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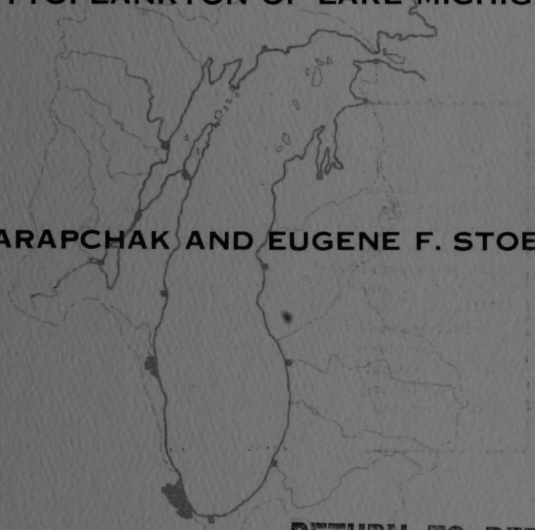

STEPHEN J. TARAPCHAK AND EUGENE F. STOERMER

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ENVIRONMENTAL STATUS OF THE LAKE MICHIGAN REGION

Volume 4. Phytoplankton of Lake Michigan

by

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December 1976

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CONTENTS

Page

PREFACE 15

ABSTRACT 17

INTRODUCTION 18

HISTORICAL SYNOPSIS 19

Investigations Prior to 1960 20
Investigations After 1960 21

FLORAL COMPOSITION AND COMMUNITY STRUCTURE 23

Species Composition of the Flora 23
Recent Numerical Changes in the Flora 25
Response of Species and Community Structure to Nutrient Enrichment . . . 26
Indicator Species 26
Species Diversity 38
Diatom Assemblages 39
Phytoplankton Assemblages 40
Spatial and Temporal Variations in the Standing Crop and Composition of Diatoms 46
Inshore-Offshore Differences and Related Phenomena 46
Ambient Concentrations of Silica and the Growth of Diatoms 63
Spatial and Temporal Variations in the Standing Crop and Composition of Phytoplankton 65
Early Studies in Southern Lake Michigan 66
Long-Term Studies at Chicago and Milwaukee 68
Inshore-Offshore Differences and Related Phenomena 72
Conclusions and Discussion 92
Species Composition of the Flora 92
Recent Numerical Changes in the Flora 94
Response of Species and Community Structure to Nutrient Enrichment, Indicator Species, and Species Diversity 94
Spatial and Temporal Variations in the Standing Crop and Composition of Diatoms and Phytoplankton 95

PRIMARY PRODUCTIVITY 98

Methodology of Measuring Phytoplankton Photosynthesis 98
Application of the Radiocarbon Technique and Experimental and Theoretical Procedures for Estimating Primary Productivity in Lake Michigan 99
Nutrient-Enrichment Experiments 101

CONTENTS

Page

Seasonal Variations in Primary Productivity at Fixed Stations 103
Grand Haven Area 103
Waukegan-Zion Area 104
Grand Traverse Bay 105
Regional Variations in Primary Productivity 106
North-to-South Transects 106
Northern versus Southern Basin and Green Bay 107
Grand Traverse Bay 109
Milwaukee-to-Ludington Transects 110
Conclusions and Discussion 113

PHOSPHORUS, SILICA, AND EUTROPHICATION 114

The Phosphorus, Silica, and Eutrophication Hypothesis 114
Changes in the Phytoplankton 115
Concentration of Silica in Surface Water 120
Seasonal Depletion of Silica in Surface Water 121
Nutrient-Enrichment Experiments 130
Correlation of Particulate Phosphorus with Primary Productivity . . . 139
Ratios of Silica to Phosphorus in Diatoms and the Loading Rates of Silica and Phosphorus 139
Conclusions and Discussion 143
Loading Rates of Phosphorus and Nitrogen and the Trophic State of Lake Michigan 148
Relative Trophic Status of Lake Michigan and Selected Great Lakes . . 153
Conclusions and Discussion 159

PHYTOPLANKTON ECOLOGY IN GREEN BAY 160

Trophic Conditions 160
Floral Composition and Community Structure 160
Nitrogen-Fixation Studies 161
Summer 1971 162
Summer 1972 164
Conclusions and Discussion 167

SAMPLING PROBLEMS AND QUANTITATIVE PHYTOPLANKTON METHODS 169

Sampling Problems 169
Quantitative Techniques 169
Concentration of Samples 170
Units of Measurement 171

GENERAL SUMMARY 172

Historical Synopsis of Phytoplankton Investigations 173
Floral Composition and Community Structure 173
Primary Productivity 175
Phosphorus, Silica, and Eutrophication 175

CONTENTS

Page

Phytoplankton Ecology in Green Bay 177
Sampling Problems and Quantitative Phytoplankton Methods 177

ACKNOWLEDGEMENTS 178

APPENDIX OF METRIC/ENGLISH EQUIVALENTS 179

CREDITS 180

REFERENCES CITED 187

FIGURES

No.		Page
1	Percentage abundance of *Cyclotella comta*	29
2	Percentage abundance of *Cyclotella kuetzingiana*	29
3	Percentage abundance of *Cyclotella ocellata*	30
4	Percentage abundance of *Cyclotella michiganiana*	30
5	Percentage abundance of *Melosira islandica*	31
6	Percentage abundance of *Tabellaria fenestrata*	31
7	Percentage abundance of *Asterionella formosa*	32
8	Percentage abundance of *Fragilaria crotonensis*	32
9	Percentage abundance of *Stephanodiscus hantzschii*	33
10	Percentage abundance of *Stephanodiscus minutus*	33
11	Percentage abundance of *Fragilaria capucina*	34
12	Percentage abundance of *Melosira granulata*	34
13	Percentage abundance of *Stephanodiscus tenuis*	35
14	Percentage abundance of *Diatoma tenue* v. *elongatum*	35
15	Percentage abundance of *Nitzschia dissipata*	36
16	Percentage abundance of *Stephanodiscus binderanus*	36
17	Percentage abundance of *Stephanodiscus subtilis*	37
18	Physical, Chemical, and Biological Parameters at Inshore and Offshore Stations near Grand Haven, Michigan	43
19	Shannon's Information--Theoretical Diversity and Evenness Indices of Lake Michigan Phytoplankton	45
20	Map of Grand Traverse Bay with Station Locations	46
21	Seasonal Abundance of Predominant Species of *Melosira* in Southern Green Bay and Lake Michigan	49

FIGURES

No.		Page
22	Seasonal Abundance of Total Diatoms in Southern Green Bay and Lake Michigan	51
23	Abundance of Diatoms (*Cyclotella, Stephanodiscus, Tabellaria,* and *Melosira*) at Sampling Stations in Lake Michigan and Green Bay	52
24	Abundance of Diatoms (*Cyclotella, Asterionella, Fragilaria,* and *Melosira*) at Sampling Stations in Lake Michigan and Green Bay	53
25	Abundance of Predominant Diatom Species at Five Stations along the Milwaukee-Ludington Transect	55
26	Doubling Times for Populations of *Fragilaria crotonensis, Melosira islandica,* and *Tabellaria flocculosa* at Four Locations in Lake Michigan	57
27	Temperature and Abundance of Dominant Phytoplankton in Lake Michigan near Zion, Illinois	59
28	Temperature and Abundance of Dominant Phytoplankton in Lake Michigan near Dead River, Zion, Illinois	60
29	Generalized Contours of Secchi-Disc Transparency and Surface Temperature near Grand Haven, Michigan	61
30	Generalized Contours of Additive Totals of Algal Cells near Grand Haven, Michigan	62
31	Generalized Contours of Relative Abundance of *Melosira granulata* near Grand Haven, Michigan	62
32	Generalized Contours of Relative Abundance of *Melosira binderana* near Grand Haven, Michigan	63
33	Generalized Contours of Relative Abundance of *Melosira islandica* near Grand Haven, Michigan	64
34	Generalized Contours of Relative Abundance of *Asterionella formosa* near Grand Haven, Michigan	64
35	Seasonal Distribution of Phytoplankton in Lake Michigan at Evanston, Illinois	66
36	Comparison of Phytoplankton Abundance in 1937-1938 with Phytoplankton Abundance in 1938-1939, at Evanston, Illinois	67
37	Graphs Showing Phylum Yields for Each Collection	69

FIGURES

No.		Page
38	Seasonal Periodicity of Total Plankton at Four Mile Crib, Chicago, Illinois	70
39	Seasonal Periodicity of Total Plankton at Milwaukee, Wisconsin	71
40	Regression of Annual Average Total Plankton Abundance against Year of Collection in Lake Michigan at Chicago, Illinois	71
41	Map of Study Area Showing Sampling Stations	72
42	Relative Abundance and Percentage Composition of Total Phytoplankton Populations at Stations 1-4 on 7 August 1962, and Stations 1-3 on 22 August 1962	74
43	Relative Abundance and Percentage Composition of Total Phytoplankton Populations at Stations 1-4 on 26 September and 24 October 1962	75
44	Relative Abundance and Percentage Composition of Total Phytoplankton Populations at Stations 1-5 on 21 April 1963	76
45	Relative Abundance and Percentage Composition of Total Phytoplankton Populations at Stations 1-5 on 22 May 1963	77
46	Relative Abundance and Percentage Composition of Total Phytoplankton Populations at Stations 1-4 on 8 June 1963	78
47	Major Lake Michigan Phytoplankton Groups near the Zion Nuclear Power Plant, Zion, Illinois	82
48	Temperature and Abundance of Offshore Phytoplankton near Zion, Illinois	83
49	Major Phytoplankton Groups and Corresponding Water Temperatures near Zion, Illinois	84
50	Major Phytoplankton Groups and Corresponding Water Temperatures near Kenosha, Wisconsin	85
51	Productivity in Lake Michigan Surface Water, Trip 1	88
52	Productivity in Lake Michigan Surface Water, Trip 3	88
53	Rates of Carbon Fixation Determined by ^{14}C Method at Inshore and Offshore Stations	104
54	Computed Daily Integral Primary Productivity at Five Stations in Lake Michigan	111

FIGURES

No.		Page
55	Phytoplankton Abundance and Percentage Composition of Blue-Green Algae in Lake Michigan Surface Water during Early April 1971	116
56	Phytoplankton Abundance and Percentage Composition of Blue-Green Algae in Lake Michigan Surface Water during Mid-May 1971	117
57	Phytoplankton Abundance and Percentage Composition of Blue-Green Algae in Lake Michigan Surface Water during Late June 1971	117
58	Phytoplankton Abundance and Percentage Composition of Blue-Green Algae in Lake Michigan Surface Water during Mid-July 1971	118
59	Phytoplankton Abundance and Percentage Composition of Blue-Green Algae in Lake Michigan Surface Water during Late August 1971	118
60	Phytoplankton Abundance and Percentage Composition of Blue-Green Algae in Lake Michigan Surface Water during Mid-September 1971	119
61	Phytoplankton Abundance and Percentage Composition of Blue-Green Algae in Lake Michigan Surface Water during Early October 1971	119
62	Phytoplankton Abundance and Percentage Composition of Blue-Green Algae in Lake Michigan Surface Water during Late October 1971	120
63	Concentrations of Silica in Water Samples Collected from Municipal Water Intakes at Chicago, Illinois; Milwaukee, Wisconsin; and Grand Rapids, Michigan	121
64	Concentrations of Silica in Lake Michigan Surface Water, 9 August 1955	122
65	Concentrations of Silica in Lake Michigan Surface Water, 10 August 1955	122
66	Subsurface Concentrations of Dissolved Silica along Seven Transects in Lake Michigan	124
67	Subsurface Concentrations of Dissolved Silica along Eight Transects in Lake Michigan	125
68	Concentrations of Chlorophyll *a* and Soluble Silica in Lake Michigan Surface Water during Early April 1971	126

FIGURES

No.		Page
69	Concentrations of Chlorophyll *a* and Soluble Silica in Lake Michigan Surface Water during Mid-May 1971	126
70	Concentrations of Chlorophyll *a* and Soluble Silica in Lake Michigan Surface Water during Late June 1971	127
71	Concentrations of Chlorophyll *a* and Soluble Silica in Lake Michigan Surface Water during Mid-July 1971	127
72	Concentrations of Chlorophyll *a* and Soluble Silica in Lake Michigan Surface Water during Late August 1971	128
73	Concentrations of Chlorophyll *a* and Soluble Silica in Lake Michigan Surface Water during Mid-September 1971	128
74	Concentrations of Chlorophyll *a* and Soluble Silica in Lake Michigan Surface Water during Early October 1971	129
75	Concentrations of Chlorophyll *a* and Soluble Silica in Lake Michigan Surface Water during Late October 1971	129
76	General Patterns of Temperature and Dissolved Silica Concentrations at Various Depths along Three Transects in Southern Lake Michigan	131
77	Results of Nutrient-Enrichment Experiments at an Offshore Station	133
78	Results of Nutrient-Enrichment Experiments at an Inshore Station	136
79	Plot of Productivity versus Concentration of Particulate Phosphorus	140
80	Map of Lake Michigan Drainage Basin Showing Major Tributaries	141
81	Relationship between Annual Primary Production and Annual Phosphorus Loading	156
82	Chlorophyll *a*, Primary Productivity, Total Phosphorus, and Secchi-Disc Transparency in the Great Lakes	157
83	Silica and Nitrate-Nitrogen in the Upper Great Lakes	159
84	Location of Fifteen Sites Visited Weekly	162
85	Variations in the Algal Population as Indicated by Total Nitrogen at Several Sites	163

FIGURES

No.		Page
86	Comparison of Acetylene Reduction with Concentrations of Algal Nitrogen, Phosphate, Ammonia, Nitrite, and Nitrate in Green Bay	164
87	Variation with Time and Position in the Algal Population as Indicated by Total Algal Nitrogen	165
88	Variation in Dissolved Oxygen, Air and Water Temperature, Acetylene Reduction, Total Algal Nitrogen, Phosphate, Ammonia, and Nitrate	166
89	Comparison of Acetylene Reduction in 1971 and 1972	167

TABLES

No.		Page
1	A Summary of Differences between 1936 and 1967 in the Total Numbers of Euplanktonic and Tychoplanktonic Algal Species in Lake Michigan	26
2	Apparent Trophic Preferences and Abundance of Selected Diatoms in Lake Michigan	38
3	Cell Counts and Percent Abundance of Selected Species at Station 1, June 1969	40
4	Cell Counts and Percent Abundance of Selected Species at Stations 1 and 2, July 1969	41
5	Cell Counts and Percent Abundance of Selected Species at Stations 1 and 2, August and September 1969	42
6	Cell Counts and Percent Abundance of Selected Species at Station 1, September 1969	42
7	Number of Species, Number of Individuals, and Diversity of Phytoplankton near the Donald C. Cook Power Plant	44
8	Abundance of Dominant Species in Samples from 5 m, Grand Traverse Bay, Lake Michigan	47
9	Productivity-Related Parameters Measured at 12 Stations in Grand Traverse Bay, Lake Michigan	48
10	Average Concentrations of Phosphorus, Nitrate-Nitrogen, and Chlorophyll *a* Compared with Cell Volume and Total Biomass of Predominant Species of *Melosira* at Times of Peak Abundance	50
11	Average Values for Various Parameters from Milwaukee to Ludington	54
12	Approximate Generation Times and Seasons of Exponential Growth for Some Principal Species of Diatoms in Lake Michigan and Green Bay	56
13	Lake Michigan Plankton	89
14	Relative Frequency of Pollution-Tolerant Taxa in Samples Collected at 5-m Depth from Grand Traverse Bay, Lake Michigan	92

