with a long hydraulic residence time.

In such cases, one of the sediment removal approaches described in this section should be considered, as they are often one-time remedies having long-lasting effects. The immobilization techniques are also effective. However, they require maintenance or repeated treatments to maintain improved water quality. It must be emphasized that to obtain optimal results and duration of the restorative effect, sediment removal or immobilization should be conducted after, or concurrently with, restoration efforts to reduce external nutrient inputs.

Lake restoration techniques covered under this heading include those involving the removal of sediment from the lake bed and those which attempt to inactivate or isolate the lake's sediments to reduce the internal phosphorus load. Dredging of sediments is generally conducted to:

1. Deepen a lake to change its mixing characteristics such that intermittent destratifications and turnovers during the growing season are terminated, and stable thermal stratification is established.
2. Remove phosphorus rich sediment in cases where the sediment is responsible for a high internal phosphorus load due to anoxic hypolimnetic conditions or intermittent destratification and lake turnover during the growing season.

Increasing Lake Depth (Dredging)

The techniques employing the removal of sediment (primarily to deepen a lake) are restricted to relatively small lakes. Lakes in the projects reported below ranged in size from 4 to 225 ha (about 10 to 560 acres). Hydraulic dredging is the preferred means of removing the sediment. In some cases lake drawdown combined with lake bed excavation is used. In either case, several years (e.g., at least 3 or 4) must be allotted for the dredging effort. Thus, these are not methods providing immediate relief from poor water quality, require considerable planning, and may require the closing of the lake while restoration is underway.

Although dredging is an expensive procedure, the long-term benefits may outweigh the one-time treatment costs incurred. Data pertaining to the costs and effectiveness of dredging projects are available in the literature. Among these, Stefan and Hanson (1981) described a modeling procedure for predicting the effect of dredging, and presented some results from the Fairmont Lakes project in Minnesota; Dunst (1981) discussed the Wisconsin Inland Lakes Renewal Program dredging projects conducted by the Wisconsin Department of Natural Resources. At the time of the Dunst report for Wisconsin, four projects had been completed, two were in progress, and six were in the planning stages. Dunst (1981) reported the Wisconsin experience indicated hydraulic dredging cost, on the average, \$1.12 per m³ of sediment removed compared to \$1.29 for lake drawdown/excavation (apparently for the late 1970's time period, e.g., 1977 and 1978). The range of costs incurred in Wisconsin ranged from \$0.37 to \$1.96 per m³ of sediment removed; the \$0.37 value was from a hydraulic dredging project. Stefan and Hanson (1981) stated the expenses for the Fairmont Lakes projects averaged \$0.72 per m³ of sediment removed.

One obstacle is finding a disposal site for the dredged material. Worth (1981) indicated that contractors were willing to pay for the dredged material because there was a demand for it, largely for reuse as a soil conditioner. This would have reduced the cost of dredging in Nutting Lake, Massachusetts from \$1.87 per m³ to well under \$1.00 (Worth, 1981). However, this would not be appropriate for many sediments due to the presence of deleterious or toxic substances; a complete chemical analysis must be performed in each case. Jorgensen (1980) lists practical experience with this method in several lakes; Gelin and Rippl (1978) reported:

1. A decrease in phosphorus concentration from 200 µg/l to less than 10 µg/l.
2. A reduction in primary productivity from 370 g C/m² to 225 g C/m².
3. A shift from blue-greens to nanoplankton.

Immobilization of the leakage of nutrients from sediments, either by physical coverage (plastic sheet or clay liners) or chemical immobilization, has also been suggested. Such techniques provide only a temporary improvement, and the natural conditions for benthic organisms are altered by the liner.

D. LAKE DILUTION/FLUSHING

The goal of dilution is to increase the flow of low nutrient, nonpolluted water into a lake to improve the lake's water quality through the dilution of nutrients and the reduction of algal standing crop via the washout of algal cells. Although Welch (1979) has shown that flushing can control algal biomass through cell washout, the minimal data presently available for dilution/flushing restoration projects suggest the primary factor affecting water quality is simple dilution. Prior to implementation, several problems must be considered:

1. Sufficient water of good quality is not always readily available.
2. The potential for deleterious impacts of an increased nutrient load on downstream lakes and streams must be considered.
3. The design must insure an effective distribution of the dilution water throughout the lake.
4. The thermal structure of the lake may be adversely affected by the temperature difference between dilution water and lake water.
5. Flushing must be continuous or a reversion to the former state will occur.

Jorgensen (1980) presented some case studies which had positive results, including a shift from blue-green algae toward diatoms. The diatom shift could be due to the dilution of blue-green excretory (allelopathic) products.

E. ALGAE REMOVAL/HARVESTING

This method only treats the symptoms of an algal bloom problem, and is not highly recommended. Oswald (1976) reported on several mechanical ways to skim the surface of a lake to remove algal growths, but these were in the development stages. It was felt that skimming was quite expensive, unless combined with the utilization of the algal biomass for methane production or other algal products.

Thus, the mechanical removal of algal blooms does not appear economically feasible for large lakes, although it might be an effective means to remove algal scums from localized, high-use, near-shore areas such as beaches. Such small scale projects might be more economically handled by the use of artificially induced surface currents, rather than through mechanical skimming.

F. LIGHT MODIFICATION

The differential utilization of both the light gradient (flux) and color (wavelength) suggests there is a potential for using light modification to control algal blooms. One way to achieve this is through the application of dyes to modify light penetration and spectral composition. This approach is only in its infancy. Wall and Briand (1979) tested colored plexiglass cubes in short-term lake experiments (6 days) and concluded:

1. A variable effect of high and low light fluxes occurred and was dependent on the algal taxa.
2. A variable effect according to the spectral composition and the algal taxa also was observed:
 - a. Blue radiation favored chrysophytes and cryptophytes and reduced dinoflagellates; this is why they are typically found at lower levels in the water column than other algae.
 - b. Red radiation reduced blue-greens, diatoms, and green algae.

V. CHEMICAL APPROACHES TO BLOOM CONTROL

Methods Discussed In This Section

1. Nutrient manipulation.
 2. Acid (pH) and CO₂ shifts.
 3. Phosphorus removal (nutrient precipitation).
 4. Algicides.
 5. Bactericides.
 6. Metabolic inhibitors.
-

A. NUTRIENT MANIPULATION

The nutrients which most commonly limit algal growth are, in order of general occurrence, nitrogen, phosphorus, and silica or trace metals (e.g., iron). The manipulation of nutrients to control algal growths is based on the limiting nutrient concept. A limiting nutrient is one which exists at a suboptimal level, and thereby prevents algae from attaining their full growth potential. The limiting nutrient is generally ascertained using nutrient limitation bioassays (EPA, 1971), or, in the case of nitrogen and phosphorus, can be inferred through the ratio of nitrogen to phosphorus (N:P) (Smith 1982; 1983a,b).

Nitrogen and Phosphorus

In general, nitrogen is limiting if the total nitrogen to total phosphorus ratio (TN:TP) is less than 10. Phosphorus is generally limiting at ratios greater than 15. Therefore, the status of lake nutrition can be assessed from the TN:TP ratio in the epilimnion. Through modeling, this can be related to nitrogen and phosphorus external loadings.

(Smith 1982; 1983a,b) and others have discussed several general trends of blue-green algae growths related to different TN:TP ratios:

1. Many lakes having a TN:TP ratio greater than 29 will exhibit low proportions of blue-green algae, with green algae and diatoms prevailing.

2. Blue-greens tend to dominate in lakes where the TN:TP ratio is less than 29, although many other algae will also be present.
3. For a TN:TP ratio of less than 10, a nitrogen deficit should trigger the appearance of nitrogen-fixing blue-green species because they are able to compensate for a relative lack of nitrogen in the lake environment. Although Toetz (1982) was able to demonstrate an increase in the proportion of nitrogen-fixing blue-green algae in a lake under low TN:TP loading (7:1), nitrogen fixation accounted only for 0.5 percent of the total nitrogen input.

The modification of TN:TP ratios can be achieved by manipulating internal and external nutrient sources.

Schindler (1974) was the first to apply nutrient manipulation in field experiments. The addition of nitrogen to a lake undergoing an algal bloom resulted in a complete recovery, the bloom having declined. Barica et al. (1980) carried out experiments in nitrogen-limited lakes and enclosures. Small additions of nitrogen before the appearance of an Aphanizomenon bloom resulted in a Microcystis bloom in the limnocorrals while the lake and control enclosures experienced an Aphanizomenon bloom. In a parallel experiment, a large addition of nitrogen resulted in the complete absence of the traditional Anabaena flos-aquae bloom, the community shifting to green algae and cryptomonads.

The above measures, while dramatically changing an existing situation at a particular point in time, are temporary measures which must be repeated each season. Nutrient manipulation of diatom blooms through silica enrichment is perhaps better justified. Vigon and Armstrong (1977) tested an addition of soluble silica salts to stimulate a diatom population and reduce the phosphorus of the water body; subsequently, the blue-green algae bloom was reduced. The success of phosphorus removal (via stimulation of diatom growth) comes from the nature of phosphorus (and silica) regeneration from sedimented diatom cells. During the post-growth period, only a portion of the particulate phosphorus (29%) and silica (42%) became available by remineralization through the water column. Sze (1980) also achieved a period of diatom bloom following silica enrichment.

B. pH AND CO₂ SHIFTS

No whole-lake studies of the effects of pH and carbon dioxide (CO₂) shifts have been performed with the proper experimental back-up or with data collection at all trophic levels. Furthermore, the method has an effect of short duration.