TABLES

No.		Page
15	A Summary of Diatom and Total Phytoplankton Abundance Measurements for Lake Michigan	96
16	A Summary of Primary Productivity Measurements Made in Lake Michigan	100
17	Carbon Fixation and Other Selected Parameters at Northern Lake Michigan Stations	108
18	Carbon Fixation and Other Selected Parameters at Southern Lake Michigan Stations	109
19	Average and Estimated Annual Primary Production Rates at Five Stations in Lake Michigan	112
20	Means and Ranges of Primary Production Rates at Five Stations in Lake Michigan	112
21	Concentrations of Total Phosphate, Nitrate-Nitrogen, and Silica in Southern Lake Michigan	123
22	Summary of Physical, Chemical, and Biological Conditions at Inshore and Offshore Stations at the Beginning of Nutrient-Enrichment Experiments	132
23	Responses of Experimental Systems to Nutrient Additions	134
24	Summary of Relative Increases in Cell Counts at an Offshore Station in Lake Michigan in Response to Nutrient Treatments	134
25	Concentration of Particulate Phosphorus in Nutrient-Enrichment Experiments	137
26	Effects of Phosphorus and Nitrogen on ^{14}C-Carbon Fixation in Nutrient-Enrichment Experiments in Little Traverse Bay near Petoskey	138
27	Contributions of Total Soluble Phosphorus and Silica to Lake Michigan by 19 Tributaries	142
28	Critical Total Phosphate-Phosphorus Concentrations in Lakes of Dissimilar Trophic State	148
29	Permissible and Dangerous Loading Levels for Nitrogen and Phosphorus in Lakes	149
30	Estimated Long-Term Inputs and Outputs of Some Nutrients for Lake Michigan	149

TABLES

No.		Page
31	Total Phosphorus Loading to Lake Michigan from Tributaries	151
32	Sources and Computed Annual Loadings of Phosphorus in Lake Michigan	152
33	Loading Values of Phosphorus Assuming an 80 or 90% Reduction in Waste Water Entering Lake Michigan	152
34	Estimates of Phosphorus Loadings, Morphometric Characteristics, and Hydrologic Data for the Great Lakes	154
35	A Summary of Phosphorus Loadings into the Great Lakes, Relative to Vollenweider's Critical Limits for Permissible and Dangerous Supply Levels	155
36	Average and Standard Deviations of Chlorophyll *a*, Primary Productivity, Secchi-Disc Transparency, and Total Phosphorus in the Great Lakes	157
37	Average Concentrations and Standard Deviations of Soluble Silica and Nitrate-Nitrogen in the Great Lakes	158

PREFACE

Assessments of the environmental impacts of individual nuclear power plants sited on the shores of Lake Michigan have led to increased recognition of the need for regional considerations of the environmental impacts of various human activities, and a compendium of information on the environmental status of the region for use in assessing such impacts. In response to these needs, a report series describing the status of Lake Michigan and its watershed is in preparation. This series is entitled "Environmental Status of the Lake Michigan Region"; this report is part of that series.

The report series provides a reasonably comprehensive descriptive review and analysis of natural features and characteristics, as well as past, present, and proposed natural processes and human activities that influence the environmental conditions of Lake Michigan, its watershed, and certain adjacent metropolitan areas. This series will constitute a regional reference document useful both to scientific investigators and to other persons involved in environmental protection, resource planning, and management. In these regards, the "Environmental Status of the Lake Michigan Region" will serve in part as an adjunct to reports of broader scope, such as the Great Lakes Basin Commission's Framework Study.

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ENVIRONMENTAL STATUS OF THE LAKE MICHIGAN REGION

VOL. 4. PHYTOPLANKTON OF LAKE MICHIGAN

by

Stephen J. Tarapchak and Eugene F. Stoermer

Abstract

For nearly 100 years, studies on the phytoplankton of Lake Michigan have provided a wealth of information on the flora, its quantitative composition, and the effects of cultural eutrophication on algal abundance and species composition.

The flora, consisting of over 2000 known taxa, contains species characteristic of oligotrophic and eutrophic environments. Phytoplankton abundance and primary productivity vary seasonally and generally are higher and more variable inshore than offshore. Seasonal phytoplankton development is bimodal in the southern and nearshore water of the central basin but exhibits a unimodal pattern (a peak in summer) offshore in the central basin. These dissimilarities are attributed to differential effects of critical water temperatures, higher nutrient concentrations in the southern basin, and differences in critical mixing depths.

The phytoplankton of the Lake historically has been dominated by diatoms. Recently there has been a significant increase in algal abundance inshore near Milwaukee and Chicago and a shift to a significant fraction of green and blue-green algae in the offshore community in the southern basin. This observation is one line of evidence suggesting that the Lake is undergoing serious cultural eutrophication due to increases in phosphorus loading rates.

The trophic state of Lake Michigan, in general, is intermediate between Lake Superior and the western basin of Lake Erie. The present-day loading rate of phosphorus into the Lake is tolerable, according to Vollenweider's (1971) nutrient loading model; however, on a limited scale, southern Green Bay and certain inshore regions in the southern and central basin are receiving unacceptable loadings.

INTRODUCTION

The first studies on the phytoplankton of Lake Michigan were undertaken over 100 years ago. Most of the information pertinent to an assessment of the quality of the Lake's waters, however, has been generated during the last decade. Presently, there is growing concern among those charged with setting and enforcing management practices that the deep-water, offshore environment of the Lake has been affected by increased rates of nutrient supply to inshore water.* Evidence for the enrichment of inshore water and for the spread of nutrients into the open water is partially demonstrable through an examination of data on water chemistry (especially phosphorus, silica, and nitrogen) and by an evaluation of the species composition and standing crop of phytoplankton.

If conditions similar to those of polluted inshore waters were to develop offshore, drastic qualitative and quantitative alterations of the biota would certainly occur over vast areas of the Lake. The cultural eutrophication of western and central Lake Erie, southern Green Bay, and Saginaw Bay are notable examples. Not only would such changes in Lake Michigan be aesthetically undesirable and detract from the recreational value of the Lake, but municipal and industrial costs for water treatment would increase, and the fisheries industry would be adversely affected.

Symptoms of advanced eutrophication have not yet been detected in the offshore environment of Lake Michigan, but they are apparent inshore in the southern basin, in the lower half of Green Bay, and near the mouths of polluted tributaries. These conditions can be attributed directly to high loading rates of nutrients, especially phosphorus and nitrogen, or to toxic pollutants. In such situations, the standing crop and primary productivity of the phytoplankton are either high or severely reduced (depending upon addition of nutrients or toxic compounds), water transparency is low, and there is marked depletion of oxygen in bottom waters. Phytoplankton in nutrient-enriched situations generally is dominated by blue-green and green algae and by diatoms normally recognized as pollution-tolerant or eutrophic forms. Although gross effects of cultural eutrophication are not evident in offshore waters, changes in phytoplankton species composition and seasonal succession patterns indicate incipient damage to the entire system.

The phytoplankton of the Lake Michigan ecosystem occupies a unique position in the metabolism of the Lake. Algal populations are extremely sensitive to environmental perturbations and can signal that the system has been disturbed. Indications of disturbances can be reflected through changes in the flora or through variations in phytoplankton standing crop and composition. Since the doubling time of some phytoplankton populations is on the order of hours or days (Fogg, 1965), response to environmental disturbances can be rapid.

Phytoplankton represents the interface between the physicochemical environment and biological communities of higher trophic levels (*cf.* Saunders,

---

**The reader should note that in this volume the terms inshore, nearshore, and offshore largely reflect their usage in the original reports. In other volumes of this series [Mortimer (1975) and Torrey (1976)], the use of the terms coastal, inshore, and nearshore imply distances from shore <16 km; the terms open water and offshore imply distances from shore >16 km.*

1963). As the primary producer of organic matter in most aquatic systems, the characteristics of phytoplankton assemblages can determine the size and composition of consumer levels. Changes in the composition of the phytoplankton induced by cultural eutrophication, for example, can result in shifts in the composition of consumers, *e.g.* zooplankton, that graze algal populations (*cf.* Saunders, 1969; Brooks, 1969).

Information on the phytoplankton of Lake Michigan is widely scattered and appears in a variety of scientific journals and in numerous state, federal and private reports. To provide some degree of uniformity to presentation of data, this report has been divided arbitrarily into seven major sections. Each section provides a coherent body of information that relates to a specific facet of research. The sections, however, are not mutually exclusive; rather, they are designed to be complementary. Data or the conclusions drawn in one series of studies are included or referenced in other sections. The content of the sections is as follows. The first section, Historical Synopsis, summarizes the nature of phytoplankton studies within a historical framework. The second section, Floral Composition and Community Structure, includes a diverse body of information on the flora, indicator species, and species diversity, and the standing crop and composition of diatom and phytoplankton assemblages. The third section, Primary Productivity, presents data on regional and seasonal variations in primary productivity, and includes information on the design, use, and interpretation of nutrient-enrichment experiments. The fourth section--Phosphorus, Silica, and Eutrophication--is a detailed treatment of a hypothesis advanced recently to explain the relationships between phosphorus, silica, phytoplankton, and the mechanisms responsible for recently observed shifts in species composition. This section also includes a general discussion on eutrophication and the trophic status of Lake Michigan. The fifth section, Phytoplankton Ecology in Green Bay, contains the results of recent studies on the significance of atmospheric nitrogen fixation by planktonic populations. The sixth section, Sampling Problems and Quantitative Phytoplankton Methods, is devoted to a general discussion and evaluation of sampling problems, methodology, and quantitative phytoplankton techniques. The last section, General Summary, is a synopsis of the previous sections.

There are no previous extensive reviews of phytoplankton in Lake Michigan. Davis (1966) discussed the nature and scope of phytoplankton studies in Lake Michigan as part of a larger, general review of plankton investigations in the Great Lakes. Recently, Vollenweider *et al.* (1974) summarized and compared selected data on phytoplankton and primary productivity in the Great Lakes.

This report should be viewed as a status assessment of information on phytoplankton in Lake Michigan. It is not only a guide to literature on phytoplankton research in Lake Michigan, but should serve as a synopsis of significant information. An effort has been made to compare or contrast the results of studies in Lake Michigan with investigations conducted in other Great Lakes or in smaller north-temperate lakes. Many investigations of Lake Michigan phytoplankton are in progress, and additional information is expected in the immediate future.

HISTORICAL SYNOPSIS

Studies of the phytoplankton of Lake Michigan, especially prior to 1960, have described the flora, its composition, and algal abundance in specific

localities within the Lake. With few exceptions these investigations were confined to inshore environments; only since 1960 have investigations included observations of phytoplankton in deep-water, offshore regions of the Lake. With the development in the late 1950's of the radiocarbon technique for measuring primary productivity, investigations in Lake Michigan were no longer limited to purely descriptive aspects of phytoplankton taxonomy and ecology. This technique not only permits measurement of primary productivity, but is also an important tool in studies of nutrient limitation and other aspects of phytoplankton physiology.

Most information on phytoplankton dealing with water quality and cultural eutrophication of the Lake have been generated since 1960. Several earlier studies of species occurrence and distribution, however, provide a basis for important comparison with characteristics of phytoplankton in the Lake today. A general account of the investigations follows. These reports are the source for most data included in this volume.

INVESTIGATIONS PRIOR TO 1960

The first reported collections of algae apparently were taken from Lake Michigan by Ehrenberg (1854-1856). The first published records on the flora of the Lake were by Briggs (1872) and Thomas and Chase (1887), all of whom were amateur diatomologists. Further reports on the flora, prior to the turn of the century, were made by Forbes (1882a, 1882b, 1882c, 1883), Kofoid (1896), Ward (1896), and Thompson (1896). Immediately after the turn of the century, Chase (1904) published a list of diatoms, some of which were collected in Lake Michigan, and Whipple (1907) and Leighton (1907) published taxonomic records of algae in the southern part of the Lake.

After 1925, studies of phytoplankton taxonomy and abundance occurred with greater frequency. Baylis and Gerstein (1929) published a report on water quality in southern Lake Michigan that included records on the algal flora. Eddy published two reports, the first in 1927 and the second in 1934. The initial paper included taxonomic records (119 species) from 56 net samples collected during 1887 and 1888 from the breakwater at Chicago, and from collections made in 1926 and 1927 at other locations in the southern basin. This report was the first detailed treatment of net phytoplankton, and the earliest report that included estimates of standing crop. Further studies on species occurrence, species distribution, and standing crop in southern Lake Michigan were reported by Eddy in 1934. Shortly after Eddy's studies, Ahlstrom (1936) published the results of a detailed species analysis of 115 samples collected during 1930 and 1931 from inshore and offshore localities over most of the Lake. This report was followed by Skvortzow's (1937) study on diatoms in the vicinity of Chicago, and by Lackey's (1944) observations of diatoms and other algae from samples near Chicago. These investigations, published after 1925, represented all of the information on the flora of the Lake. Although they contained records of species occurrence, taxonomic notes, and estimates of phytoplankton abundance, all of the studies except Ahlstrom's were confined to inshore sites. None of these investigations provided information on annual cycles or on seasonal succession of algal populations.

Quantitative studies on yearly cycles of phytoplankton in the Lake were initiated at Northwestern University. Daily (1938), Damann (1941), and Griffith (1955) investigated annual phytoplankton cycles at a single inshore station at Evanston, Illinois. Long-term quantitative cycles of phytoplankton

have been monitored at the water filtration plants at Chicago and Milwaukee. Some of these data have been summarized and published by Damann (1945, 1960, 1966); however, much of these data are unpublished. Vaughn (1961, 1962) has reported on species causing serious clogging problems in the filtration system of these installations.

INVESTIGATIONS AFTER 1960

Since the late 1950's and early 1960's, studies of phytoplankton in Lake Michigan have become more numerous and sophisticated, and more diverse in scope and objective. Unlike earlier studies, recent investigations have coordinated taxonomy and quantification of phytoplankton with measurements of water chemistry, primary productivity,* and nutrient-enrichment experiments.

Detailed investigations of the flora were undertaken by Stoermer and Yang (1969, 1970), Stoermer (1967), Holland (1969), and Holland and Beeton (1972). The collective results of these investigations have greatly increased the number of species known to be in the Lake, especially the diatoms. These reports also provide details on occurrence and distribution of particular species. Stoermer and Yang (1969, 1971) and Patrick and Reimer (1966) also carried out specialized studies on diatom systematics.

Investigations evaluating species occurrence, regional distribution, and species abundance as indicators of water quality and trophic conditions were conducted by Holland (1968, 1969), Holland and Beeton (1972), and Stoermer and Yang (1969, 1970). A comparative study of the contemporary flora and that present in the Lake in the early 1930's has been made by Stoermer (1967).

A number of studies have been designed specifically to assess water quality in various regions of the Lake, and have included a species analysis of the flora and description of its quantitative composition (Copeland and Ayers, 1972; Cook and Risley, 1963--unpublished; Ayers, 1970; and U. S. Dep. Inter., 1968a). Data gathered by the National Water Quality Network has been published partially by Williams (1962, 1964, 1972) and Williams and Scott (1962). Recent investigations on phytoplankton at power plants are part of the limnological survey being conducted in the vicinity of the Donald C. Cook power plant at Benton Harbor in southern Lake Michigan (*cf.* Ayers and Seibel, 1973). Similar monitoring studies are being undertaken by the Nalco Chemical Company Environmental Sciences Group (formerly Industrial Bio-Test Laboratories) at the Zion power plant in the southern region of the Lake (*cf.* Huh *et al.*, 1972) and at a number of other sites (Limnetics, 1974; Beeton and Barker, 1974).