However, the approach does show some promise. The application of acidic substances (e.g., hydrochloric acid or CO₂) is usually accompanied by nutrient addition. Acidification as a means to control or eliminate blue-greens is based on the observation by Brock (1973) in Yellowstone National park that blue-greens were completely absent when the pH was less than 4 while prokaryotes usually flourished; blue-greens dominated when the pH was greater than 5. Shapiro (1983; 1973) and Shapiro et al. (1977) conducted numerous enclosure experiments, with highly reproducible results. Of 20 experiments involving additions of CO₂ to pH 5.5 (with concurrent additions of nitrogen and phosphorus), 19 indicated dominance shifted from blue-greens (Phormidium, Anabaena, Chroococcus, Gomphosphaerium, and Aphanizomenon) to green algae (largely Chlorella and Scenedesmus). Enrichment with nitrogen and phosphorus facilitated these shifts. The relative ability to utilize CO₂ was believed to be only partially responsible for the shifts; pH was felt to be the major controlling factor. The end result was an algal population with a high proportion of species grazable (edible) by zooplankton rather than the relatively ungrazable blue-greens. The effects of a pH shift was more pronounced when accompanied by nutrient additions. If nitrogen and phosphorus were not added, the shift, even at a pH of 5.5, was slow and partial. However, upon the addition of nitrogen and phosphorus, the shift was more dramatic, even when green algae were initially rare. Shifts were also reversible; by changing the pH from low to high values, green algae shifted to blue-greens.

C. IN-LAKE PHOSPHORUS REMOVAL

The precipitation of phosphorus in a lake is usually achieved through the use of aluminium sulfate (alum). Other agents, such as ferric chloride or calcium hydroxide, are not suitable. The ferric ion is easily released after its reduction to ferrous, and calcium hydroxide results in a pH increase. Cooke and Kennedy (1981) observed a reduced algal standing crop and improved transparency after the addition of aluminum sulfate to a lake. Alum is particularly useful for inactivating phosphorus when the soluble reactive phosphorus concentration is at a maximum, or dissolved organic phosphorus is at a minimum (Vigon and Armstrong, 1977). The following restrictions or problems are typical for this treatment:

1. There is no rational basis for dosing (amount added).
2. Data on the longevity of effectiveness are not available. Jorgensen (1980) documents a short-lived effect. The longevity of the effectiveness versus initial cost is not known.

3. There is no knowledge about the impact of the treatment upon the levels of biological organization or long-term toxicity.
4. Methods of applying alum are inefficient and need to be improved. The water body must be stratified during the application to prevent the disruption of flocculation by wind mixing.
5. Cost restricts the application to small water bodies only.
6. The method should only be effective in sufficiently deep lakes to prevent disruption of the floc by wind mixing, where the algal abundance can be ascribed to variations in the suspected limiting nutrient, and where nutrient correlations can be demonstrated.

D. ALGICIDES

Algicides generally produce a considerable improvement in lakes, resulting in the reduction or elimination of algal blooms and their accompanying problems. However, the effect is only a temporary cosmetic one, and the high cost of copper sulfate, the traditional algicide of choice, is prohibitive except for use in the smallest of lakes. Potassium permanganate has also been used effectively.

Recently, organic chelations of copper have appeared which are based on triethylaniline, citrate, or gluconate. In contrast to copper sulfate, whose toxicity to most aquatic organisms is well documented, the organic chelations of copper appear to be relatively safe although considerable caution is still necessary. Further testing is required to evaluate their biodegradability and ultimate fate in the aquatic system. These new algicides may eliminate most of the toxicity problems copper sulfate produces, while at the same time keeping the copper in solution longer by preventing its precipitation. This reduces the quantity of copper required for the administration of an effective dose, thereby reducing the potential toxicity problems and the cost.

Some species specific organic algicides are also available. This is a field for future research and development. The most selective agents which work against blue-green algae appear to be phenanthraquinone, dichlone (2,3-dichloronaphthoquinone), rosin amine D acetate, and simazine. Some of the tests which have been conducted with these algicides have been described by Prows and McIlhenny (1974), Prescott (1981a,b), and Fitzgerald (1981).

E. BACTERICIDES

Bactericides have been given only passing attention despite the numerous interactions between bacteria and algae. The rationale behind the application of bactericides is the reduction of CO₂ availability to the algae (CO₂ can be the limiting nutrient in a dense bloom population). CO₂ is produced by the decomposition of organic compounds by bacteria. Kuentzel (1969) advocates the removal of the biodegradable organic matter (or an arrest in its degradation) as a necessary control step in the overall attempt to reduce massive algal blooms. However, no serious tests have been carried out to study the effects of a reduced bacterial population on the rest of the freshwater community.

F. METABOLIC INHIBITORS

It may be worth seriously looking into the possibility of the chemical control of algal blooms. This control could occur via metabolic inhibitors of phosphate uptake by algae, including arsenic, potassium, chloride and others, such as the photosynthetic inhibitors CNCH and DCDU. These may make it possible to develop new "algicides".

It is known that an increased concentration of sodium can contribute to the increased eutrophication of some water bodies near the sea. It appears that potassium ions have the opposite effect, inhibiting phosphate uptake (Mohleji and Verhoff, 1980). Microcystis is better at phosphate uptake than Selenastrum, therefore Microcystis can be preferentially inhibited by potassium. Shapiro et al. (1977) demonstrate that arsenate can limit phosphate uptake by green algae, while chlorine limits the uptake rate more in blue-greens than in greens.

VI. EXPERIMENTAL BIOLOGICAL APPROACHES OF BLOOM CONTROL

Methods Discussed In This Section

1. Allelopathy by algae
 2. Macrophytes
 3. Pathogens: Viruses (phages)
 4. Pathogens: Bacteria and Fungi (actinomycetes)
 5. Grazing/predation
 6. Fish
-

Presently, all methods relating to biological control of algal blooms must be considered experimental.

A. ALLELOPATHY

Allelopathy can be defined as the chemical inhibition of one organism by another, and occurs via inhibitory compounds excreted by algae and plants. Allelopathy offers an explanation for the most offensive characteristic of accelerated eutrophication, the rapid take-over of the vernal diatom bloom population by blue-green algae. Keating (1976, 1977, 1978) reports extensively on the inhibition of diatom growth by cell-free extracts of blue-green algae. The extent of interaction is so great that the diatom bloom population varies inversely with the level of the preceding blue-green algal population. Keating (1976) noted that an inhibition of diatom development in the spring was overcome by an addition of silica. This notion can serve as a basis for management, as it suggests that through eliminating winter blue-green algal blooms and stimulating the more desirable vernal diatom blooms, summer blue-green blooms can be diminished. Such an approach would involve:

1. Winter blue-green blooms should be eliminated by algicides. This would remove the allelopathic inhibition of the spring diatom bloom.
2. Spring diatom blooms should be enhanced by the addition of silica. Silica would lessen the effect of the utilization of blue-green metabolites and would extend the diatom bloom.
3. These effects should increase the period of diatom domination and decrease the nutrient levels left over after diatom die-off. This, in turn, would shorten the subsequent (summer) blue-green bloom.

This control alternative must be tested in whole-lake experiments, but presents an interesting possibility as a

short-term measure.

B. MACROPHYTES

Aquatic macrophytes, especially submersed ones, can inhibit the development of phytoplankton. Canfield et al. (1984) improved a nutrient-chlorophyll model by incorporating the inhibitory effect of macrophytes.

C. PATHOGENS: VIRUSES

The utilization of viruses to combat algal blooms would emulate processes which occur in nature. Viruses which attack blue-green algae (cyanophages) are present in many ecological situations. Although cyanophages are not often reported as occurring, this may be attributable to the lack of good methods for their identification and enumeration. Jenifer (1971) monitored the appearance of viruses which attack algae (phycoviruses) in natural water bodies and found a direct relationship between their presence and the frequency of blue-green algae. This suggests that phycoviruses may play a role in the natural control of algal growths, and indicates there is a potential for their use as biological control agents.

According to Desjardins (1983), the advantages of cyanophages as algae control agents are:

1. They are selective and specific for problem species. This allows for the replacement of problem species with more desirable ones without the annihilation of the entire algal population.
2. They are nontoxic to other microorganisms in the food chain.
3. They are harmless to man and animal.
4. Their utilization should be relatively inexpensive because they would reproduce rapidly in the aquatic environment.
5. They are noncorrosive to mechanical equipment.

Disadvantages of cyanophages as control agents include:

1. A potential problem is the development of host algae which are immune to the virus.

2. A broad spectrum of cyanophages must be available for controlling the species of concern, and the species which replace them.

To date, studies involving the applications of cyanophages to natural waters are few in number. Martin (1982) successfully applied a combination of biological agents (bacteria and viruses) to field enclosures containing developing blooms of Anabaena, Aphanizomenon, Microcystis, and Oscillatoria. Desjardins (1983) tested them on a blue-green bloom in 8000-liter outdoor ponds. In this case, the blue-green alga Plectonema never grew again, although other blue-green algae replaced it as bloom species.

The practical application of cyanophages is only in the initial stages of development. According to Desjardins (1983), aspects requiring further research include:

1. Evaluation of the role of lysogeny in the ecology of cyanophage-host interactions and how it might affect the control of blue-greens.
2. Determination of the effects of environmental factors on the infection and survival capabilities of cyanophages.
3. Development of cyanophages to which problem and toxic species of blue-green algae are susceptible.
4. Checking the development of resistancy (or application of mixed, broad-spectrum species).
5. Determination of the survival capabilities and longevity in natural environments.
6. Performance of field tests under controlled conditions.
7. Giving consideration to the development of available off-the-shelf viable cultures (e.g., seed and an introductory media supplement). These would be a mixture of cyanophages especially developed for certain types of blue-green algal blooms. Methods of preservation and storage of these materials should be developed. Freezing significantly reduces the infectivity of cyanophages (Desjardins, 1983).
8. Application of an integrated approach for the use of cyanophages and bacterial agents to complement zooplankton grazing.