Studies by Ayers and Seibel (1973) and Huh *et al.* (1972) contain information on inshore phytoplankton distribution, abundance, and seasonal variability. Holland (1969), Holland and Beeton (1972), Stoermer and Kopczynska (1967), Stoermer *et al.* (1971), Schelske *et al.* (1971), and Stoermer (1974) also have published detailed data on seasonal variability of phytoplankton assemblages.

**The terms primary productivity, primary production, photosynthetic carbon fixation, and photosynthesis frequently are used interchangeably. Primary productivity denotes the rate at which organic matter is produced by phytoplankton (see Saunders, 1963). The term primary production implies a rate process, also, and is used to denote a summation of individual productivity measurements with respect to time, such as an estimate of annual primary productivity.*

Most studies also provide detailed information on differences between inshore and offshore phytoplankton communities. An investigation of thermal bar effects on phytoplankton development and species distribution has been carried out by Stoermer (1968), and studies on phytoplankton abundance in Grand Traverse Bay and Little Traverse Bay have been undertaken by Stoermer *et al.* (1972) and Schelske *et al.* (1973--unpublished), respectively. Data on the variability of phytoplankton along north-to-south transects are given by Parkos *et al.* (1969).

Investigations on the rate of primary production in Lake Michigan have been undertaken only since the late 1950's. Studies on ^{14}C techniques and the comparability of measurements based on *in situ* and *in vitro* estimates of photosynthesis were carried out by Saunders *et al.* (1962). More recently, Fee (1969, 1973a, 1973b) developed a numerical model for measuring integral primary productivity, and provided the first estimates of annual primary production beneath a unit of surface water in the Lake. Verduin (1972) investigated differences in simultaneous measurements of primary productivity using the ^{14}C method and the pH-alkalinity technique. Variations in primary productivity in surface water along north-to-south transects were described by Parkos *et al.* (1969), and Schleske and Callender (1970) have compared primary productivity in the northern and southern regions of the Lake. Schelske and Roth (1973) estimated primary productivity in northern Lake Michigan, and photosynthesis in Grand Traverse Bay was studied by Stoermer *et al.* (1972) and Saunders *et al.* (1962). The effects of upwelling on primary productivity near Grand Haven, Michigan, have been studied by Schelske *et al.* (1971). A number of authors have compared rates of primary production in Lake Michigan with other north-temperate lakes (including Lakes Superior, Huron, Erie, and Ontario): Parkos *et al.* (1969), Schelske and Callender (1970), Schelske and Roth (1973), Saunders *et al.* (1962), Saunders (1964), and Verduin (1972).

Investigations to assess nutrient limitation and the physiology of phytoplankton were carried out by Schelske and Stoermer (1971, 1972) and Schelske *et al.* (1974). The results of nutrient-enrichment experiments at inshore and offshore stations were described by Stoermer *et al.* (1971). A hypothesis to explain recent culturally induced changes in the phytoplankton of Lake Michigan has been proposed by Schelske and Stoermer (1971, 1972). Data generated by nutrient-enrichment experiments form one major line of evidence supporting their contentions that the Lake is undergoing accelerated eutrophication.

Several papers discuss cultural eutrophication of Lake Michigan and the other Great Lakes. Each paper considers changes in nutrient inputs, nutrient concentrations, and characteristics of the biota as indications that the Lake has been disturbed (Beeton 1965, 1966, 1969; Beeton and Edmondson, 1972; Schelske 1974, 1975; Lee, 1974). Bibliographies including citations of phytoplankton studies have been compiled by Gannon (1969), Environmental Protection Agency (1973), and Van Oosten (1957). The first treats the plankton of the Great Lakes, and the second includes studies on the effects of power-plant cooling water on the biota. There are only two publications summarizing information on comparative aspects of phytoplankton in the Great Lakes. A review by Davis (1966) is based primarily on studies prior to 1960. A recent paper by Vollenweider *et al.* (1974) is especially valuable because it includes estimates of phosphorus loadings, primary productivity, and phytoplankton standing crop in the Great Lakes and provides comparative information on the trophic state of the lakes.

FLORAL COMPOSITION AND COMMUNITY STRUCTURE

Information on species composition of the flora and seasonal variations in the size of phytoplankton communities in Lake Michigan is widely scattered in the literature. The design and scope of most studies are dissimilar; many investigations focus primarily on diatoms, and others consider characteristics of total phytoplankton assemblages. To provide some degree of uniformity in the presentation of data, this section is divided arbitrarily into five major parts: (*i*) the species composition of the flora, (*ii*) recent numerical changes in phytoplankton and indicator species, (*iii*) community structure of diatom and total phytoplankton assemblages related to nutrient enrichment (data for the third subsection have been extracted in part from the previous two subsections), (*iv*) investigations yielding information specifically on seasonal fluctuations in standing crop and composition of diatom communities, and (*v*) a diverse body of information on spatial and temporal variations in total phytoplankton composition and standing crop. Some aspects of phytoplankton studies in Green Bay are discussed in the latter part. Additional information on phytoplankton in Green Bay is discussed in the section on Phytoplankton Ecology in Green Bay.

SPECIES COMPOSITION OF THE FLORA

Investigations prior to 1960 resulted in a known flora of approximately 600 taxa, about one-half of which were diatoms. Since the early 1960's, studies on the phytoplankton have increased and broadened to detect ecological, geographical, and seasonal differences within the Lake.

Since 1900, over 2000 species, varieties, and forms of algae have been recorded from the open water of the Lake. The flora is represented by the five major divisions normally found in north-temperate lakes. Approximately 1300 Bacillariophyceae* (diatoms) have been identified, and the remaining 700-800 taxa are members of the Chlorophyta (green algae), Cyanophyta (blue-green algae), Chrysophyceae* (golden-brown algae), Euglenophyta (euglenoids), and Pyrrophyta (dinoflagellates and cryptomonads).

A complete inventory of species in the planktonic environment of the Lake is beyond the scope of this volume. Three taxonomic listings are representative of the types of analyses yielding information on the flora of the Lake. An inventory compiled by Stoermer (1968) is based upon 150 samples collected with a phytoplankton net throughout the Lake. The listing is of particular interest because it includes detailed comparisons with an investigation conducted in the early 1930's by Ahlstrom (1936). The results of both studies are contrasted in the next subsection, Recent Numerical Changes in the Flora (p. 25).

A second taxonomic inventory by Huh *et al.* (1972) is based on monthly sampling during April 1971-March 1972 at locations near the Zion power plant in southwestern Lake Michigan. The species identifications were based on samples sedimented with detergent (Mackenthun, 1969) and counted by Lackey's technique (*cf.* Vollenweider, 1968). The results of this study and two related

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**The Bacillariophyceae and Chrysophyceae are two of three major Classes of the Chrysophyta (Prescott, 1962).*

studies are presented in a subsequent subsection, Southern Lake Michigan (p. 72).

A third inventory is that of Ayers *et al.* (1972b). This listing was compiled from seasonal studies of phytoplankton near the Donald C. Cook power plant in southeastern Lake Michigan. Samples were enumerated by using the inverted microscope in conjunction with natural settling in Utermöhl chambers or the settle-freeze method of Sanford *et al.* (1969).

The above listings do not include all reports containing significant information on the flora. Additional reports of species occurrence near Waukegan are given in Delinck and Lamble (1971), Piala and Lamble (1971), and Gulo and Lamble (1971); species occurrence near Benton Harbor is reported in Ayers *et al.* (1971, 1972a, 1972b), Ayers and Seibel (1973), and Seibel and Ayers (1974). In addition, a report by Stoermer and Kopczynska (1967) includes quantitative records of diatoms and other algae in the southern basin. More information on species distribution and abundance is included in Holland (1968, 1969) and Holland and Beeton (1972). Stoermer and Yang (1969, 1970) document regional distribution patterns and abundance of several hundred diatom species.

All of the available records indicate that diatoms (Bacillariophyceae),* as opposed to other groups of algae, constitute nearly 60% of the flora. The Centrales include the genera *Melosira, Coscinodiscus, Cyclotella, Stephanodiscus, Rhizosolenia,* and *Thalassiosira*; the Araphidineae (suborder of Pennales) are represented by species of the genera *Fragilaria, Tabellaria, Diatoma, Asterionella,* and *Synedra*. Many species in these groupings are euplanktonic and occur repeatedly in open water.

The suborders Monoraphidineae and Biraphidineae (with the exception of several species of *Nitzschia* and *Surirella*) generally are recognized as littoral or benthic forms living in epipelic and epilithic habitats or growing as epiphytes on littoral vegetation. Species of the Monoraphidineae such as *Achnanthes, Eunotia,* and *Cocconeis*, however, are widely distributed but in very low abundance in open water. Species of the Biraphidineae, likewise, are frequently detected both inshore and offshore. Among the 30 genera found in Lake Michigan, the following are most common: *Anomoeoneis, Navicula, Cymbella, Stauroneis, Mastogloia, Amphipleura, Frustula, Diploneis, Amphora, Gomphonema, Nitzshia, Cymatopleura, Surirella, Gomphoneis, Pinnularia, Campylodiscus, Caloneis, Amphiprora, Epithemia, Denticulata, Neidium, Rhopalodia, Hantzschia, Gyrosigma,* and *Pleurosigma*.

There are two explanations for the occurrence of littoral and benthic forms in open water. Such species can occur as chance plankters; these forms become detached from solid substrates and are carried passively by currents into the open water. These algae may not survive for appreciable periods of time because of lower nutrient levels. A second explanation was advanced

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**The Bacillariophyceae (diatoms) are divided into two Orders: the Centrales (radially symmetrical cells) and the Pennales (elongate, bilaterally symmetrical cells). The three major suborders of Pennales are divided on the basis of the raphe: Araphidineae (lacking a raphe), Monoraphidineae (cells with one raphe), and Biraphidineae (cells with two raphes).*

recently by Stoermer (1967). He contends that nutrient enrichment of the offshore environment in the southern basin has reached levels sufficient to allow such algal forms to colonize the planktonic environment. This contention is discussed below in Recent Numerical Changes in the Flora (p. 25) and Indicator Species (p. 26).

The flora, exclusive of diatoms, consists largely of a diverse assemblage of green algae in the Order Chlorococcales. This group includes the genera *Golenkinia, Pediastrum, Coelastrum, Botryococcus, Westella, Dictyosphaerium, Planktosphaeria, Oocystis, Nephrocytium, Lagerheimia, Ankistrodesmus, Closteriopsis, Selanastrum, Kirchnierella, Quadrigula, Tetraëdron, Scenedesmus, Crucigenia, Actinastrum, Micractinium, Tetradesmus,* and *Tetrastrum*. At least one species in each of these genera has been reported from the plankton. The only other Order of green algae that occurs regularly in the plankton is the Volvocales, which includes species of the genera *Chlamydomonas, Gonium, Eudorina,* and *Volvox*. In addition, *Planctonema lauterbornii*, a filamentous green alga in the Order Ulotrichales, occurs as a spring dominant in the Lake. Although desmids often are a significant component of the flora in freshwater lakes (*cf.* review by Hutchinson, 1967), they appear to be poorly represented in the plankton of Lake Michigan. Only a few species of the genera *Staurastrum, Closterium, Cosmarium, Xanthidium,* and *Staurodesmus* (= *Arthodesmus*) have been recorded.

The Chrysophyceae, Euglenophyta, and Pyrrophyta collectively total less than 200 taxa. The Chrysophyceae (golden-brown algae) are represented principally by species of the genera *Mallomonas, Dinobryon, Synura,* and *Chrysosphaeria*. Although species of these genera can become abundant in the Lake, less than 40 taxa have been recorded. Euglenophyta are represented by two pigmented genera, *Euglena* and *Trachelomonas*, which have been rarely observed in the Lake. Species of Dinophyceae* (dinoflagellates) are members of several genera, including *Ceratium, Gymnodinium, Glenodinium,* and *Peridinium*. Cryptophyceae (cryptomonads) consist primarily of species in the genera *Chroomonas, Cryptomonas,* and *Rhodomonas* and have been reported infrequently. The number of dinoflagellate and cryptomonad species identified in the Lake is less than 30. Cyanophyta (blue-green algae) are found frequently, especially in southern Lake Michigan; they are members of two Orders, the Chroococcales and Oscillatoriales (*cf.* Prescott, 1962). Species in the Chroococcales are members of the genera *Chroococcus, Aphanocapsa, Microcystis, Merismopedia, Rhabdoderma, Dactylococcopsis, Aphanothece, Coelosphaerium,* and *Gomphosphaeria*. The principal species in the Oscillatoriales are members of the genera *Oscillatoria, Anabaena,* and *Lyngbya*. The literature indicates that about 75 species of blue-green algae occur in the Lake.

RECENT NUMERICAL CHANGES IN THE FLORA

One of the questions posed in the early 1960's was: To what extent has cultural eutrophication affected the species composition of the flora? An investigation was undertaken at the Great Lakes Research Division, University of Michigan, to address this question. Two approaches were taken in these studies. First, a detailed analysis of present-day flora was carried out

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**The Pyrrophyta consist of two principal Classes, the Dinophyceae and Cryptophyceae (Prescott, 1962).*

(Stoermer, 1967) and was contrasted with the results of a previous investigation (Ahlstrom, 1936). Second, present-day diatoms in the Lake were compared with collections of plankton made since the early 1900's (Stoermer and Yang, 1969, 1970). The results of the first study are discussed here; results of the second study are presented below in the subsection on Indicator Species (p. 26).

The investigation by Stoermer (1967), based on an analysis of 158 samples, was designed to be compared with the results of the survey by Ahlstrom (1936). Ahlstrom's investigation, the only previous study that included offshore regions of the Lake, was based on an examination of 115 samples collected by net tow in 1930-1931. Although the studies differed in sample number and seasonal representation, Stoermer was able to perceive certain other dissimilarities. Three major points are apparent from the data (Table 1): (*i*) there has been an increase in the total number of taxa occurring in offshore water, (*ii*) there has been an increase in the number of euplanktonic (adapted to open water) and tychoplanktonic (adapted to the littoral zone) forms found in the plankton, and (*iii*) euplanktonic species not recorded by Ahlstrom but observed today are regarded as taxa adapted to eutrophic water.

Table 1. A Summary of Differences between 1936 and 1967 in the Total Numbers of Euplanktonic and Tychoplanktonic Algal Species in Lake Michigan*

	1936		*1967*		*Increase in Algal Species from 1936 to 1967*			
Algal Species	*Number*	*% of Total*	*Number*	*% of Total*	*Number*	*%*	*% of Total*	*% Eutrophic Species*
Total	160	100	247	100	87	65	100	? (insufficient evidence)
Euplanktonic	96	60	131	53	35	73	40	71
Tychoplanktonic	64	40	116	47	52	55	60	? (insufficient evidence)

**Data from Stoermer (1967).*

References: 1936, Ahlstrom (1936); 1967, Stoermer (1967).

Stoermer concluded that changes in flora have occurred in the last 30 years and that these alterations are indicative of accelerated eutrophication, particularly in the southern basin. He attributed the increase in numbers of euplanktonic species to the introduction of *new* species and to increases in the number of tychoplanktonic taxa in open water. The latter situation is brought about by the presence of larger and more diverse periphyton communities that *seed* the offshore environment. The survival of tychoplanktonic forms for appreciable periods of time in offshore water also suggests chemical alteration of these environments by the spread of nutrients from inshore to offshore regions.

RESPONSE OF SPECIES AND COMMUNITY STRUCTURE TO NUTRIENT ENRICHMENT

Indicator Species

The investigations of indicator species in Lake Michigan are primarily on diatoms. As in other freshwater studies, investigators have made the assumption that different taxa are either adapted to or tolerate water of dissimilar nutrient content. The two principal studies of indicator species in Lake Michigan were designed specifically to detect diatoms that show *preferences* for different trophic conditions. Several limnological investigations also

have added information on species preference. In this section, results of studies by Stoermer and Yang (1969, 1970), Holland (1968, 1969), and Holland and Beeton (1972) are summarized, and diatoms with moderate to highly distinct trophic preferences are tabulated for future reference.

Stoermer and Yang (1969, 1970), in the most extensive study on indicator species in Lake Michigan, documented regional differences in occurrence, distribution, and abundance of planktonic diatoms. They also examined plankton samples collected in the late 1880's through the 1940's to determine the extent of recent changes in species distributional patterns. Their analysis of the present-day flora was based on collections during 1964-1967 from inshore and offshore environments, including the northern basin, Green Bay, and entrances to most major harbors. Stoermer and Yang identified approximately 700 species of diatoms. Earlier collections made near Chicago in 1876-1881, near Evanston and Chicago in 1937-1938, and near Chicago during 1945-1947 also were examined by Stoermer and Yang. In these analyses, detailed counts of about 50,000 individuals per sample were made for 320 collections. The results of an additional 600 collections, examined in less detail, were also included in the reports.

Based on these observations, six categories of diatoms were established: (*i*) species characteristic of highly oligotrophic regions, (*ii*) dominant species in offshore water, (*iii*) eurytopic dominant species, (*iv*) eutrophic species normally characteristic of small, nutrient-enriched lakes, (*v*) species characteristic of disturbed habitats in large lakes, and (*vi*) species with poorly defined distributional patterns. Stoermer and Yang (1970) described the distributional patterns of nearly 50 diatoms that fit into these categories. The patterns of a number of important species are discussed in the following text.

Species characteristic of oligotrophic water are illustrated by the distributional patterns of *Cyclotella comta* (Fig. 1), *Cyclotella kuetzingiana* (Fig. 2), and *Cyclotella ocellata* (Fig. 3). These species generally are abundant offshore but can become abundant in inshore regions that are not enriched significantly. The majority of oligotrophic species respond to increased enrichment by decreases in relative abundance over time, a trend observable by comparing relative abundance in the early 1900's with recent data.

Several diatoms characteristic of mesotrophic environments which decrease in relative abundance in enriched regions are: *Cyclotella michiganiana* (Fig. 4), *Melosira islandica* (Fig. 5), and *Tabellaria fenestrata* (Fig. 6). These diatoms can be ephemeral dominant species offshore and also can occur in low percentages nearshore. Their relative abundance, however, is dramatically reduced in highly enriched regions, such as southern Green Bay and inshore areas in southern Lake Michigan.

Species considered to be mesotrophic, which can tolerate moderate enrichment, are represented by *Asterionella formosa* (Fig. 7), *Fragilaria crotonensis* (Fig. 8), *Stephanodiscus hantzschii* (Fig. 9), and *Stephanodiscus minutus* (Fig. 10). These diatoms tend to increase in relative abundance following nutrient enrichment and apparently can tolerate moderate eutrophy. Their relative abundance is reduced markedly only in highly eutrophic or oligotrophic areas.

Species considered to be eutrophic indicators are represented by the distributional patterns and relative abundance of *Fragilaria capucina* (Fig. 11),

Melosira granulata (Fig. 12), and *Stephanodiscus tenuis* (Fig. 13). *Fragilaria capucina* appears to show the most clear-cut response to nutrient enrichment of the eutrophic species. Presently, it is most abundant in polluted harbors, rare at offshore stations, and is the dominant diatom in spring and fall in southern Green Bay.

Eutrophic species, as a group, are abundant nearshore and in polluted harbors; they are markedly reduced in open-water regions, particularly in the northern basin. The data generated by Stoermer and Yang (1969, 1970) suggest that the relative abundances of eutrophic species have increased with accelerated inshore nutrient loadings.

The diatoms listed as introduced eutrophic forms by Stoermer and Yang (1969, 1970) are either species that were present previously in small percentages and have become dominant in nutrient-enriched water, or species that actually did not exist in the Lake prior to cultural eutrophication. *Diatoma tenue* v. *elongatum* (Fig. 14), for example, first appeared in collections made near Chicago. It is now present in low abundance in most areas of the Lake and is of quantitative significance primarily in spring. Its occurrence is restricted almost exclusively to inshore water. Most records indicate that it becomes abundant in chloride-rich habitats. *Nitzschia dissipata* (Fig. 15), a species that responds to high levels of organic pollution, is listed tentatively as an indicator of advanced eutrophication, but its distributional pattern is not entirely distinct. *Stephanodiscus binderanus* (Fig. 16) was first observed in 1938 in very low abundances (Note: *S. binderanus* and *Melosira binderana* are taxonomic synonyms. Although observed frequently in 1964-1967 collections, it constituted 1.0% of the community at only one station in 1964. During 1967, it was abundant at offshore locations, in southern Green Bay, and in polluted harbors. Stoermer and Yang (1970) cited the distributional pattern of *S. binderanus* as an indication of serious eutrophication of the Lake. *Stephanodiscus subtilis* (Fig. 17) generally occurs in highly eutrophic regions that are slightly to moderately brackish. Its distribution is confined primarily to harbors and inshore areas, although it can occur in low abundance offshore.

Studies undertaken by Holland (1968, 1969) and Holland and Beeton (1972) in central Lake Michigan were designed (*i*) to detect seasonal abundance patterns and variations in regional distribution of diatoms at inshore and offshore Lake sites and in Green Bay and (*ii*) to provide information on the trophic preferences of diatoms. The observations of these investigators were in relatively good agreement with those of Stoermer and Yang (1969, 1970). Many species considered as indicators of oligotrophic, mesotrophic, and eutrophic environments by Stoermer and Yang appear to fit similar categories inferred by Holland. One notable exception, however, is the classification of *Cyclotella stelligera* as a diatom adapted to the low-nutrient conditions of central Lake Michigan. Holland and Beeton detected maximum abundance of this species in July and August, whereas Stoermer and Yang detected relatively lower abundances in their studies. Holland and Beeton attributed this discrepancy to sampling differences. Their samples were filtered onto Millipore filters and counted; Stoermer and Yang collected samples by net tow. Since *C. stelligera* ranges from 3.0 to 5.0 μm in diameter and is unicellular, it is not captured effectively by a plankton net. Its abundance, therefore, is underrepresented in the studies of Stoermer and Yang.

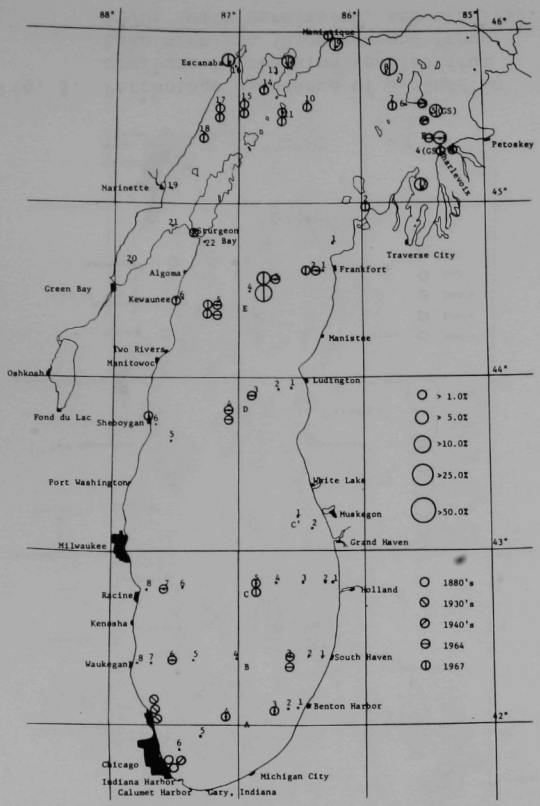

Fig. 1. Percentage abundance of *Cyclotella comta* in plankton samples from Lake Michigan (Stoermer and Yang, 1970) (with permission, see credits).

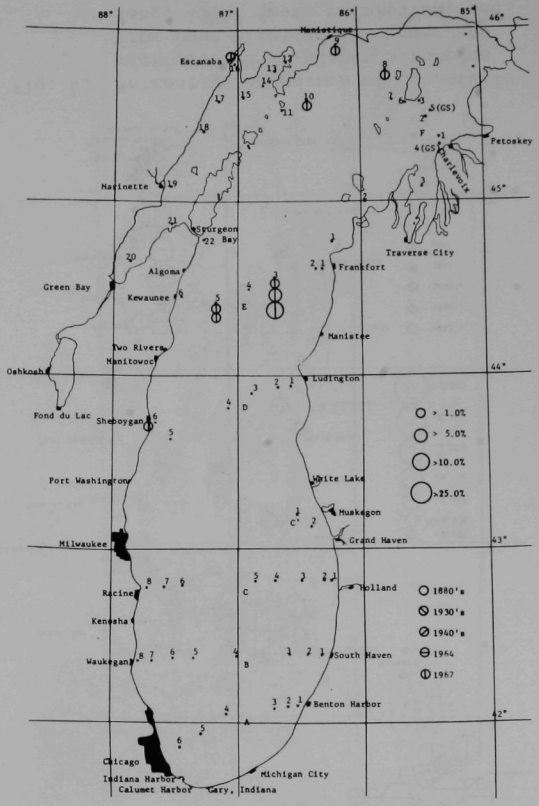

Fig. 2. Percentage abundance of *Cyclotella kuetzingiana* in plankton samples from Lake Michigan (Stoermer and Yang, 1970) (with permission, see credits).

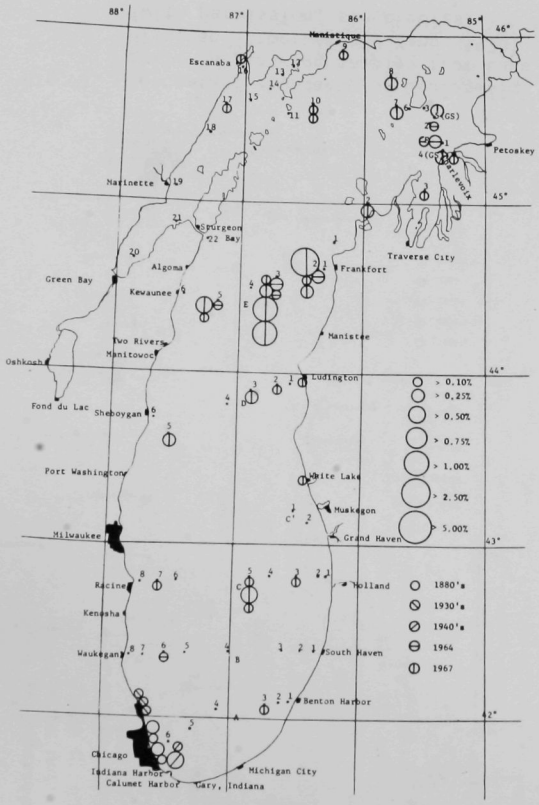

Fig. 3. Percentage abundance of *Cyclotella ocellata* in plankton samples from Lake Michigan (Stoermer and Yang, 1970) (with permission, see credits).

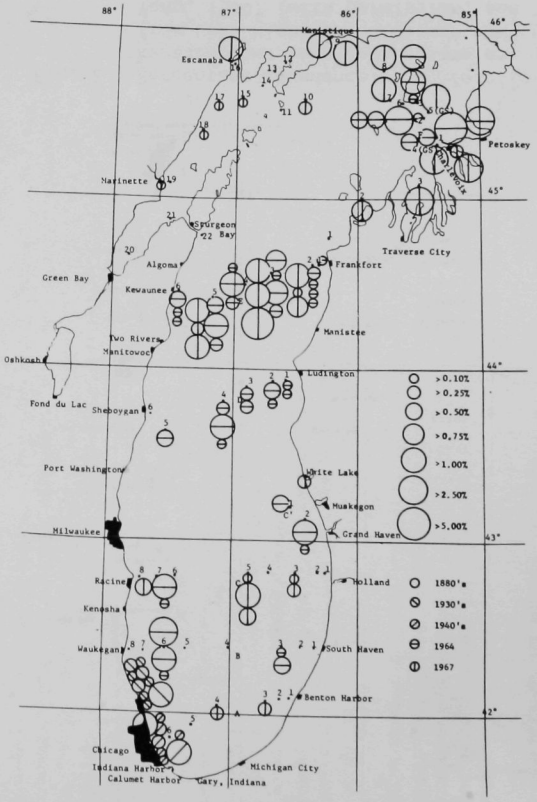

Fig. 4. Percentage abundance of *Cyclotella michiganiana* in plankton samples from Lake Michigan (Stoermer and Yang, 1970) (with permission, see credits).

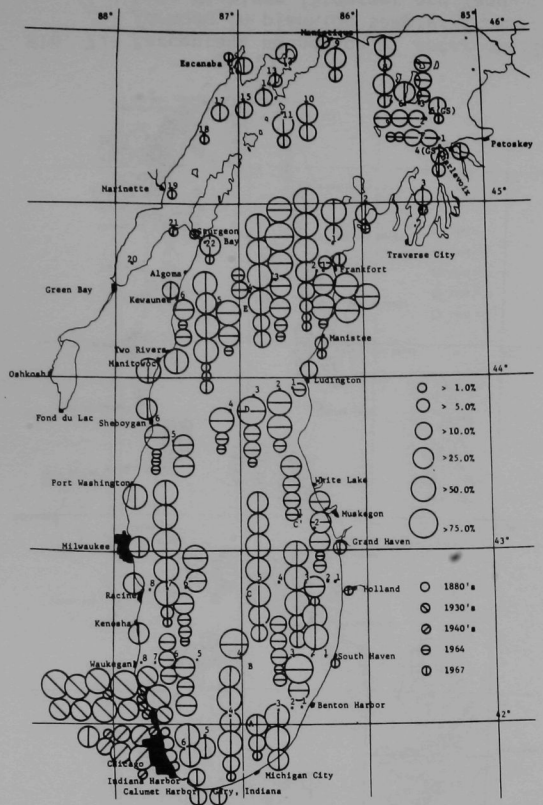

Fig. 5. Percentage abundance of *Melosira islandica* in plankton samples from Lake Michigan (Stoermer and Yang, 1970) (with permission, see credits).

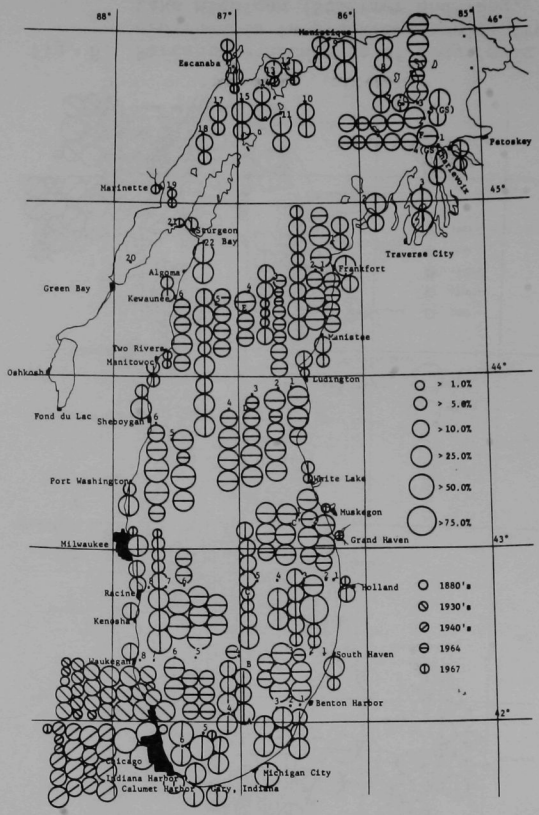

Fig. 6. Percentage abundance of *Tabellaria fenestrata* in plankton samples from Lake Michigan (Stoermer and Yang, 1970) (with permission, see credits).