D. BACTERIA AND ACTINOMYCETES

Tests with lytic bacteria are in their infancy and have a great potential (Martin, 1982). Certain antagonistic bacteria (mostly myxobacteria) can disrupt the peptidoglycan cell wall

layer of blue-green algae. Usually, a cell-to-cell contact is required, even though the lytic agent is extracellular, having proteolytic and cell wall lytic activity (Martin, 1976; Burnham, 1981). Tests have been successful with Aphanizomenon, Microcystis and Anabaena. To increase the potential of the myxococcal predatory system, co-predation can be used: an actinomycete occupying the core of the colony and myxococcus occupying the periphery (Burnham and Fraleigh, 1983). The advantages of bacterial lytic systems are:

1. A low inoculum is requirement.
2. Low-specific host requirement.
3. Survival in the environment (tests in controlled natural ecosystem are required).
4. Blue-greens may become more available to heterotrophs following their lysis. In food chains, this may lead to predation at a higher trophic level (e.g., at the level of fish).

E. GRAZING

Grazing is the use of plants as a food source; grazing organisms are usually referred to as herbivores. In the present context, grazing refers to the consumption of phytoplankton (algae) by zooplankton and fish. A considerable portion of the zooplanktonic community is herbivorous. Some animals, referred to as omnivores, are not selective feeders and utilize both animals and plants for nutrition. Table 2 provides examples of some of the more common grazers, omnivores, and predators found in the zooplanktonic community of lakes.

Grazing of herbivorous zooplankton on algae is a topic under considerable discussion, especially for the colonial and filamentous blue-greens. The ability of zooplankton to utilize algae is highly variable, being dependent on a number of factors:

1. Type of algae.
2. Size and shape of algae.
3. Zooplankter's means of feeding.
4. Selective feeding mechanisms of zooplankter.
5. Nutritional quality and digestibility of algae.
6. Survival and reproductive rates of zooplankton.
7. Relative and absolute abundance of algae.
8. Palatability and toxicity of algae.

Table 2: Some Common Members of Freshwater Communities.

Trophic Level	Group	Typical Genera/Species	Method Of Feeding	
Primary Producers:	Algae and Macrophytes			
Herbivores:	Large Cladocerans	<u>Daphnia</u>	NSF	
		<u>Diaphanosoma</u>	NSF	
	Small Cladocerans	<u>Bosmina</u>	NSF	
		<u>Ceriodaphnia</u>	NSF	
		<u>Holopedium</u>	NSF	
	Copepod Nauplii	<u>Cyclops</u>	SF	
		<u>Diaptomus</u>	SF	
		<u>Limnocalanus</u>	SF	
	Small Copepods	<u>Diaptomus</u>	SF	
		<u>Eurytemora</u>	SF	
	Small Rotifers		SF	
Primary Predators:	Large Cladocerans	<u>Leptodora</u>	R	
		<u>Polyphemus</u>	R	
	Large Copepods	<u>Cyclops (large)</u>	SF	
		<u>Epischura</u>	SF	
		<u>Senecella</u>	SF	
	Large Rotifers	<u>Asplanchna</u>	R	
		<u>Drachionus</u>	R	
		Macroinvertebrates	e.g., Insects, Snails	
		Small Vertebrates		
	Secondary Predators:	Zooplanktivorous Fish (prey on zooplankton)		
Top Predators:	Piscivorous Fish (prey mostly on fish)			

R = Raptorial
 SF = Sective Filter Feeders
 NSF = Non-Selective Filter Feeders

The belief of some people that blue-green algae are totally ungrazable by zooplankton is not fully justified. Blue-green species such as Aphanizomenon (Blazka, 1966; Holm et al., 1983), Microcystis (DeBernardi et al., 1981), and Anabaena can, under certain conditions, be grazed. The major problem associated with grazing upon blue-green algae is a decrease in the filtering rate of filter-feeding zooplankton. This is due to the mechanical difficulties of handling filamentous algae (Webster and Peters, 1978). The vast amount of literature on grazing emphasizes conditions relating to the edibility of algae. These include factors such as toxins in Anabaena, Aphanizomenon, Microcystis and Lyngbya (see e.g., Moore, 1977, Gentile and Maloney, 1969, Lampert, 1981).

The zooplankton community exhibits a seasonal patterns of growth, as does the phytoplankton community. In addition to absolute measures of organisms (e.g., dry weight or organism counts), the system's structure is vitally important. System structure includes the ratio of herbivores to predators and the proportions of individual grazer groups. Herbivore counts are usually the highest in spring and late summer, that is, during the periods of peak algal biomass and growth (Adalsteinsson, 1979). This pattern is interpreted to be the result of the following two factors (in addition to the appearance of large cladocerans such as Daphnia):

1. Zooplankton mortality from either zooplanktivorous fish pressure or invertebrate predators.
2. Large and filamentous algal forms contributing a selective interference factor with the filtration mechanism.

Thus, a typical succession of zooplankton in eutrophic lakes would be (Gliwicz, 1977):

1. Spring development of mostly large cladocerans (e.g., Daphnia, Bosmina).
2. Summer recession of the above, accompanied by abundance of Diaphanosoma, and Chydorus, Ceriodaphnia.
3. A temporary return of large cladocerans in autumn.

With continued eutrophication, the appearance of large cladocerans changes to the appearance of small cladocerans or small copepods (i.e. microzooplankton). This shift from large cladocerans to the microzooplankton, which can utilize finer particulate matter of microbial-detrital origin, means a shift from the phytoplanktonic/large zooplanktonic community structure which provides a food source for higher trophic levels, to the microbial-detritus system characterized by microzooplankton. This is a shift toward a less efficient and less desirable food chain. The goal in lake restoration is to maintain the community dominated by herbivorous zooplankton.

Experiments have been conducted to modify phytoplanktonic/zooplanktonic communities. McCauley and Briand (1979) demonstrated that phytoplankton composition could be changed by the removal of large (predatory) zooplankton. This was accomplished by filtering out the zooplankters with netting. In this case, blue-green algae shifted to green and diatom dominance. Bailey-Watts (1982) introduced the large zooplankton Daphnia and Cyclops in order to decrease the number of smaller-sized algae. Schoenberg and Carlson (1984), using lake enclosures, added small Bosmina to green algae (Scenedesmus, Ankistrodesmus). They obtained increased algal biomass, productivity, pH, and Microcystis population. On the other hand, a reverse experiment with the large cladoceran Daphnia lead to lowered biomass, production rate, pH, and to a reduced proportion of blue-greens. Thus, heavy grazing on large and colonial algae (e.g. Daphnia grazing on Microcystis) resulted in a set of abiotic factors favoring edible and non-edible green algae. The authors also reported on several documented cases in which the proportion of more edible algae either increased or was unchanged, contrary to the expected result of selective grazing behavior. This anomalous pattern can be explained by grazing on large blue-green algae (by large grazers) and/or differential stimulation of the nanoplankton.

F. GENERAL ECOSYSTEM MODELS

Ecosystem Structure

The previous sections dealt only with a two-level (link) interaction, such as algae/herbivore interactions. Studies involving the effects of fish, as well as modifications of the system's trophic structure have illustrated potential means of algal control. In general terms, the total energy available to a food chain is dependent on the solar energy that is fixed by plants during photosynthesis (e.g., freshwater algae in the case of lakes). As one moves to higher trophic levels in the food chain, most of the energy contained within the previous trophic level is dissipated. The efficiency of energy transfer is the

ratio of energy available in the higher trophic level to that in the lower trophic level, or when considering the entire system, the ratio of energy leaving the system to the energy entering the system.

Using net productivity and production data, Wetzel (1975) lists a few documented examples of phytoplankton - zooplankton predator - top predator (fish) food chains. The efficiency of transfer is nearly constant at about 10 percent. The chain length (i.e. the number of trophic levels) depends on the amount of energy available (resources) at the lowest level, and is greater as the productivity of phytoplankton increases.

There is a general pattern between the food chain structure and the dominant controlling factor for the system. This is highly significant for the purpose of controlling the algal standing crop. The controlling factor is dependent upon whether the whole system is odd-linked (one, three, five trophic levels) or even-linked (two, four, six trophic levels) (Table 3) (Fretwell, 1977; Hairston et al., 1960).

The biological dynamics which tend to result in relatively lower algal standing crop with an even number of trophic levels (even-linked) and relatively higher algal standing crops with an odd number of trophic levels (odd-linked) is actually a simple concept. The following is a simplistic, generalized description. The first trophic level is always the producers, that is, the algae and macrophytes which form the basis for the food chain (Table 3). This single trophic level alone would be an odd-linked system (one trophic level) and would result in biologically unchecked algal growth. The second trophic level (even-linked system) is generally the herbivorous zooplankton which feed on the algae, thereby providing a control mechanism to restrict algal growth. This even-linked (two trophic level) system would result in relatively lower algal standing crops. The third trophic level (odd-linked system) is generally carnivorous zooplankton which feed on the herbivorous zooplankton. Thus, the control exerted by herbivorous zooplankton on algal standing crops in the two trophic level system is now removed through the introduction of the third trophic level. The fourth trophic level (even-linked system) may be zooplanktivorous fish which feed mainly on the carnivorous zooplankton which tend to be larger in size than the herbivorous zooplankton. This permits a greater number of herbivorous zooplankton which can, again, keep the standing crop of algae relatively low.

Table 3: Generalized Concept of Even/Odd Linked Systems and Their Effect on Ecosystem Composition.

System Type and Linkage	Relative Size of Algal Standing Crop	Control Type	Herbivores (Zooplank.)	Primary Predators (Zooplank.)	Zooplanktivorous Fish	Piscivorous Fish
1 - Odd	High	Resource	X			
2 - Even	Low	Grazers	X	X		
3 - Odd	High	Resource	X	X	X	
4 - Even	Low	Predator	X	X	X	X

Several limitations make it difficult to apply the concept of even- and odd-linked systems, and ecosystem models in general, to freshwater systems. First, it is sometimes difficult to properly define both the number of trophic levels and the community structure. It is misleading to use only the standing crop of each group because it is a result of the dynamics of the growth and loss (e.g., death, sinking, grazing, predation) processes. For example, an active, healthy zooplankton population can be very small under heavy predator pressure. As a result, one might have the tendency to neglect it in the overall model. As an alternative, productivity and turnover rates (e.g., grazing, predation rates, growth rates) could be used. However, methods for estimation of these are elaborate and sometimes unavailable. Another serious problem in many investigations has been the failure to separate the zooplankton into grazing, omnivorous, and predatory components. Likewise, the fish population must be properly characterized (e.g., grazers, piscivorous, zooplanktivorous).

Figure 2: Branched Food Chains With Different Numbers of Trophic Levels.



The number of trophic levels may vary according to the initial input of resources and may sometimes be difficult to assign. For a highly complex system with many parallel branches, one can end up with a non-integer-length food chain, because energy may flow through different parallel branches, each having a different number of trophic levels (links) (Fretwell, 1977). Furthermore, the length of the food chain (number of trophic levels) is, among other factors, dependent on the size of the ecosystem and the resources available. Total length is ecosystem size dependent. For example, a top predator (e.g., piscivorous fish) may occur whenever there are sufficient resources. The importance of top predators will become apparent in later sections.

The number of trophic levels is the result of the "will of man" to some extent. As was illustrated in the discussion on even- and odd-linked systems (Table 3), only even-linked systems are desirable from the viewpoint of obtaining low standing crops of phytoplankton. Thus, a top predator (e.g., fish) is recommended (either piscivorous or zooplanktivorous).

In oligotrophic systems, the carrying capacity (number of organisms the system can support) may limit the trophic structure; insufficient resources may result in limited trophic levels with no top predators present. Therefore, the addition of nutrients (nutrient manipulation) may result in a desirable shift in trophic structure in an oligotrophic lake by adding a desirable trophic level.

Addition and Removal of Trophic Levels

It is clear from the previous section on ecosystem structure that algal biomass is controlled by ecosystem structure. Thus, if one can control the ecosystem structure, one can control the standing crop of algae. Recent data on the effect of addition or

removal of some trophic levels, obtained largely from lake manipulation studies, are summarized in Table 4.

Table 4: Trophic Levels Interaction

Authors	Algae	Herbi- vores (Zoo- plank.)	Preda- tors (Zoo- plank.)	Zooplank- tivorous Fish	Pisciv- orous Fish	Total # of Trophic Levels	Effect On Total Phyto- plankton
Elliot et al. (1983)	X					1	Increase
	X	X				2	Decrease
	X	X		X		3	Increase
Sirenko et al. (1983)	X	X	X		X	4	Decrease
Henrick- son et al. (1980)	X	(X)	X			2	Decrease
Lynch & Shapiro (1981)	X					1	Increase
	X	X	(X)			2	Decrease
	X	X	(X)	X		3	Increase
Andersson et al. (1978)	X	X	X	X	X	5	Increase
	X	X	X			3	Decrease

(X) Authors did not include in the total number of trophic levels.

The only well-defined data are from Elliot et al. (1983). In the other reports, there is uncertainty, especially in terms of the number of trophic levels. These data generally conform to the outline of ecosystem structure presented above. The only exception is the data of Anderson et al. (1978) on fish removal. In some experiments, fish removal via chemical means (rotenone) was used, and it is not clear what effect the chemicals had on other trophic levels.

Sirenko et al. (1976) reported on heavy grazing by piscivorous fish on Aphanizomenon, Oscillatoria, Anabaena and Microcystis. Siegfried (1983) reported on the shift in dominance from diatom-cryptomonads to coccoid blue-greens (Anacystis and Aphanotheca). This occurred with the increase of a population of rainbow smelt, a zooplanktivorous fish, due to predation on large zooplankton.

Fish (Top Predators)

As indicated Table 4, studies on the effect of piscivorous and zooplanktivorous fish, separately or together, in a food chain with all of the links present are very rare. For example, a controlled study of the effects of piscivorous fish on phytoplankton-herbivores-predators is not available. Control of fish populations and types was suggested by Carlson and Schoenberg (1983) as a possibility for reducing the algal standing crop and at the same time the blue-green/green ratio. The conceptual model originated from a study of phytoplankton-herbivore interaction. An increased nutrient load leads to a decrease in CO_2 concentration and an increase in pH, the consequence of photosynthetic consumption of CO_2 , resulting in an increase of blue-green algae. The resulting high primary productivity and high algal densities decrease the available light (transparency), thereby fostering the growth of blue-greens. The observed decrease in the grazing of either the inedible green algae (filamentous or big colonial) or toxic blue-greens may be the result of increased fish predation on large herbivores (zooplankton). This leads to a decrease in the mean size of zooplankton, caused either by an increase in the macrophyte cover suitable for fish or by a decreased zooplanktivore search volume resulting from the depletion of hypolimnetic oxygen. The higher algal biomass significantly increases the sedimentation rate of dead algal cells. The decay of these cells causes hypolimnetic oxygen decreases. With lowered hypolimnetic oxygen concentrations, nutrient release is increased, and the cycle repeats.

To reverse the process just described, Carlson and Schoenberg (1983) suggest an effective method of reducing blue-greens. They do this by promoting the growth of larger zooplankton by decreasing the abundance of zooplanktivorous fish. Zooplanktivorous fish selectively prey on large zooplankton. Therefore, their absence should lead to a decline in carnivorous zooplankton and, therefore, an increase in herbivorous zooplankton and a decrease in algal abundance. Furthermore, the intensive selective grazing by herbivores on small particles should decrease the primary productivity and increase the ambient light to the water column. As a result, blue-green algae will decline, even though they are not grazed, and greens will proportionally dominate the population because of their better light competition characteristics.

Thus, control measures should try to reduce the predation pressure of zooplanktivorous fish via:

1. Fish poisons, although this measure is questionable, because such poisons also affect other food chain links.
2. Establishment of a fish community that does not use primarily zooplankton as its food (e.g., piscivorous fish).

3. Reduction of macrophytes, because zooplankton are strongly inhibited or repelled by substances secreted into the water.
4. Destratification, which increases the volume available for zooplankton and decreases the impact of fish predation on them.
5. Introduction of large zooplankton species.
6. Creation of zooplankton refuges in water bodies (zones of highly oxygenated water near the surface of the water body, containing high water temperatures, unsuitable for zooplanktivorous fish).
7. Providing an alternate food supply (organic carbon source) to increase the zooplankton population and to maintain it during periods of low algal abundance.
8. Introduction of other herbivorous animals (snails).

Summary of Control With Top Predators

From field observations, there is no doubt that the effect of the top predator on the trophic biomass pyramid causes a series of alterations in underlying trophic levels. Furthermore, it causes physical and chemical conditions in the water to change and may cause a shift in the direction of eutrophication. This, in turn, would eventually lead to a shift from a high primary productivity, microzooplankton - microbial - detritus recycle food chain to a low primary productivity, large zooplankton - fish food chain. This latter food chain is the more desirable one and is a more ecologically balanced system. It can be achieved by the introduction of top fish predators, either piscivorous fish which eat other fish or zooplanktivorous fish which eat zooplankton. At the same time, some nutrient manipulation may be required to adjust the length of food chain.

Many problems are to be addressed before this kind of control is fully implementable. One of the major problems is the long-term effect of predators and/or grazers over the whole range of pressures. Also, large-scale manipulation studies are required. However, biological top control has the potential of being relatively inexpensive, perhaps self-perpetuating, and may be the most "natural" method available.

VII. CONCLUSIONS

Table 5 provides a summary of management practices based on the previous discussion of water quality problems and restoration approaches. It appears that more basic research is needed in almost all areas, especially in the cause-effect relations of bloom formation and in the corresponding fundamentals of control methods, which includes individual studies of two-link interactions between trophic levels. Well-controlled field tests are necessary in which data is appropriately collected at all trophic levels.

Priority should be given to the biological methods because of low initial cost and their self-perpetuating effect. Highest priority should be given to control via top predators. It is suggested that a special review of control methods be devoted to this problem since the authors did not collect all available data. The complexity of the problems mandate that an interdisciplinary effort should be launched. Large-scale and long-term experiments will require a high initial concentration of manpower and money.

Besides control at the purely biological level, some combination of all three kinds of basic methods should be attempted. The most obvious seems to be top biological control (perhaps supplemented by specific removal of nongrazable phytoplankton via parasites), accompanied by the following: suitable nutrient manipulation, destratification when appropriate, and system modeling and simulation to reinforce the entire control strategy.

Table 5: Summary of Algal Bloom Management Strategies.

Method	Lab Tests	Field Tests	Cost	Prospect	Comments
<u>Chapter III: Nutrient Load Reductions</u>					
External Nutrient Load Manipulation			High	X	Well established in wastewater treatment.
<u>Chapter IV: Physical, Mechanical & Engineering Methods</u>					
A. Artificial Circulation/ Destratification		X	May Be Low	X	Intermittent; combine with wind induced or low intensity mixing.
Hypolimnetic Aeration		X	High	?	
B. Hypolimnetic Diversion					May create problems downstream.
C. Sediment Removal/ Immobilization		X	High	X	Short-term remedy.
D. Lake Dilution/ Flushing				X	Short-term remedy, may cause problems downstream.
E. Algae Removal/ Harvesting	X	X	High	X	Cost lower if utilize harvested algae.
F. Light Modification	X	X	High	?	In early stages of development.
<u>Chapter V: Chemical Methods</u>					
A. Nutrient Manipulation		X	Low	X	
B. pH and CO ₂ Manipulation	X	X	High	?	Short-term remedy.
C. Phosphorus Removal (Precipitation)	X	X	High		

Table 5: Continued.