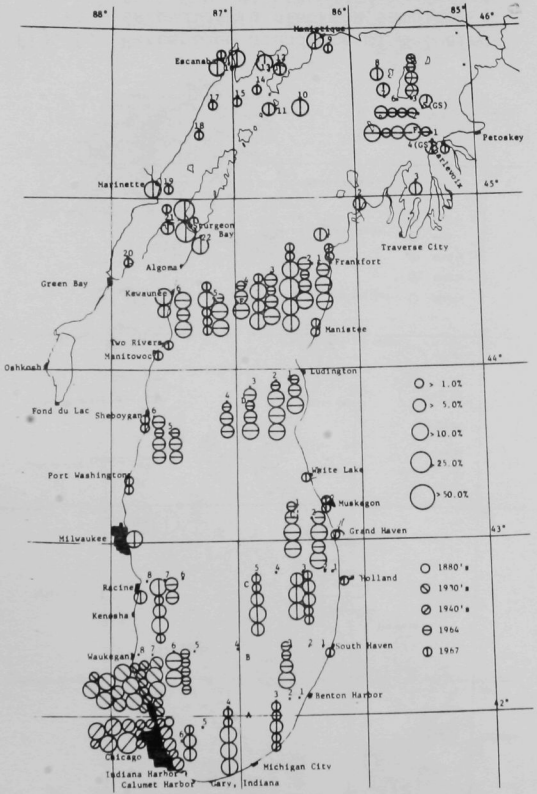

Fig. 7. Percentage abundance of *Asterionella formosa* in plankton samples from Lake Michigan (Stoermer and Yang, 1970) (with permission, see credits).

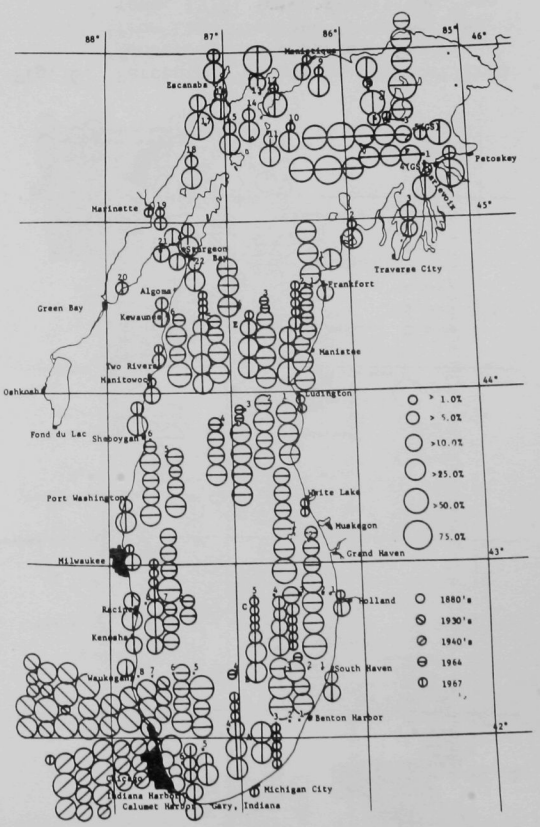

Fig. 8. Percentage abundance of *Fragilaria crotonensis* in plankton samples from Lake Michigan (Stoermer and Yang, 1970) (with permission, see credits).

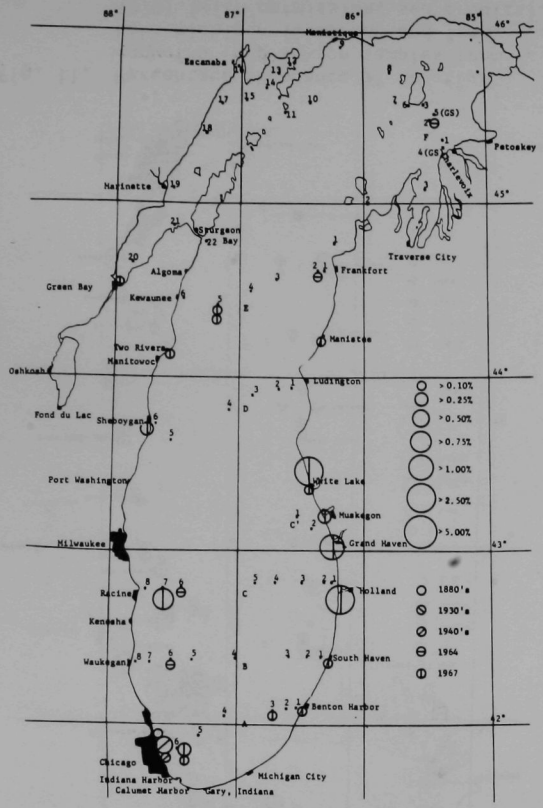

Fig. 9. Percentage abundance of *Stephanodiscus hantzschii* in plankton samples from Lake Michigan (Stoermer and Yang, 1970) (with permission, see credits).

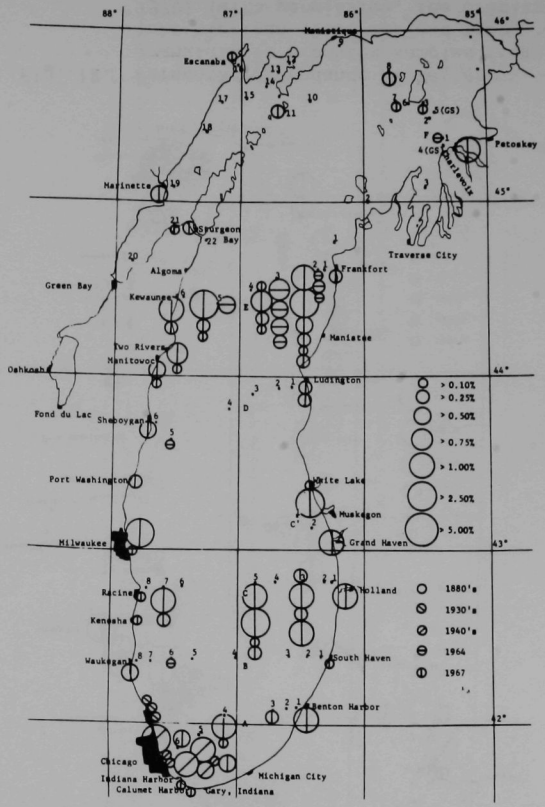

Fig. 10. Percentage abundance of *Stephanodiscus minutus* in plankton samples from Lake Michigan (Stoermer and Yang, 1970) (with permission, see credits).

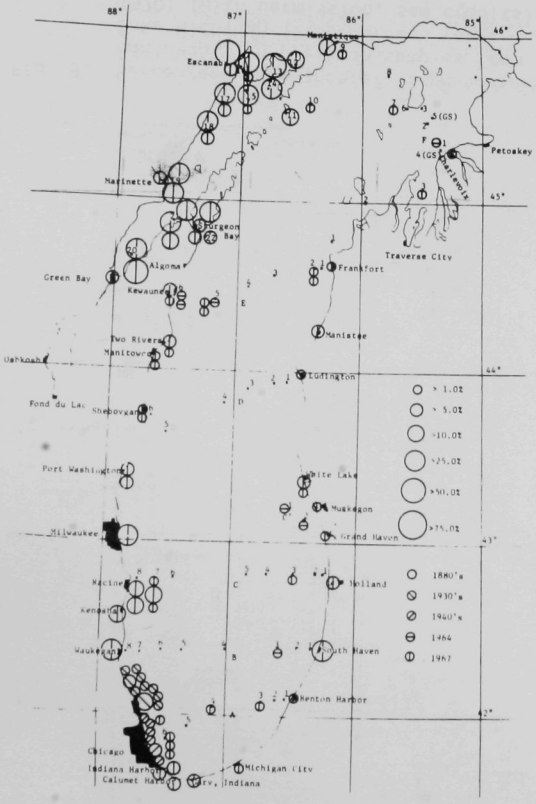

Fig. 11. Percentage abundance of *Fragilaria capucina* in plankton samples from Lake Michigan (Stoermer and Yang, 1970) (with permission, see credits).

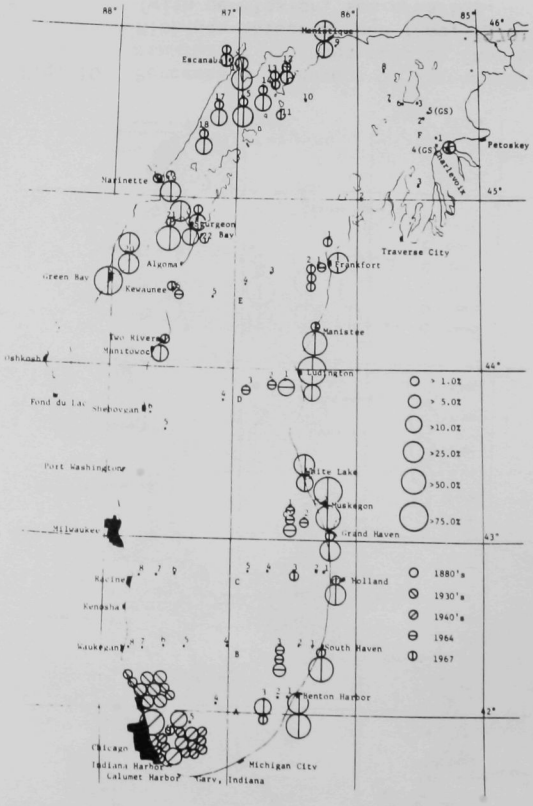

Fig. 12. Percentage abundance of *Melosira granulata* in plankton samples from Lake Michigan (Stoermer and Yang, 1970) (with permission, see credits).

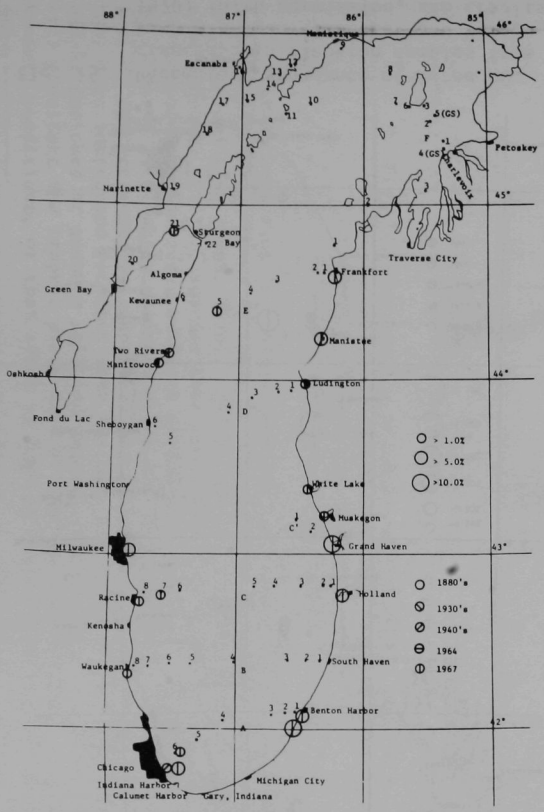

Fig. 13. Percentage abundance of *Stephanodiscus tenuis* in plankton samples from Lake Michigan (Stoermer and Yang, 1970) (with permission, see credits).

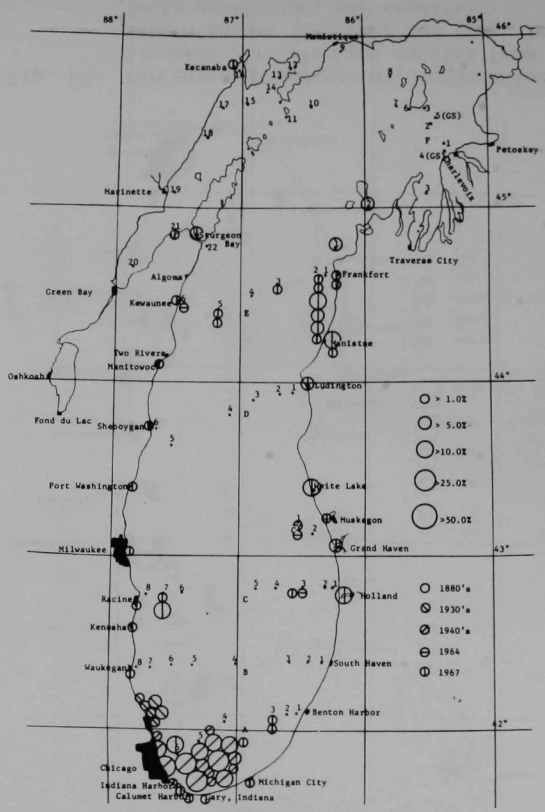

Fig. 14. Percentage abundance of *Diatoma tenue* v. *elongatum* in plankton samples from Lake Michigan (Stoermer and Yang, 1970) (with permission, see credits).

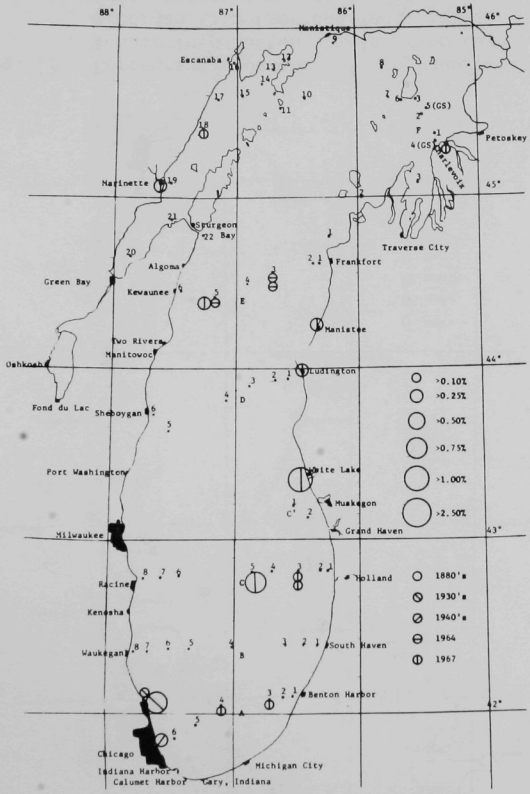

Fig. 15. Percentage abundance of *Nitzschia dissipata* in plankton samples from Lake Michigan (Stoermer and Yang, 1970) (with permission, see credits).