Method	Lab Tests	Field Tests	Cost	Prospect	Comments
D. Algicides	X	X	High	X	Short-term remedy.
E. Bactericides	X	X	High	?	
F. Metabolic Inhibitors	X	X	High	?	
<u>Chapter VI: Biological Methods</u>					
A. Allelopathy	X	X	Low	?	With silicon enrichment.
B. Macrophytes	X	X	Low	?	Must be investigated.
C. Viruses	X	X	Low	X	With other biol. methods.
D. Bacteria	X	X	Low	X	Too early to assess.
E. Grazing/ Predation	X		Low	X	
F. Fish	X	X	Very Low	X	

LITERATURE CITED

- Adalsteinsson, H., 1979. Zooplankton and Its Relation to Available Food in Lake Myvatn. OIKOS 32: 162-194.
- Ahlgren, I., 1977. Role of Sediments in the Progress of Recovery of a Eutrophicated Lake. In: Golterman, H.L. (Ed.), Interactions Between Sediments and Freshwater, Dr. W. Junk Publishers, pp. 372-377.
- Armstrong, D.E., and R.E. Stauffer, 1980. Internal Loading in Shagawa Lake. Ecological Research Series Report, U.S. EPA, Corvallis, OR.
- Ashley, K.I., 1983. Hypolimnetic Aeration of a Naturally Eutrophic Lake: Physical and Chemical Effects. Can. J. Fish. Aquat. Sci. 40(9): 1343-1359.
- Bailey-Watts, A., 1982. The Composition and Abundance of Phytoplankton in Loch Leven (Scotland) 1977-1979 and a Comparison. With the Succession in Earlier Years. Int. Revue ges. Hydrobiol. 67(1): 1-25.
- Banse, K., 1976. Rates of Growth, Respiration and Photosynthesis of Unicellular Algae as Related to Cell Size - A Review. J. Phycol. 12: 135-140.
- Barcia, J., H. Kling, and J. Gibson, 1980. Experimental Manipulation of Algal Bloom Composition by Nitrogen Addition. Can. J. Fish. Aquat. Sci. 37: 1175-1183.
- Baybutt, R.I., and J.C. Makarewicz, 1981. Multivariate Analysis of the Lake Michigan Phytoplankton Community at Chicago. Bulletin of the Torrey Botanical Society 108(2): 255-267.
- Berman, T., B.F. Sherr, E. Sherr, D. Wynne, and J.J. McCarthy, 1984. The characteristics of Ammonium and Nitrate Uptake by Phytoplankton in Lake Kinneret. Limnol. Oceanogr. 29(2): 287-297.

- Bierman, V.J., Jr., 1976. Mathematical Model of the Selective Enhancement of Blue-Green Algae by Nutrient Enrichment. In: Canale, R.P. (Ed.), Modeling Biochemical Processes in Aquatic Ecosystems. Ann Arbor Science, Ann Arbor, MI, pp. 1-31.
- Blazka, P., 1966. Metabolism of Natural and Cultured Populations of Daphnia Related to Secondary Production. Verh. Int. Verein. Limnol. 16: 380-385.
- Brock, T.D., 1973. Lower pH Limit for the Existence of Blue-Green Algae: Evolutionary and Ecological Implications. Science 179: 480-483.
- Burnham, J.C., 1981. The Utilization of Bacteria in Managing Cyanobacterial Populations: A Review and Update. In: Taylor, W.D. and V.W. Lambon (Eds.), Proceedings of Workshop on Algal Management and Control. Technical Report E-81-7 (Army Corps of Engineers). Prepared by U.S. EPA, Las Vegas, NV, pp. 230-258.
- Burnham, J.C., and P.C. Fraleigh, 1983. Predatory Myxobacteria: Lytic Mechanisms and Prospects as Biological Control Agents for Cyanobacteria (Blue-Green Algae). In: Lake Restoration, Protection and Management, Proceedings of Second Annual Conference, October 26-29, 1982. EPA-440/5-83-001, U.S. EPA, Washington, D.C., pp. 249-256.
- Canale, R.P., L.M. DePalma, and A.H. Vogel, 1976. A Plankton-Based Food Web Model for Lake Michigan. In: Canale, R.P. (Ed.), Modeling Biochemical Processes in Aquatic Ecosystems. Ann Arbor Science, Ann Arbor, MI, pp. 33-72.
- Canfield, D.E., Jr., J.V. Shireman, D.E. Colle, W.T. Haller, C.E. Watkins II, and M.T. Maceina, 1984. Predictions of Chlorophyll a Concentrations in Florida Lakes: Importance of Aquatic Macrophytes. Can. J. Fish. Aquat. Sci. 41: 497-501.
- Carlson, R.E., and S.A. Schoenberg, 1983. Controlling Blue-Green Algae by Zooplankton Grazing. In: Lake Restoration, Protection and Management, Proceedings of Second Annual Conference, North American Lake Management Society,

October 26-29, 1982. EPA 440/5-83-001, U.S. EPA, Washington, D.C., pp. 228-233.

- Carpenter, E.J., and R.L. Guillard, 1971. Intraspecific Differences in Nitrate Half-Saturation Constants for Three Species of Marine Phytoplankton. *Ecology* 52: 183-185.
- Cembella, A.D., N.J. Antia, and P.J. Harrison, 1984a. The Utilization of Inorganic and Organic Phosphorus Compounds as Nutrients by Eukaryotic Microalgae: A Multidisciplinary Perspective: Part I. *CRC Critical Reviews in Microbiology* 10(4): 317-391.
- Cembella, A.D., N.J. Antia, and P.J. Harrison, 1984b. The Utilization of Inorganic and Organic Phosphorus Compounds as Nutrients by Eukaryotic Microalgae: A Multidisciplinary Perspective: Part 2. *CRC Critical Reviews in Microbiology* 11(1): 13-81.
- Chapra, S.C., and K.H. Reckhow, 1983. *Engineering Approaches for Lake Management, Volume 2: Mechanistic Modeling*. Ann Arbor Science, Ann Arbor, MI, 492 pp.
- Chow-Fraser, P., and H.C. Duthie, 1983. Assessment of Phosphorus Limitation in an Oligotrophic Lake Using Radiophosphorus Uptake Kinetics. *Can. J. Fish. Aquat. Sci.* 40: 817-821.
- Cole, J.J., 1982. Interactions Between Bacteria and Algae in Aquatic Ecosystems. *Ann. Rev. Ecol. Syst.* 13: 291-314.
- Collins, C.D., and C.W. Boylen, 1982. Ecological Consequences of Long-Term Exposure of *Anabaena ariabilis* (Cyanophyceae) to Shifts in Environmental Factors. *Applied and Environmental Microbiology* 44(1): 141-148.
- Cooke, G.D., and R.H. Kennedy, 1981. State-of-the-art Summary of Phosphorus Inactivation as a Lake Restoration Technique. In: Taylor, W.D. and V.W. Lambon (Eds.), *Proceedings of Workshop on Algal Management and Control*. Technical Report E-81-7 (Army Corps of Engineers). Prepared by U.S. EPA, Las Vegas, NV, pp. 32-56.

- Cordeiro, C.F., W.F. Echelberger, Jr., and F.H. Verhoff, 1977. Rates of Carbon, Oxygen, Nitrogen, and Phosphorus Cycling Through Microbial Populations in Stratified Lakes. In: Middlebrooks, E.J. (Ed.), Modeling the Eutrophication Process. Ann Arbor Science, Ann Arbor, MI, pp. 111-120.
- Currie, D.J., and J. Kalff, 1984a. A Comparison of the Abilities of Freshwater Algae and Bacteria to Acquire and Retain Phosphorus. *Limnol. Oceanogr.* 29(2): 298-310.
- Currie, D.J., and J. Kalff, 1984b. The Relative Importance of Bacterioplankton and Phytoplankton in Phosphorus Uptake in Freshwater. *Limnol. Oceanogr.* 29(2): 311-321.
- DeBernardi, R., G.G. Giussani, and E.L. Pedretti, 1981. The Significance of Blue-Green Algae as Food for Filterfeeding Zooplankton: Experimental Studies on Daphnia spp. fed by Microcystis aeruginosa. *Verh. Internat. Verein. Limnol.* 21: 477-483.
- DePinto, J.V., V.J. Bierman, Jr., and F.H. Verhoff, 1976. Seasonal Phytoplankton Succession as a Function of Species Competition for Phosphorus and Nitrogen. In: Canale, R.P. (Ed.), Modeling Biochemical Processes in Aquatic Ecosystems. Ann Arbor Science, Ann Arbor, MI, pp. 141-169.
- Desjardins, P.R., 1983. Cyanophage: History and Likelihood as a Control. In: Lake Restoration, Protection and Management, Proceedings of Second Annual Conference, October 26-29, 1982. EPA 440/5-83-001, U.S. EPA, Washington, D.C., pp. 242-248.
- Dillon, P.J., N.D. Yan, and H.H. Harvey, 1984. Acidic Deposition: Effects on Aquatic Ecosystems. *CRC Crit. Rev. Environ. Control* 13(3): 167-194.
- Dorich, R.A., D.W. Nelson, and L.E. Sommers, 1980. Algal Availability of Sediment Phosphorus in Drainage Water of the Black Creek Watershed. *J. Envir. Qual.* 9: 557-563.
- Dunst, R.C., 1981. Dredging Activities in Wisconsin's Lake Renewal Program. In: Restoration of Lakes and Inland Waters: International Symposium on Inland Waters and Lake

Restoration, EPA 440/5-81-010 Sept. 8-12, 1980, Portland, ME. U.S. EPA, Office of Water Regulations and Standards, Washington, D.C., pp. 86-88.