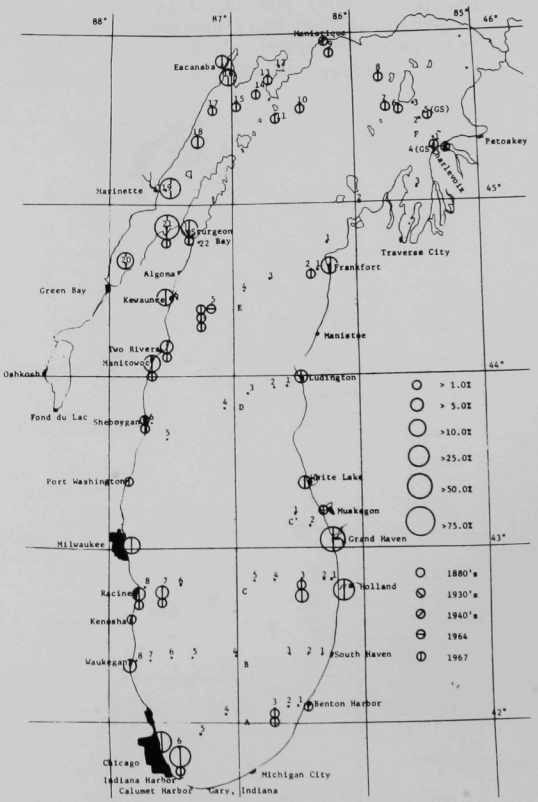

Fig. 16. Percentage abundance of *Stephanodiscus binderanus* in plankton samples from Lake Michigan (Stoermer and Yang, 1970) (with permission, see credits).

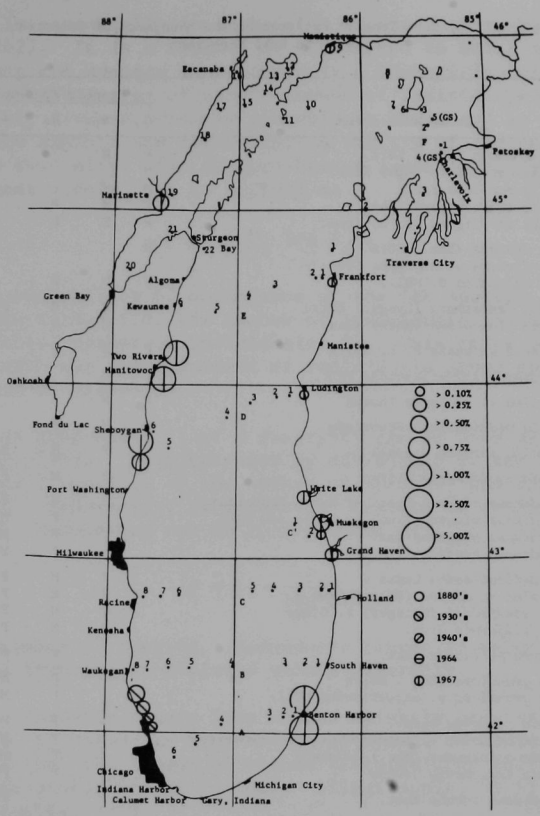

Fig. 17. Percentage abundance of *Stephanodiscus subtilis* in plankton samples from Lake Michigan (Stoermer and Yang, 1970) (with permission, see credits).

Diatoms appearing to exhibit moderately distinct trophic preferences in Lake Michigan are listed in Table 2. The trophic categories are adopted from Stoermer and Yang (1969, 1970): (*i*) O, species in low-nutrient (oligotrophic) environments, (*ii*) M_1, species that are adapted to slightly enriched water and cannot tolerate increased nutrient enrichment, (*iii*) M_2, species that are normally found in slightly enriched water and can tolerate moderate enrichment, (*iv*) E, species normally adapted to eutrophic water,* and (*v*) EI, species that have been introduced recently into the Lake and occur almost exclusively in highly enriched or grossly polluted waters. It is expected that further study will elucidate the trophic preference of diatoms that tolerate a broad range of trophic conditions, or that adapt to low- or high-nutrient environments.

**Some of the diatom genera--e.g. Coscinodiscus, Skeletonema, and Thalassiosira--recently introduced into the Lake require or tolerate elevated salinity levels.*

Table 2. Apparent Trophic Preferences and Abundance of Selected Diatoms in Lake Michigan

Selected Diatoms	Trophic Preference				
	O	M_1	M_2	*E*	*EI*
Cyclotella comta (Ehr.) Kütz.	P	M	P		
Cyclotella operculata (Ag.) Kütz.	M				
Cyclotella ocellata Pant.	M	P			
Cyclotella kuetzingiana Thwaites	P	M	P		
Cyclotella stelligera Cl. u. Grun.	P	M	P		
Melosira distans (Ehr.) Kütz.	M				
Melosira distans v. *alpigena* Grun.					M
Melosira islandica O. Müll.	P	M	P		
Tabellaria fenestrata (Lyngb.) Kütz.		P	M	P	
Tabellaria flocculosa (Roth) Kütz.		M	P		
Rhizosolenia eriensis H. L. Smith	P	M	P		
Stephanodiscus transilvanicus Pant.	P	M			
Synedra ulna v. *chaseana* Thomas	P	M			
Cyclotella michiganiana Skvortzow	P	M	P		
Asterionella formosa Hassall		P	M	P	
Fragilaria crotonensis Kitton		P	M	P	
Stephanodiscus alpinus Hust. *ex* Huber-Pestalozzi		P	M	P	
Stephanodiscus minutus Grun. *ex* Cleve and Möll.			P	M	
Stephanodiscus niagarae Ehr.			P	M	
Stephanodiscus hantzschii Grun.			P	M	
Synedra delicatissima Lewis		P	M	P	
Synedra ulna v. *danica* (Kütz.) Grun.		P	M	P	
Synedra ostenfeldii (Krieger) A. Cleve		P	M	P	
Synedra filiformis Grun.		P	M	P	
Amphipleura pellucida Kütz.			P	M	P
Melosira granulata (Ehr.) Ralfs			P	M	
Melosira granulata v. *angustissima* Müll.			P	M	
Fragilaria capucina Desm.			P	M	
Fragilaria capucina v. *mesolepta* (Rabh.) Grunow			P	M	
Fragilaria construens (Ehr.) Grunow			P	M	
Fragilaria intermedia Grunow			P	M	
Stephanodiscus tenuis Hust.				P	M
Asterionella bleakeleyi Wm. Smith				P	M
Diatoma tenue v. *elongatum* Lyngb.				P	M
Stephanodiscus binderanus (Kütz.) Krieger				P	M
Stephanodiscus subtilis (Van Goor) A. Cleve				P	M
Nitzschia dissipata (Kütz.) Grun.				M	P
Coscinodiscus subsalsa Juhl.-Dannf.					M

Symbols: *O, oligotrophic;* M_1*, mesotrophic but intolerant of nutrient enrichment;* M_2*, mesotrophic and tolerant of moderate nutrient enrichment; E, eutrophic; EI recently introduced eutrophic species; P, presence of species; and M, apparent maximum abundance of the species.*

References: *Holland (1968, 1969); Stoermer and Yang (1969, 1970); Holland and Beeton (1972).*

Species Diversity

The diversity of phytoplankton communities can be used to compare different assemblages and to indicate trophic state (Margalef, 1958a, 1958b, 1964). Species diversity of phytoplankton communities has not been widely investigated in north-temperate lakes; however, numerous estimates for Lake Michigan phytoplankton are available.

Diversity is essentially an expression of the structure of communities (*cf.* Patten, 1962). It is a measure of the degree to which individuals are distributed among the species in a community. Communities with large numbers of species and a high degree of apportionment of individuals among species are regarded as highly diverse, whereas assemblages dominated by one or a few taxa are considered to exhibit low diversity. A variety of indices can be used to express species diversity. The Shannon-Weaver index (Shannon and Weaver, 1963) has been used most widely. It is defined as

$$H = -\Sigma\, p_i \log p_i \,, \tag{1}$$

where p_i is the probability of occurrence of the ith species. In samples, p_i is estimated from n_i/N_s, *i.e.* the number of individuals in the ith species divided by the total number of individuals, N_s. This index combines the number of species with the apportionment of individuals among species (evenness) into the estimate of diversity.

The evenness component, J, of H diversity can be used as a community property (Pielou, 1969). J is computed by dividing H by the theoretical maximum diversity (logarithm of the number of species) and ranges in value from zero to 1.0. Redundancy, R, a relative measure of dominance, is a function of J and H. Redundancy can be approximated by

$$R = 1 - \frac{H}{\log S} \,, \tag{2}$$

where S is the number of species. Redundancy ranges in value from zero to 1.0 and generally is inversely correlated with H diversity.

In lakes, H normally ranges from values slightly greater than zero, in bloom situations, to values as high as 4.5 bits/cell or individual. Margalef (1968) indicated that the ranges of values (bits/cell or individual) defining different trophic states are as follows: oligotrophic, >3.5; mesotrophic, 2.5 to 3.5; and eutrophic, <2.5.

Diatom Assemblages

Species diversity of diatom communities was studied extensively by Stoermer and Yang (1969). Their analyses, based on 422 lake-wide collections, were designed in part to determine relationships between diversity and trophic characteristics of different regions of the Lake. Estimates of H and R ranged from 0.513 to 3.574 bits/cell and from 0.358 to 0.881 bits/cell, respectively. The modal values of H and R were 1.80 and 0.60 bits/cell, respectively. Although these values fall within the expected range, the authors concluded that species diversity furnishes little information regarding trophic conditions of different regions of the Lake. When individual locations in harbor areas were examined, for example, very high and very low values occurred together. At offshore stations, the range of index values on successive sampling dates at the same station can be extremely large.

The authors noted, however, that there is a tendency for diversity to increase rather than to decrease with eutrophication as might be expected on the basis of theory. They hypothesized that diversity of diatom assemblages was low prior to cultural eutrophication of the Lake. They predicted that

continued nutrient additions to the Lake will cause benthic and littoral diatoms to invade the plankton, thus increasing diversity. However, if the habitat becomes highly eutrophic or polluted by toxic wastes, species survival will decrease with a dramatic decrease in diversity.

According to Stoermer and Yang (1969), the situation in the Lake seems to be one in which populations of some species are large, tending to lower the diversity index. This is balanced, however, by invasion of the plankton by benthic and littoral diatom populations. Stoermer and Yang suggested that species diversity of diatom assemblages, therefore, is probably near the maximum values that may be expected in many areas of the Lake.

Phytoplankton Assemblages

Several recent investigations have included species diversity of total phytoplankton assemblages. The study sites were (*i*) at Grand Haven, (*ii*) near the Donald C. Cook and Waukegan-Zion power plants in southern Lake Michigan, and (*iii*) in Grand Traverse Bay. In addition, one experimental investigation on the effects of nutrient enrichment on species diversity was conducted in the Lake.

Observations at Grand Haven (Schelske *et al.*, 1971) were made at an inshore and an offshore station during June-September 1969. At each location, physical, biological (Tables 3-6), and chemical variables were monitored (Fig. 18). During July-September at the inshore station, *H* ranged from 1.79 to 2.86 bits/cell, with a mean of 2.34. The range and mean at the offshore station were 1.85-2.55 and 2.29 bits/cell, respectively. Diversity at both stations varied irregularly over the study period and was equivalent to or possibly slightly greater than diversity at the offshore station. Theoretically, one would expect higher diversity in the low-nutrient and more stable offshore water.

Table 3. Cell Counts and Percent* Abundance of Selected Species at Station 1, June 1969**

Most Abundant Species	*9 June*		*18 June*		*29 June*	
	Cells/ml	*%*	*Cells/ml*	*%*	*Cells/ml*	*%*
Station 1, Inshore						
Melosira granulata (Ehr.) Ralfs	320	22	326	17	158	15
Synedra filiformis Grun.	193	13	16	1	-	-
Rhizosolenia eriensis H. L. Smith	152	10	119	6	14	1
Rhizosolenia gracilis H. L. Smith	99	7	66	3	-	-
Fragilaria capucina Desm.	96	7	45	2	106	10
Stephanodiscus binderanus (Kütz.) Krieger	78	5	174	9	30	3
Fragilaria crotonensis Kitton	70	5	230	12	221	20
Diatoma tenue v. *elongatum* Lyngb.	54	4	217	11	49	5
Tabellaria fenestrata (Lyngb.) Kütz.	55	4	149	8	221	20
Unidentified flagellates	23	2	110	6	82	8
Fragilaria intermedia v. *fallax* (Grun.) A. Cleve	-	-	114	6	-	-
Total of most abundant species	1140	78	1566	79	881	82
Total number of species identified	40		50		40	
Total number of cells/ml in sample	1463		1970		1079	
Shannon-Weaver diversity index, bits/cell	2.64		2.79		2.45	

*% = Total number of cells/ml of given species divided by the total number of cells/ml of all species identified.

**Data from Schelske et al. (1971).

Table 4. Cell Counts and Percent* Abundance of Selected Species at Stations 1 and 2, July 1969**

Most Abundant Species	19 July		21 July		25 July		28 July	
	Cells/ml	%	Cells/ml	%	Cells/ml	%	Cells/ml	%
Station 1, Inshore								
Tabellaria fenestrata	198	26	162	13	197	10	107	20
Fragilaria crotonensis	135	17	327	26	265	14	105	19
Cyclotella stelligera (Grun. & Cl.) V. H.	126	16	382	31	554	29	59	11
Unidentified flagellates	78	10	20	2	70	4	40	7
Dinobryon divergens Imhof	44	6	14	1	107	6	22	4
Cyclotella michiganiana Skv.	27	3	96	8	115	6	3	-
Cyclotella meneghiniana v. *plana* Fricke	22	3	51	4	85	4	8	1
Melosira granulata	11	1	12	1	179	9	9	2
Anabaena flos-aquae (Lyngb.) Bréb.	4	-	5	-	8	-	19	4
Total of most abundant species	645	83	1069	86	1580	83	372	69
Total number of species identified	46		48		49		57	
Total number of cells/ml in sample	772		1244		1899		539	
Shannon-Weaver diversity index, bits/cell	2.44		2.14		2.50		2.86	
Station 2, Offshore								
Cyclotella stelligera	622	53	613	49	173	31	322	30
Dinobryon divergens	125	11	132	11	7	1	167	15
Tabellaria fenestrata	86	7	60	5	6	1	138	13
Fragilaria crotonensis	81	7	132	11	55	10	135	12
Cyclotella michiganiana	75	6	84	7	37	7	60	6
Unidentified flagellates	66	6	70	6	61	11	32	3
Cyclotella ocellata Pant.	13	1	14	1	16	3	6	-
Rhizosolenia eriensis	12	1	3	-	13	2	1	-
Unidentified coccoid green	11	1	25	2	21	4	5	-
Rhizosolenia gracilis	2	0.2	7	0.6	30	5	7	-
Anabaena flos-aquae	9	0.8	13	1	29	5	4	-
Total of most abundant species	1102	94	1153	92	448	81	877	81
Total number of species identified	49		39		34		51	
Total number of cells/ml in sample	1174		1249		550		1089	
Shannon-Weaver diversity index, bits/cell	1.85		1.93		2.54		2.42	

*% = Total number of cells/ml of given species divided by the total number of cells/ml of all species identified.

**Data from Schelske *et al.* (1971).

During investigations on phytoplankton diversity at the Donald C. Cook power plant, Ayers *et al.* (1972a) observed that *H* ranged from 0.49 to 4.27 bits/individual during a survey on 10 July 1970 (Table 7). Their observations indicated that *H* varies greatly between adjacent stations, and that both high and low values occur simultaneously in nearshore and offshore water. The authors concluded that a high degree of patchiness occurs in the composition and relative size of phytoplankton populations, and that diversity index values serve only as a mathematical summary of data from biologically different water masses.

Studies near the Waukegan Generating Station yielded results differing from those of the investigations of Schelske *et al.* (1971) and Ayers *et al.* (1972b). Piala and Lamble (1971) presented data on seasonal variations of *H* and *J* from three stations in the southwestern part of the Lake (Fig. 19). Phytoplankton diversity near Zion and Waukegan varied monthly, with high values in late August, September, and January and low values during May, June, and November. The authors interpreted these observations as evidence that *H* and *J* do not show significant differences between adjacent stations or with time of day. Observations made at the offshore station show similar seasonal

Table 5. Cell Counts and Percent* Abundance of Selected Species at Stations 1 and 2, August and September 1969**

Most Abundant Species	26 August Cells/ml	%	27 August Cells/ml	%	29 August Cells/ml	%	2 September Cells/ml	%	8 September Cells/ml	%
Station 1, Inshore										
Melosira granulata	487	37	1158	56	719	40	258	28	305	35
Fragilaria capucina	217	17	99	5	81	4	–	–	48	5
Fragilaria crotonensis	128	10	328	16	302	17	32	3	161	18
Cyclotella stelligera	66	5	104	5	161	9	18	2	35	4
Cyclotella meneghiniana v. *plana*	66	5	38	2	74	4	71	8	33	4
Dinobryon divergens	22	2	6	–	25	1	229	25	10	1
Unidentified flagellates	53	4	76	4	56	3	112	12	66	7
Anacystis dimidiata (Kütz.) Dr. & Daily	12	1	17	1	15	1	25	3	31	3
Anacystis sp.	11	1	20	1	14	1	45	5	40	4
Total of most abundant species	1062	81	1846	89	1447	80	790	86	729	83
Total number of species identified	44		50		62		44		45	
Total number of cells/ml in sample	1304		2083		1800		916		881	
Shannon-Weaver diversity index, bits/cells	2.32		1.79		2.31		2.30		2.41	
Station 2, Offshore										
Unidentified flagellates	85	23			61	17	121	34	90	31
Cyclotella stelligera	56	15			20	6	9	2	24	8
Anacystis dimidiata	39	11			58	17	56	16	35	12
Gloeocystis sp.	39	11			60	17	21	6	3	1
Fragilaria crotonensis	27	7			28	8	2	–	4	1
Anacystis sp.	22	6			51	15	66	19	24	8
Oocystis sp.	12	3			20	6	17	5	6	2
Unidentified coccoid green	6	2			4	1	17	5	33	11
Cyclotella michiganiana	17	5			7	2	3	1	5	2
Total of most abundant species	303	83			309	88	312	88	224	78
Total number of species identified	32				29		25		39	
Total number of cells/ml in sample	365				351		355		287	
Shannon-Weaver diversity index, bits/cell	2.55				2.40		2.13		2.55	

*% = Total number of cells/ml of given species divided by the total number of cells/ml of all species identified.

**Data from Schelske et al. (1971).

Table 6. Cell Counts and Percent* Abundance of Selected Species at Station 1, September 1969**

Most Abundant Species	16 September Cells/ml	%	17 September Cells/ml	%	18 September Cells/ml	%	19 September Cells/ml	%	22 September Cells/ml	%	26 September Cells/ml	%
Station 1, Inshore												
Fragilaria crotonensis	151	32	153	26	63	14	134	24	20	5	40	9
Unidentified flagellates	66	14	42	7	55	12	60	11	101	24	86	21
Unidentified coccoid green	51	11	43	7	45	10	58	10	59	14	45	11
Anacystis dimidiata	44	9	41	7	38	8	25	4	46	11	40	9
Cyclotella stelligera	29	6	19	3	32	7	35	6	32	8	39	9
Melosira granulata	26	5	80	14	56	12	102	18	5	1	10	2
Anacystis sp.	22	5	28	5	22	5	23	4	27	6	35	8
Cyclotella michiganiana	18	4	17	3	9	2	12	2	19	4	23	5
Fragilaria capucina	–	–	–	–	4	1	–	–	56	13	11	3
Dinobryon divergens	–	–	26	4	4	1	–	–	–	–	49	12
Total of most abundant species	407	85	449	78	328	73	449	81	365	87	378	90
Total number of species identified	40		45		51		42		31		37	
Total number of cells/ml in sample	479		586		450		553		418		419	
Shannon-Weaver diversity index, bits/cell	2.45		2.70		2.93		2.56		2.45		2.57	

*% = Total number of cells/ml of given species divided by the total number of cells/ml of all species identified.

**Data from Schelske et al. (1971).

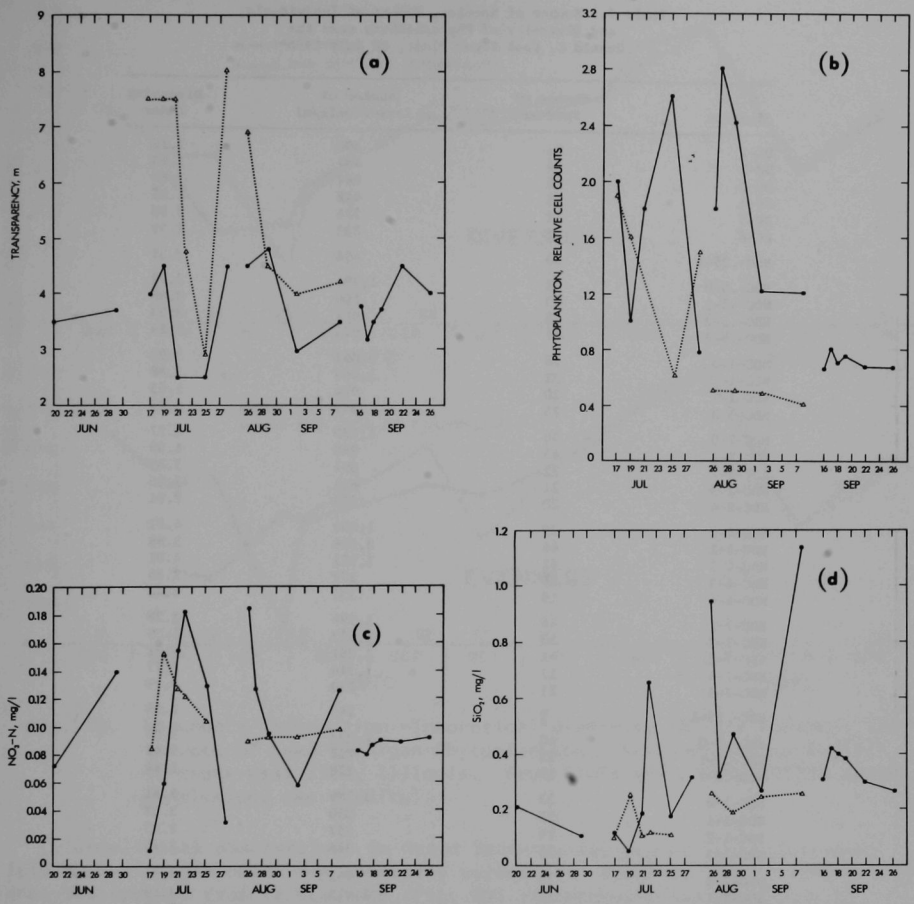

Fig. 18. Physical, Chemical, and Biological Parameters at Inshore (Station 1, solid line) and Offshore (Station 2, dotted line) Stations near Grand Haven, Michigan. Modified from Schelske *et al.* (1971) (with permission, see credits).

trends in the surface water and near the thermocline. Diversity and evenness decrease through June and July and then increase through late summer, fall, and early winter. Based on these and similar studies for April 1971-March 1972 (Huh *et al.*, 1972), it appears that *H* diversity and evenness tend to be higher offshore than nearshore. This trend appears to agree with that postulated for north-temperate waters, and apparently differs from the findings of Schelske *et al.* (1971).

Table 7. Number of Species, Number of Individuals, and Diversity of Phytoplankton near the Donald C. Cook Power Plant, 10 July 1970*

Station	*Number of Species*	*Number of Individuals/ml*	*Diversity Index*
DC-1	23	390	3.18
DC-2	24	407	3.63
DC-3	30	647	3.60
DC-4	15	448	1.85
DC-5	12	286	2.88
DC-6	11	333	2.39
NDC-.25-1	26	458	3.39
NDC-.5-0	42	1,794	3.92
NDC-.5-1	43	504	3.88
NDC-.5-2	26	647	3.53
NDC-.5-3	17	528	2.89
NDC-1-0	36	3,052	3.90
NDC-1-1	31	1,244	3.88
NDC-1-2	20	974	1.65
NDC-1-3	25	543	3.28
NDC-2-0	36	1,180	4.27
NDC-2-1	43	940	4.05
NDC-2-2	21	504	3.85
NDC-2-3	21	601	3.46
NDC-2-4	20	515	2.91
NDC-4-0	30	1,856	4.01
NDC-4-1	46	3,024	3.89
NDC-4-2	42	1,521	4.01
NDC-4-3	19	277	2.85
NDC-4-4	19	331	3.40
NDC-7-1	46	1,594	3.78
NDC-7-2	50	11,523	1.09
NDC-7-3	41	1,081	3.92
NDC-7-4	17	1,344	2.77
NDC-7-5	21	220	3.29
SDC-.25-1	9	143	1.94
SDC-.5-0	40	1,038	3.90
SDC-.5-1	33	718	3.62
SDC-.5-2	17	278	2.84
SDC-1-0	33	1,396	3.81
SDC-1-1	27	830	3.33
SDC-1-2	19	757	2.03
SDC-1-3	16	386	2.75
SDC-2-0	34	962	3.55
SDC-2-1	29	1,012	3.58
SDC-2-2	13	265	2.55
SDC-2-3	18	337	3.23
SDC-2-4	12	316	2.29
SDC-4-0	40	1,104	4.22
SDC-4-1	31	567	3.56
SDC-4-2	26	798	3.08
SDC-4-3	18	438	2.84
SDC-4-4	17	331	3.15
SDC-7-1	32	632	3.68
SDC-7-2	42	13,274	0.49
SDC-7-3	37	630	3.54
SDC-7-4	26	712	3.20
SDC-7-5	23	413	2.88
Average diversity index			3.20

*Data from Ayers *et al.* (1972a).

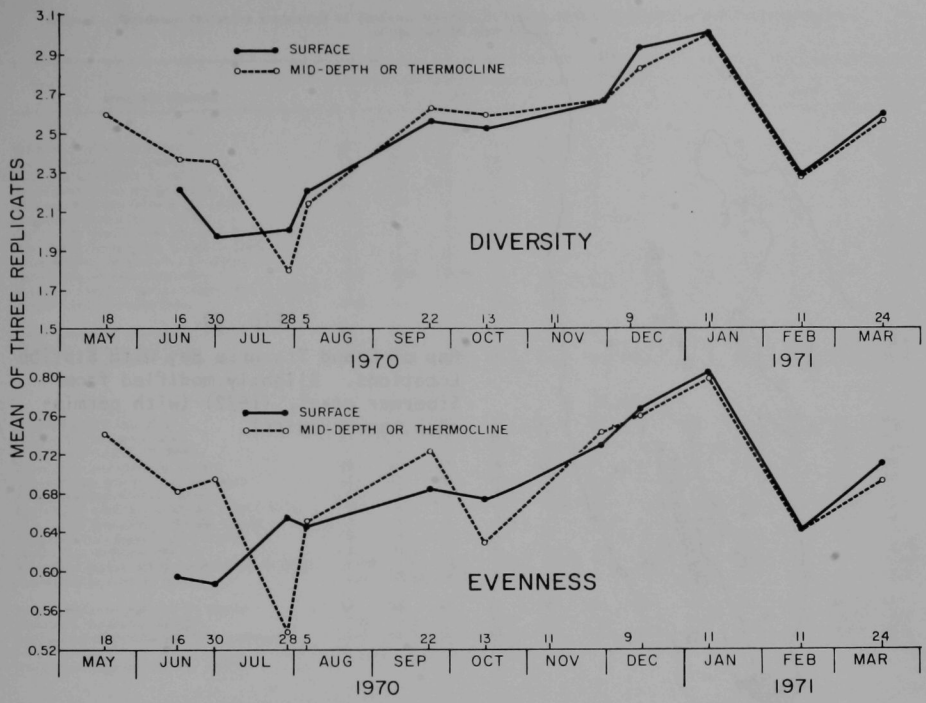

Fig. 19. Shannon's Information--Theoretical Diversity (H) and Evenness (J) Indices of Lake Michigan Phytoplankton. Station located 6 miles offshore near Zion, Illinois. From Pjala and Lamble (1971) (with permission, see credits).

Limnological observations in Grand Traverse Bay resulted in additional information on phytoplankton community structure. Stoermer *et al.* (1972) analyzed samples from 12 stations (Fig. 20) to determine the influence of nutrient enrichment on phytoplankton productivity and standing crop in the bay (Tables 8 and 9). Diversity was higher in May (2.3-2.6 bits/cell) than in June (1.8-2.0 bits/cell), and appeared to be negatively correlated with an overall increase in standing crop. Despite the fact that the lower end of the bay received nutrients and was more productive than the central and northern regions, diversity was remarkably uniform at all stations during each month. Species diversity did not appear to reflect obvious differences in water quality in the bay.

Stoermer *et al.* (1971) conducted an experimental study on phytoplankton diversity at an inshore and an offshore station near Grand Haven. Lake water was enclosed in large plastic bags and enriched with different concentrations of nitrogen, phosphorus, and silica. In treatments receiving all three nutrients, diversity decreased significantly after one week; by the second week, diversity increased and varied irregularly after that. The decrease in diversity at the inshore station was due to a sharp decline in abundance of several

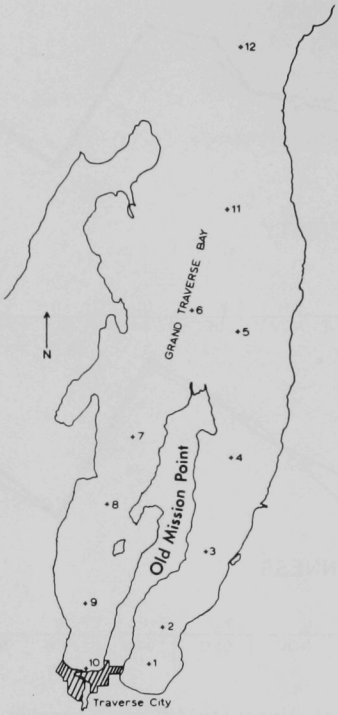

Fig. 20.

Map of Grand Traverse Bay with Station Locations. Slightly modified from Stoermer *et al.* (1972) (with permission, see credits).

species and to a large increase in the abundance of *Fragilaria crotonensis*. Likewise, at the offshore station, the diatom *Cyclotella stelligera* increased dramatically while several other species decreased in abundance.

These experimental results are difficult to interpret. Species diversity decreased after nutrient enrichment, but the trend was not sustained over the course of the experiment. The authors concluded that additional studies or further analysis of existing data is necessary.

SPATIAL AND TEMPORAL VARIATIONS IN THE STANDING CROP AND COMPOSITION OF DIATOMS

There have been several studies undertaken specifically on spatial and temporal variations in diatom abundance in Lake Michigan. In this section, the salient observations of each study are presented, and a hypothesis involving the relationship between ambient silica concentrations and the growth of diatoms is presented.

Inshore-Offshore Differences and Related Phenomena

Since these investigations were undertaken in different regions of the Lake, they are organized by geographic location for convenience.