- Elliot, E.T., L.G. Castanares, D. Perlmutter, and K.G. Porter, 1983. Trophic-level Control of Production and Nutrient Dynamics in an Experimental Planktonic Community. OIKOS 41: 7-16.
- Ellis, B.K., and J.A. Stanford, 1982. Comparative Photoheterotrophy, Chemoheterotrophy, and Photolithotrophy in a Eutrophic Reservoir and an Oligotrophic Lake. Limnol. Oceanogr. 27(3): 440-454.
- Falkner, G., P. Strasser, and D. Graffius, 1984. Phosphate Uptake by Blue Green Algae *in vitro* and in a Lake During an Algal Bloom: Useful Application of a Force-Flow Relationship. Hydrobiologia 108: 265-271.
- Fallon, R.D., and T.D. Brock, 1980. Planktonic Blue-Green Algae: Production, Sedimentation and Decomposition in Lake Mendota, Wisconsin. Limnol. Oceanogr. 25(1): 72-88.
- Fallon, R.D., and T.D. Brock, 1979. Decomposition of Blue-Green Algal (Cyanobacterial) Blooms in Lake Mendota, Wisconsin. Applied and Environmental Microbiology 37(5): 820-830.
- Fast, A.W., and M. Lorenzen, 1978. Effects of Aeration/Mixing on Lake Biology. In: Mitchell, R. (Ed.), Water Pollution Microbiology (Volume 2), John Wiley & Sons, New York, NY, pp. 415-430.
- Fee, E.J., 1979. A Relation Between Lake Morphometry and Primary Productivity and its use in Interpreting Whole-Lake Eutrophication Experiments. Limnol. Oceanogr. 24(3): 401-416.
- Ferris, J.J., N.L. Clesceri, 1977. A Description of the Trophic Status and Nutrient Loading for Lake George, New York. North American Project -- A Study of U.S. Water Bodies. EPA-600/3-77-086, U.S. EPA, Corvallis, OR, 135-178.
- Fitzgerald, G.P., 1981. Selective Algalcides. In: Taylor,

W.D. and V.W. Lambon (Eds.), Proceedings of Workshop on Algal Management and Control. Technical Report E-81-7 (Army Corps of Engineers). Prepared by U.S. EPA, Las Vegas, NV, pp. 15-31.

Fogg, G.E., 1969. The Physiology of an Algal Nuisance. Proc. Roy. Soc. B. 173: 175-189.

French, R.H., 1984. Lake Modeling: State of the Art. CRC Crit. Rev. Environ. Control 13: 311-357.

Fretwell, S.D., 1977. The Regulation of Plant Communities by the Food Chains Exploiting Them. Perspectives in Biology and Medicine 20: 169-185.

Ganf, G.G., and R.L. Oliver, 1982. Vertical Separation of Light and Available Nutrients as a Factor Causing Replacement of Green Algae by Blue-Green Algae in the Plankton of a Stratified Lake. J. of Ecology 70: 829-844.

Gates, M.A., A.P. Zimmerman, W.G. Sprules, and R. Knoechel, 1983. Planktonic Biomass Trajectories in Lake Ecosystems. Can. J. Fish. Aquat. Sci. 40(10): 1752-1760.

Gelin, C., and W. Ripl, 1978. Nutrient Decrease and Response of Various Phytoplankton Size Fractions Following the Restoration of Lake Trummen, Sweden. Arch. Hydrobiol. 81(3): 339-367.

Gentile, J.H., and T.E. Maloney, 1969. Toxicity and Environmental Requirements of a Strain of Aphanizomenon flos-aquae (L.) Ralfs. Can. J. Microbiol. 15: 165-173.

George, D.G., and S.I. Heaney, 1978. Factors Influencing the Spatial Distribution of Phytoplankton in a Small Productive Lake. J. of Ecology 66: 133-155.

Gibson, C.E., and R.V. Smith, 1983. Freshwater Plankton. In: Carr, N.G. and B.A. Whitton (Eds.), The Biology of Cyanobacteria. University of California Press, Los Angeles and Berkeley, CA, pp: 463-489.

- Gliwicz, Z.M., 1977. Food Size Selection and Seasonal Succession of Filter Feeding Zooplankton in an Eutrophic Lake. *Ekologia Polska* 25(2): 179-225.
- Gordon, D.M., C.M. Finlayson, and A.J. McComb, 1981. Nutrients and Phytoplankton in Three Shallow, Freshwater Lakes of Different Trophic Status in Western Australia. *Aust. J. Mar:Freshwater Res.* 32: 541-553.
- Haertel, L., 1976. Nutrient Limitation of Algal Standing Crops in Shallow Prairie Lakes. *Ecology* 57: 664-678.
- Hairston, N.G., F.E. Smith, and L.B. Slobodkin, 1960. Community Structure, Population Control, and Competition. *American Naturalist* 94: 421-425.
- Harris, G.P., 1980. Temporal and Spatial Scales in Phytoplankton Ecology: Mechanisms, Methods, Models, and Management. *Can. J. Fish. Aquat. Sci.* 37: 877-900.
- Holm, N.P., G.C. Ganf, and J. Shapiro, 1983. Feeding and Assimilation Rates of Daphnia pulex fed Aphanizomenon flos-aquae. *Limnol. Oceanogr.* 28(4): 677-687.
- Huff, D.D., J.F. Koonce, W.R. Ivarson, P.R. Weller, E.H. Dettmann, and R.F. Harris, 1977. Simulation of Urban Runoff, Nutrient Loading, and Biotic Response of a Shallow Eutrophic Lake. In: Middlebrooks, E.J. (Ed.), *Modeling the Eutrophication Process*, Ann Arbor Science, Ann Arbor, MI, pp. 33-55.
- Ivey, G.N., and J.C. Patterson, 1984. A Model of the Vertical Mixing in Lake Erie in Summer. *Limnol. Oceanogr.* 29(3): 553-563.
- Jenifer, G.W., and J.C. Patterson, 1977. Studies on the Natural Relationships of Cyanophages and their Hosts and the Nature of Resistance. PB-270-781, U.S. Dept. Commerce, Springfield, VA, 24 pp.
- Jensen, T.E., L. Sicko-Goad, and H. Lehman, 1976. Aspects of Phosphate Utilization by Blue-Green Algae. EPA-600/3-76-103, U.S. EPA, Corvallis, OR, 121 pp.

- Jorgensen, S.E., 1980. Lake Management. Pergamon Press, Oxford, 160 pp.
- Kalff, J. and R. Knoechel, 1978. Phytoplankton and their Dynamics in Oligotrophic and Eutrophic Lakes. *Ann. Rev. Ecol. Sys.* 9: 475-495.
- Keating, K.I., 1978. Blue-Green Algal Inhibition of Diatom Growth: Transition from Mesotrophic to Eutrophic Community Structure. *Science* 199: 971-973.
- Keating, K.I., 1977. Allelopathic Influence on Blue-Green Bloom Sequence in a Eutrophic Lake. *Science* 196: 885-887.
- Keating, K.I., 1976. Algal Metabolite Influence on Bloom Sequence in Eutrophied Freshwater Ponds. EPA-600/3-76-081, U.S. EPA, Corvallis, OR, 147 pp.
- King, D.L., 1970. The Role of Carbon in Eutrophication. *Jour. Water Poll. Control Fed.* 42(12): 2035-2051.
- Konopka, A., T.D. Brock, and A.E. Walsby, 1978. Buoyancy Regulation By Planktonic Blue-Green Algae in Lake Mendota, Wisconsin. *Arch. Hydrobiol.* 83(4): 524-537.
- Kothandaraman, V., and R.L. Evans, 1981. An Assessment of the Ecology of Fox Chain of Lakes and the Applicability of In-Lake Restoration Techniques. Illinois State Water Survey Contract Report, pp. 52-63.
- Kuentzel, L.E., 1969. Bacteria, Carbon Dioxide and Algal Blooms. Proceedings of the 24th Industrial Waste Conference May 6, 7 and 8, 1969. Purdue University, Lafayette, IN, pp. 1028-1039.
- Kuenzler, E., S. Mozley, and H. Paerl, 1980. Chowan River Nuisance Algal Blooms and Probable Causes. A Position Paper Prepared for The N.C. Department of Natural Resources and Community Development. Water Resources Research Institute, Univ. of N.C. and N.C. State Univ., Raleigh, N.C., 4 pp.

- Lampert, W., 1981. Inhibitory and Toxic Effects of Blue-Green Algae on Daphnia. Int. Revue ges. Hydrobiol. 66(3): 285-298.
- Larsen, D.P., 1979. The Effect of Wastewater Phosphorus Removal on Shagawa Lake, Minnesota. Water Research 13: 1259.
- Larsen, D.P., 1975. Response of Eutrophic Shagawa Lake, Minnesota, U.S.A., to Point Source, Phosphorus Reduction. Verh. Int. Verein. Limnol. 19: 884.
- Larsen, D.P., and K.W. Malueg, 1981. Whatever Became of Shagawa Lake? In: Restoration of Lakes and Inland Waters: International Symposium on Inland Waters and Lake Restoration, Sept. 8-12, 1980, Portland, ME. EPA 440/5-81-010, Office of Water Regulations and Standards, Washington, D.C. pp. 67-72.
- Lean, D.R.S., 1973a. Movements of Phosphorus Between its Biologically Important Forms in Lake Water. J. Fish. Res. Board Can. 30: 1525-1536.
- Lean, D.R.S., 1973b. Phosphorus Dynamics in Water. Science 179: 678-680.
- Lean, D.R.S., and E. White, 1983. Chemical and Radiotracer Measurements of Phosphorus Uptake by Lake Plankton. Can. J. Fish. Aquat. Sci. 40(2): 147-155.
- Lennox, L.J., 1984. Lough Ennell: Laboratory Studies on Sediment Phosphorus Release Under Varying Mixing, Aerobic and Anaerobic conditions. Freshwater Biology 14: 183-187.
- Lewis, W.M., Jr., 1983. A Revised Classification of Lakes Based on Mixing. Can. J. Fish. Aquat. Sci. 40(10): 1779-1787.
- Lynch, M., and J. Shapiro, 1981. Predation, Enrichment and Phytoplankton Community Structure. Limnol. Oceanogr. 26(1): 86-102.
- Lynch, M., 1979. Predation, Competition and Zooplankton Community Structure: An Experimental Study.

- Limnol. Oceanogr. 24(2): 253-272.
- Martin, E.L., 1982. Biological Regulation of Bloom-Causing Blue-Green Algae: A Feasible Alternative. PB83-220574, Nebraska Water Resources Center, Institute of Agriculture & Natural Resources, University of Nebraska, Lincoln, NE, pp. 1-36.
- Martin, E.L., 1976. Biological Control of Blue-Green Algae. Nebraska Water Resources Center, University of Nebraska, Lincoln, NE, 1-16.
- McCauley, E., and F. Briand, 1979. Zooplankton Grazing and Phytoplankton Species Richness: Field Tests of the Predation Hypothesis. Limnol. Oceanogr. 24(2): 243-252.
- Mohleji, S.C., and F.H. Verhoff, 1980. Sodium and Potassium Ions Effects on Phosphorus Transport in Algal Cells. J. Water Poll. Control Fed. 52(1): 110-125.
- Moore, R.E., 1977. Toxins From Blue-Green Algae. BioScience 27(1): 797-802.
- Murphy, T.P., D.R.S. Lean, and C. Nalewajko, 1976. Blue-Green Algae: Their Excretion of Iron-Selective Chelators Enables Them to Dominate Other Algae. In: Rosowski, J.R. and B.C. Parker (Eds.), Selected Papers in Phycology II, Phycological Society of America, Lawrence, KS, pp. 394-395.
- Norman, J.C., and P.E. Sager, 1978. Modelling Phosphorus Transfer Rates in Lake Water. J. Theor. Biol. 71: 381-385.
- Nurnburg, G.K., 1984. The Prediction of Internal Phosphorus Load in Lakes with Anoxic Hypolimnia. Limnol. Oceanogr. 29(1): 111-124.
- Nyholm, N., 1978. Dynamics of Phosphate Limited Algal Growth: Simulation of Phosphate Shocks. J. Theor. Biol. 70: 415-425.

- Odum, E.P., 1971. Fundamentals Of Ecology, Third Edition. W.B. Saunders Company, Philadelphia, PA, 574 pp.
- Olofsson, J.A., Jr., and F.E. Woodward, 1977. Effects of pH and Inorganic Carbon Concentrations Upon Competition Between Anabaena flos-aquae and Selenastrum capricornutum. PB-267-720, Land and Water Resources Institute, University of Maine at Orono, ME, 55 pp.
- Oswald, W.J., 1976. Removal of Algae in Natural Bodies of Water. EPA-600/3-76-059, U.S. EPA, Environmental Research Laboratory, Corvallis, OR, 151 pp.
- Paerl, H.W., 1983. Partitioning of CO₂ Fixation in the Colonial Cyanobacterium Microcystis aeruginosa: Mechanism Promoting Formation of Surface Scums. Applied and Environmental Microbiology 46(1): 252-259.
- Paerl, H.W., 1982. Environmental Factors Promoting and Regulating N₂ Fixing Blue-Green Algal Blooms in the Chowan River, N.C. UNC-WRRI-82-176, Water Resources Research Institute of the Univ. of North Carolina, Raleigh, N.C., 65 pp.
- Paerl, H.W., and M.F. Downes, 1978. Biological Availability of Low Versus High Molecular Weight Reactive Phosphorus. J. Fish. Res. Board Can. 35: 1639-1643.
- Paerl, H.W., and P.E. Kellar, 1979. Nitrogen-Fixing Anabaena: Physiological Adaptations Instrumental in Maintaining Surface Blooms. Science 204: 620-622.
- Paerl, H.W., J.F. Ustach, 1982. Blue-Green Algal Scums: An Explanation for their Occurrence During Freshwater Blooms. Limnol. Oceanogr. 27(2): 212-217.
- Paloheimo, J.E., and A.P. Zimmerman, 1983. Factors Influencing Phosphorus-Phytoplankton Relationships. Can. J. Fish. Aquat. Sci. 40: 1804-1812.
- Pastorok, R.A., T.C. Ginn, and M.W. Lorenzen, 1981. Aeration/Circulation for Control of Algal Production. In: Taylor, W.D. and V.W. Lambon (Eds.), Proceedings of

Workshop on Algal Management and Control. Technical Report E-81-7 (Army Corps of Engineers). Prepared by U.S. EPA, Las Vegas, NV, pp. 57-97.

Peterson, S.A., 1981. Sediment Removal As A Lake Restoration Technique. EPA-600/3-81-013, Office of Research and Development, Corvallis, OR, 55 pp.

Peters, R.H., 1979. Concentrations and Kinetics of Phosphorus Fractions along the Trophic Gradient of Lake Memphremagog. J. Fish. Res. Board Can. 36: 970-979.

Peters, R.H., 1978. Concentrations and Kinetics of Phosphorus Fractions in Water from Streams Entering Lake Memphremagog. J. Fish. Res. Board Can. 35: 315-979.

Petts, G.E., 1984. Impounded Rivers: Perspectives for Ecological Management. John Wiley & Sons, New York, NY, 326 pp.

Pianka, E.R., 1970. On r- and K-Selection. The American Naturalist 104: 592-597.

Porcella, D.B., A.B. Bishop, and W.J. Grenney, 1977. Activity Analysis and the Management of Resources: A Model for Control of Eutrophication. In: Middlebrooks, E.J. (Ed.), Modeling the Eutrophication Process. Ann Arbor Science, Ann Arbor, MI, pp. 171-186.

Porcella, D.B., S.A. Peterson, and D.P. Larsen, 1980. Index to Evaluate Lake Restoration. J. Envir. Engng. Div. Am. Soc. Civ. Engs. 106: 1151-1168.

Porcella, D.B., J.C. Andersen, O.W. Asplund, and A.B. Crawford, 1974. Comprehensive Management of Phosphorus Water Pollution, February, 1974. EPA-600/3-78-008, U.S. EPA, Washington, D.C., 429 pp.

Prepas, E.E., 1983. Orthophosphate Turnover Time in Shallow Productive Lakes. Can. J. Fish. Aquat. Sci. 40(9): 1412-1418.

Prepas, E.E., D.O. Trew, 1983. Evaluation of the

Phosphorus-Chlorophyll Relationship for Lakes Off the Precambrian Shield in Western Canada.
Can. J. Fish. Aquat. Sci. 40(1): 27-35.

- Prescott, G.W., 1981a. Algicides and Algal Management and Control Bibliography. In: Taylor, W.D. and V.W. Lambon (Eds.), Proceedings of Workshop on Algal Management and Control. Technical Report E-81-7 (Army Corps of Engineers). Prepared by U.S. EPA, Las Vegas, NV, pp. 259-299.
- Prescott, G.W., 1981b. A Review of Control Measures for Objectionable Algal "Blooms". In: Taylor, W.D. and V.W. Lambon (Eds.), Proceedings of Workshop on Algal Management and Control. Technical Report E-81-7 (Army Corps of Engineers). Prepared by U.S. EPA, Las Vegas, NV, pp. 5-14.
- Prows, B.L., and W.F. McIlhenny, 1974. Research and Development of a Selective Algaecide to Control Nuisance Algal Growth. EPA-660/3-74-019, U.S. EPA Pacific Northwest Water Laboratory, Corvallis, OR, 221 pp..
- Reckhow, K.H., and S.C. Chapra, 1983. Engineering Approaches for Lake Management, Volume 1: Data Analysis and Empirical Modeling. Ann Arbor Science, Ann Arbor, MI, 340 pp.
- Reynolds, C.E., G.H.M. Jaworski, H.A. Cmiech, and G.F. Leedale, 1981. On the Annual Cycle of the Blue-Green Alga Microcystis aeruginosa Kutz. emend. Elenkin. Phil. Transactions Royal Society of London B 293: 419-477.
- Reynolds, C.S., 1984a. The Ecology of Freshwater Phytoplankton Cambridge University Press, Cambridge, Great Britian, 384 pp.
- Reynolds, C.S., 1984b. Phytoplankton Periodicity: The Interactions of Form, Function and Environmental Variability. Freshwater Biology 14: 111-142.
- Reynolds, C.S., and A.E. Walsby, 1975. Water-Blooms. Biol. Rev. 50: 437-481.

- Rhee, G-Yull, and I.J. Gotham, 1980. Optimum N:P Ratios and Coexistence of Planktonic Algae. *J. Phycol.* 16: 486-489.
- Round, F.E., 1981. *The Ecology of Algae*. Cambridge University Press, Cambridge, Great Britian, 653 pp.
- Rueter, J.G., Jr., 1983. Alkaline Phosphatase Inhibition by Copper: Implications to Phosphorus Nutrition and Use as a Biochemical Marker of Toxicity. *Limnol. Oceanogr.* 28(4): 743-748.
- Sandusky, J.C., and A.J. Horne, 1978. A Pattern Analysis of Clear Lake Phytoplankton. *Limnol. Oceanogr.* 23(4): 636-648.
- Schanz, F., E.D. Allen, and P.R. Gorham, 1979. Bioassay of the Seasonal Ability of Water from a Eutrophic Alberta Lake to Promote Selective Growth of Strains of Anabaena flos-aquae and Other Blue-Green Algae. *Can. J. Bot.* 57: 2443-2451.
- Schindler, D.W., 1977. Evolution of Phosphorus Limitation in Lakes. *Science* 195: 260-262.
- Schindler, D.W., 1974. Eutropication and Recovery in Experimental Lakes: Implications for Lake Management. *Science* 184: 897-899.
- Schoenberg, S.A., and R.E. Carlson, 1984. Direct and Indirect Effects of Zooplankton Grazing on Phytoplankton in a Hypereutrophic Lake. *OIKOS* 42: 291-302.
- Shapiro, J., 1983. Blue-Green Dominance in Lakes: The Role and Management Significance of pH and CO₂. In: *Lake Restoration, Protection and Management, Proceedings of Second Annual Conference, North American Lakes Management Society, October 26-29, 1982*. EPA 440/5-83-001, U.S. EPA, Washington, D.C., pp. 219-227.
- Shapiro, J., 1973. Blue-Green Algae: Why They Become Dominant. *Science* 179: 382-384.

- Shapiro, J., G. Zoto, and V. Lamarra, 1977. Experimental Studies on Changing Algal Populations from Blue-Greens to Greens. PB-270-779, Contribution No. 168, Limnological Research Center, University of Minnesota, Minneapolis, MN, 27 pp.
- Shuter, B.J., 1978. Size Dependence of Phosphorus and Nitrogen Subsistence Quotas in Unicellular Microorganisms. *Limnol. Oceanogr.* 23(6): 1248-1255.
- Siegfried, C.A., 1983. Dynamics of the Crustacean Zooplankton of Lake George; Or, There's a Rainbow over Lake George but Where's the Pot of Gold. In: Desormeau, C. (Ed.), *The Lake George Ecosystem (Volume III): A Compilation of Original Research Papers Presented at the Third Lake George Research Symposium April 9, 1983.* The Lake George Association, Canada Street, Lake George, NY, pp. 13-22.
- Sirenko, L.A., P.S. Vovk, A.Ya. Malyarevskaya, and T.I. Birger, 1976. Control of Eutrophication of the Dnieper Reservoirs by Algae Removal and Herbivorous Fishes Introduction. *Limnologica (Berlin)* 10(2): 603-606.
- Smith, R.E.H., and J. Kalff, 1983. Competition for Phosphorus Among Co-Occurring Freshwater Phytoplankton. *Limnol. Oceanogr.* 28(3): 448-464.
- Smith, R.E.H., and J. Kalff, 1982. Size-Dependent Phosphorus Uptake Kinetics and Cell Quota in Phytoplankton. *J. Phycol.* 18: 275-284.
- Smith, V.H., 1983a. The Nitrogen and Phosphorus Dependence of Blue-Green Algal Dominance in Lakes. In: *Lake Restoration, Protection and Management, Proceedings of Second Annual Conference, North American Lakes Management Society, October 26-29, 1982.* EPA 440/5-83-001, U.S. EPA, Washington, D.C., pp. 237-241.
- Smith, V.H., 1983b. Low Nitrogen to Phosphorus Ratios Favor Dominance by Blue-Green Algae in Lake Phytoplankton. *Science* 221: 669-671.
- Smith, V.H., 1982. The Nitrogen and Phosphorus Dependence of Algal Blooms in Lakes: An Empirical and Theoretical Analysis. *Limnol. Oceanogr.* 27: 1101-1112.

- Smith, V.H., and J. Shapiro, 1981. Chlorophyll Phosphorus Relations in Individual Lakes: Their Importance to Lake Restoration Strategies. *Envir. Sci. Technol.* 15: 444-451.
- Spencer, D.F., and R.W. Greene, 1981. Effects of Nickel on Seven Species of Freshwater Algae. *Env. Poll. (Series A)* 25: 241-247.
- Stauffer, R.E., and D.E. Armstrong, 1984. Lake Mixing and Its Relationship to Epilimnetic Phosphorus in Shagawa Lake, Minnesota. *Can. J. Fish. Aquat. Sci.* 41: 57-69.
- Stauffer, R.E., and G.F. Lee, 1977. The Role of Thermocline Migration in Regulating Algal Blooms. In: Middlebrooks, E.J. (Ed.), *Modeling the Eutrophication Process*, Ann Arbor Science, Ann Arbor, MI, pp. 73-82.
- Stefan, H.G., and M.H. Hanson, 1981. Predicting Dredging Depths to Minimize Internal Nutrient Recycling in Shallow Lakes. In: *Restoration of Lakes and Inland Waters: International Symposium on Inland Waters and Lake Restoration*, Sept. 8-12, 1980, Portland, ME. EPA 440/5-81-010, U.S. EPA, Office of Water Regulations and Standards, Washington, D.C., pp. 79-85.
- Stewart, W.D.P., 1973. Nitrogen Fixation. In: Carr, N.G. and B.A. Whitton (Eds.), *The Biology of Blue-Green Algae* University of California Press, Berkeley and Los Angeles, CA, pp. 261-278.
- Sze, P., 1980. Seasonal Succession of Phytoplankton in Onondaga Lake, New York (USA). *Phycologia* 19(1): 54-59.
- Sze, P., 1975. Possible Effect of Lower Phosphorus Concentrations on the Phytoplankton in Onondaga Lake, New York, U.S.A. *Phycologia* 14(4): 197-204.
- Tilman, D., 1981. Tests of Resource Competition Theory Using Four Species of Lake Michigan Algae. *Ecology* 62(3): 802-815.
- Tilman, D., 1977. Resource Competition Between Planktonic Algae:

An Experimental and Theoretical Approach. Ecology 58: 338-348.

Tilman, D., S.S. Kilham, and P. Kilham, 1982. Phytoplankton Community Ecology: The Role of Limiting Nutrients. Ann. Rev. Ecol. Syst. 13: 349-372.

Toetz, D., 1983. Factors Controlling Blue-Green Algae Dominance in a Southwestern Reservoir. Oklahoma Water Resources Research Institute, Stillwater, OK, 39 pp.

Toetz, D., 1982. Nutrient Control of Blue-Green Algae in a Southwestern Reservoir. PB82-24-336-1, Oklahoma Water Resources Research Institute, Stillwater, OK, 40 pp.

Uttormark, P.D., and M.L. Hutchins, 1980. Input/Output Models as Decision Aids for Lake Restoration. Water Resources Bulletin 16: 494-500.

U.S. Environmental Protection Agency, 1979. Lake Restoration: Proceedings of National Conference, August 22-24, 1978 Minneapolis, MN. Office of Water Planning and Standards, Washington, D.C.

U.S. Environmental Protection Agency, 1976. Process Design Manual for Phosphorus Control. EPA-625/1-76-001a, U.S. EPA, Office of, Washington, D.C.,

U.S. Environmental Protection Agency, 1975. Process Design Manual for Nitrogen Control. U.S. EPA, Washington, D.C.

U.S. Environmental Protection Agency, 1971. Algal Assay Procedure Bottle Test, National Eutrophication Survey, U.S. EPA, Washington, D.C., 82 pp.

Vigon, B.W., and D.E. Armstrong, 1977. The Role of Silica and the Vernal Diatom Bloom in Controlling the Growth of Nuisance Algal Populations in Lakes. Technical Report WIS-WRC-77-06, University of Wisconsin, Water Resources Center, Madison, WI, 116 pp.

Wall, D., and F. Briand, 1979. Response of Lake Phytoplankton

Communities to in Situ Manipulations of Light Intensity and Colour. *Journal of Plankton Research* 1: 103-112.

- Webster, K.E., and R.H. Peters, 1978. Some Size-Dependent Inhibitions of Larger Cladoceran Filterers in Filamentous Suspensions. *Limnol. Oceanogr.* 23(6): 1238-1245.
- Welch, E.B., 1979. Lake Restoration by Dilution. *Lake Restoration: Proceedings of a National Conference.* EPA-400/5-79-001, U.S. EPA, Washington, D.C., pp. 133-139.
- Wetzel, R.G., 1975. *Limnology.* W.B. Saunders Company, Philadelphia, PA, 743 pp.
- Williams, J.D.H., S.S. Syers, R.F. Shukla, and R.F. Harris, 1971. Levels of Inorganic and Total Phosphorus in Lake Sediments as Related to other Sediment Parameters. *Sci. and Tech.* 5: 1113-1120.
- Woolheiser, D.A., B.A. Stewart, W.H. Wischmeier, J.H. Caro, and M.H. Trere, 1975. Control of Water Pollution from Cropland, Volume II. EPA-600/2-75-026b, U.S. EPA, Athens, GA, 187 pp.
- Worth, D.D., 1981. Nutting Lake Restoration Project: A Case Study. In: *Restoration of Lakes and Inland Waters: International Symposium on Inland Waters and Lake Restoration, Sept. 8-12, 1980, Portland, ME.* EPA 440/5-81-010, U.S. EPA, Office of Water Regulations and Standards, Washington, D.C., pp. 89-92.
- Zimmerman, A.P., K.M. Noble, M.A. Gates, and J.E. Paloheimo, 1983. Physicochemical Typologies of South-Central Ontario Lakes. *Can. J. Fish. Aquat. Sci.* 40(10): 1788-1803.