Table 8. Abundance (Relative Frequency) of Dominant Species in Samples from 5 m, Grand Traverse Bay, Lake Michigan, 18 May and 20 June 1970*

Dominant Species	Stations 1	2	3	4	5	6	7	8	9	10	11	12
						18 May						
Synedra filiformis Grun.	21	23	23	23	20	21	22	24	26	23	21	15
Unidentified flagellates	26	20	20	12	21	21	20	17	18	24	21	21
Melosira islandica O. Müll.	8	10	7	12	11	6	11	12	8	8	3	8
Fragilaria crotonensis Kitton	12	5	11	5	9	14	8	10	12	13	16	13
Rhizosolenia gracilis H. L. Smith	5	4	6	6	6	6	6	4	4	4	6	8
Stephanodiscus minutus Grun.	5	7	8	6	5	5	7	8	9	8	3	4
Cyclotella stelligera (Grun. & Cl.) V. H.	7	9	7	11	4	4	5	4	5	4	3	5
Tabellaria fenestrata (Lyngb.) Kütz.	3	6	3	4	3	2	2	3	2	2	5	1
Rhizosolenia eriensis H. L. Smith	1	2	1	1	0.9	1	0.9	0.8	0.7	1	1	1
Cyclotella michiganiana Skv.	0.8	0.6	0.09	0.5	0.3	0.3	0.4	0.1	0.3	0.5	0.3	0.2
Melosira italica subsp. *subarctica* O. Müll.	1	1	1	5	1	0.7	2	1	1	1	3	3
Asterionella formosa Hass.	0.6	1	1	0.5	0.5	1	1	0.5	0.3	0.5	1	1
Total number of species in sample	57	58	45	52	45	46	53	54	51	62	51	48
Diversity index, bits/cell	2.3	2.4	2.5	2.6	2.5	2.5	2.6	2.4	2.4	2.3	2.5	2.6
Percent of dominants in the assemblage	90.4	88.6	87.8	86.0	81.7	82.0	83.3	84.4	86.3	89.0	83.3	81.2
						20 June						
Synedra filiformis Grun.	36	35	40	37	35	41	47	46	46	39	44	16
Unidentified flagellates	14	15	12	21	12	7	7	9	12	18	13	15
Melosira islandica O. Müll.	0	1	1	0.9	0.2	0	0.4	0.5	0.4	1	0	0.8
Fragilaria crotonensis Kitton	20	18	17	14	12	9	17	20	17	16	14	26
Rhizosolenia gracilis H. L. Smith	12	13	13	14	22	24	12	9	9	9	15	15
Stephanodiscus minutus Grun.	1	1	1	0.7	0.5	0.2	2	2	2	2	1	1
Cyclotella stelligera (Grun. & Cl.) V. H.	0.7	1	1	1	0.6	0.6	0.8	0.4	0.6	0.4	0.8	1
Tabellaria fenestrata (Lyngb.) Kütz.	2	3	2	0.4	1	0.08	2	2	2	2	0.5	1
Rhizosolenia eriensis H. L. Smith	4	3	3	4	4	7	2	2	2	2	3	3
Cyclotella michiganiana Skv.	1	0.7	1	1	0.6	0.7	0.9	0.8	0.9	0.8	1	0.08
Melosira italica subsp. *subarctica* O. Müll.	0.06	0.5	0.1	0.2	0.2	0	0.2	0.2	0.1	0.3	0	0.03
Asterionella formosa Hass.	0.3	0.07	0.3	0.3	2	1	0.4	0.2	0.2	0.3	0.4	0.5
Total number of species in sample	56	51	45	55	60	50	59	54	55	59	47	48
Diversity index, bits/cell	2.0	2.0	1.9	1.8	2.0	1.8	1.8	1.8	1.8	1.9	1.8	2.2
Percent of dominants in the assemblage	91.1	91.3	91.4	94.5	90.1	90.6	91.7	92.1	92.2	90.8	92.7	79.4

*Data from Stoermer *et al.* (1972).

Central Lake Michigan

Three studies of spatial and temporal variations in diatom standing crop and composition in central Lake Michigan have been carried out at the Center for Great Lakes Studies, Milwaukee, Wisconsin. The first was a study of the seasonal abundance patterns of *Melosira* in several regions of the Lake; the second was a quantitative investigation of the total assemblage at the same locations; and the third study documented differences in composition of diatom assemblages along a transect from Milwaukee, Wisconsin, to Ludington, Michigan.

The first study, conducted by Holland (1968), explored differences among the standing crop of planktonic diatoms and determined patterns in the distribution of four species of *Melosira (M. granulata, M. ambigua, M. binderana,* and *M. islandica)* at four locations in the Lake and southern Green Bay. The distributional pattern of these species in north-temperate lakes indicates that each diatom exhibits a preference for specific lake types (*cf.* Hustedt, 1945; Lund, 1962; Hohn, 1968--unpublished, 1969; and Rawson, 1956). *Melosira binderana* and *M. granulata* normally are found in eutrophic lakes. *Melosira ambigua* apparently is favored by nutrient enrichment and flourishes in mesotrophic water; it is reduced in abundance in highly eutrophic environments and generally is replaced by either or both of the first two species. *Melosira islandica*, conversely, occurs primarily in low-nutrient environments but can tolerate some degree of nutrient enrichment; it is replaced frequently by *M. ambigua* in mesotrophic environments.

Table 9. Productivity-Related Parameters Measured at 12 Stations in Grand Traverse Bay, Lake Michigan, on 18 May and 20 June 1970*

	Secchi disc, m	*Part. P, µg/l*		*NO_3-N, mg/l*		*Diss. SiO_2, mg/l*		*Standing crop, cells/ml*	*Productivity, mg C/m³/hr*
		A	*B*	*A*	*B*	*A*	*B*	*A*	*A*
					18 May				
Stations									
1	9.0	7.2		0.234		1.07		1937	4.05
2	9.2	6.7		0.230		1.10		1697	4.13
3	8.5	7.6		0.238		1.18		1527	4.96
4	8.5	7.0		0.229		1.20		1455	4.07
5	8.0	6.9		-		1.13		1978	5.90
6	6.5	8.1		0.243		1.05		1889	4.99
7	7.0	7.4		0.238		1.01		2036	5.90
8	7.0	7.4		0.228		0.93		2730	5.66
9	7.2	8.6		0.222		0.82		2689	8.10
10	5.5	10.1		0.218		0.79		3355	8.63
11	6.5	-		0.231		1.06		2325	4.50
12	6.5	7.0		0.265		1.00		2001	5.27
Mean									
All stations	7.45	7.6		0.234		1.03		2134	5.51
East arm	8.8	7.2		0.233		1.14		1654	4.30
West arm	6.7	8.4		0.226		0.89		2703	7.07
Open bay	6.9	7.3		0.246		1.06		2048	5.16
					20 June				
Stations									
1	5.5	8.5	-	0.124	0.161	0.483	0.512	3376	4.70
2	5.5	12.9	9.1	0.153	0.209	0.457	0.809	3952	5.54
3	6.0	7.7	6.7	0.171	0.130	0.414	1.27	3188	3.10
4	7.0	8.9	11.6	0.153	0.162	0.462	1.24	3434	3.19
5	6.0	6.4	7.7	0.179	0.199	0.429	1.23	3622	3.72
6	7.5	7.5	12.2	0.149	0.135	0.498	0.809	2500	2.74
7	5.0	11.1	10.3	0.169	0.170	0.227	1.15	5748	7.39
8	4.5	9.8	8.9	0.165	0.138	0.230	-	6388	7.77
9	5.0	12.1	9.8	0.152	0.103	0.211	1.19	6089	8.39
10	4.0	15.9	15.1	0.131	0.118	0.300	0.606	6469	13.44
11	6.5	4.8	4.4	0.159	-	0.442	0.811	3262	2.76
12	4.2	5.3	6.3	0.122	0.194	0.162	1.08	3951	7.86
Mean									
All stations	5.6	9.3	9.3	0.152	0.156	0.359	0.908	4323	5.88
East arm	6.0	9.5	9.1	0.150	0.166	0.454	0.956	3462	4.13
West arm	4.6	12.2	11.0	0.154	0.132	0.242	0.784	6173	9.25
Open bay	6.0	6.0	7.7	0.152	0.176	0.383	0.983	3334	4.27

Symbols: A = samples taken at 5-m depth; B = samples taken 1 m above bottom.

**Data from Stoermer et al. (1972).*

Samples were collected from five stations (Fig. 21): inshore and offshore Michigan, inshore and offshore Wisconsin, and southern Green Bay. Measurements of total, dissolved, and particulate phosphorus indicated major differences in nutrient concentrations between Green Bay and the other four localities, and between inshore Michigan stations and the other three locations in the Lake (Table 10). The occurrence and abundance of the four predominant species are shown in Figure 21 and summarized in Table 10. *Melosira granulata* and *Melosira binderana* were found only in Green Bay, and *Melosira ambigua* was detected only in Green Bay and at the inshore station near Michigan. *Melosira islandica* was present at all stations except Green Bay. The abundance patterns of these species indicated that the abundance of the eutrophic species *M. granulata* and *M. binderana* was greatest in Green Bay, whereas *M. ambigua* seemed to be more

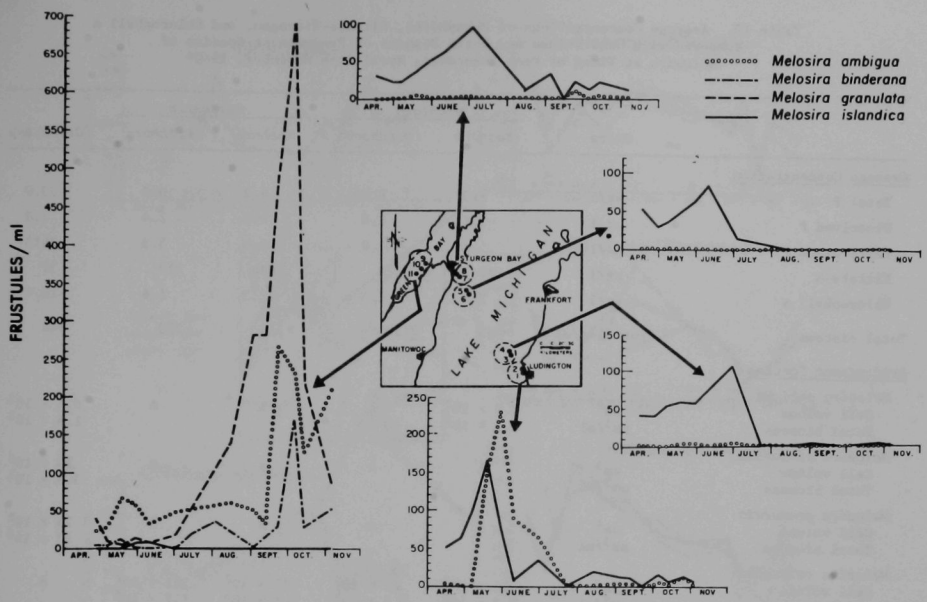

Fig. 21. Seasonal Abundance of Predominant Species of *Melosira* in Southern Green Bay and Lake Michigan, April into November 1965. Slightly modified from Holland (1968) (with permission, see credits).

abundant in eutrophic or moderately eutrophic water. *Melosira islandica* was not favored by eutrophic conditions; it was moderately abundant at all stations but absent in the bay. Holland concluded that the distributional patterns of *Melosira* apparently reflect significant differences in the trophic status of the regions investigated; Green Bay represents eutrophic conditions, whereas oligotrophic conditions prevail in offshore water and near the Wisconsin shore.

The primary objective of the second, more extensive, study (Holland, 1969) was to obtain quantitative information on seasonal variability, composition, and abundance in the same five areas (Fig. 21). Samples were collected from depths of 2, 5, and 10 m at each station, and the samples were pooled for each area. A summary of chemical measurements of phosphorus fractions, nitrate-nitrogen, and chlorophyll *a* with depth at the locations is similar to that presented in Table 10. Green Bay had extremely high concentrations of total phosphorus relative to the other locations, and inshore Lake Michigan appeared to have significantly higher concentrations than the three other locations in the Lake.

The major differences in species composition occurred between the bay and offshore locations. Principal diatoms in the Lake were *Asterionella formosa, Cyclotella michiganiana, Cyclotella glomerata-stelligera, Fragilaria crotonensis, Melosira islandica,* and *Tabellaria flocculosa*. Several species were abundant at certain times or only at some locations. *Stephanodiscus tenuis* generally was abundant in May and June near the Michigan shore. *Cyclotella bodanica-comta* was abundant at the two offshore locations.

Table 10. Average Concentrations of Phosphorus, Nitrate-Nitrogen, and Chlorophyll *a* Compared with Cell Volume and Total Biomass of Predominant Species of *Melosira* at Times of Peak Abundance, April into November, 1965*

	Units	Michigan		Wisconsin		Green Bay
		Inshore	Offshore	Inshore	Offshore	
Average Concentration						
Total P	µg/l	9.3	6.5	6.2	6.0	33.0
Dissolved P	µg/l	3.6	2.8	2.4	2.4	7.0
Particulate P	µg/l	5.5	3.9	4.0	3.3	26.3
Nitrate-N	µg/l	100	113	109	112	37
Chlorophyll *a*	µg/l	2.4	1.3	2.3	1.6	10.4
Total diatoms	frustules/ml	813	390	514	350	944
Predominant Species						
Melosira ambigua						
Cell volume	μm^3	2.9×10^2	A	A	A	6.1×10^2
Total biomass	$\mu m^3/ml$	0.7×10^5				1.6×10^5
Melosira binderana						
Cell volume	μm^3	A	A	A	A	23×10^2
Total biomass	$\mu m^3/ml$					3.8×10^5
Melosira granulata						
Cell volume	μm^3	A	A	A	A	24×10^2
Total biomass	$\mu m^3/ml$					17×10^5
Melosira islandica						
Cell volume	μm^3	25×10^2	22×10^2	25×10^2	21×10^2	A
Total biomass	$\mu m^3/ml$	4.2×10^5	2.3×10^5	2.3×10^5	1.7×10^5	

**From Holland (1968). Phosphorus and nitrate data from Allen (1966--unpublished). Chlorophyll a data (concentration at 2 m) added (Holland, 1969).*

Symbols: A = absent or uncommon.

The populations in Green Bay had several distinct characteristics. *Stephanodiscus niagarae* dominated the assemblage at nearly all times, and *Melosira granulata* was a principal species in the fall along with *Melosira binderana* and *Fragilaria capucina*. *Amphipleura pellucida*, *Amphitrora ornata*, and *Surirella* spp. (members of the benthic and periphyton communities) were more common in the bay than in the Lake.

The seasonal abundance of diatoms appeared to have one seasonal maximum in the Lake and two peaks in the bay (Fig. 22). The peaks in Green Bay occurred in spring and fall. The inshore Wisconsin location did not exhibit a pronounced peak; however, one did occur in late June at the offshore location. The two locations on the Michigan side of the Lake exhibited pronounced peaks in May (inshore) and in August (offshore). Diatom abundance, based on a comparison of average values for the five locations, was greatest in the bay, intermediate at inshore locations, and least at offshore locations.

The seasonal abundance patterns of selected diatoms are shown in Figures 23 and 24. Some of these species fluctuated so rapidly that progressive plankton phases were suggested. Rapidly declining numbers of *Cyclotella glomerata-stelligera* and *Stephanodiscus tenuis* appeared to signal the end of a late winter or early spring phase. The abundance patterns of *Tabellaria flocculosa* and *Melosira islandica* appeared as a second phase that terminated with a sudden decline in the abundance of the latter species. *Tabellaria flocculosa* was abundant along with *Asterionella formosa* and *Rhizosolenia eriensis* at offshore areas. The fourth phase was initiated by rapid increases in the

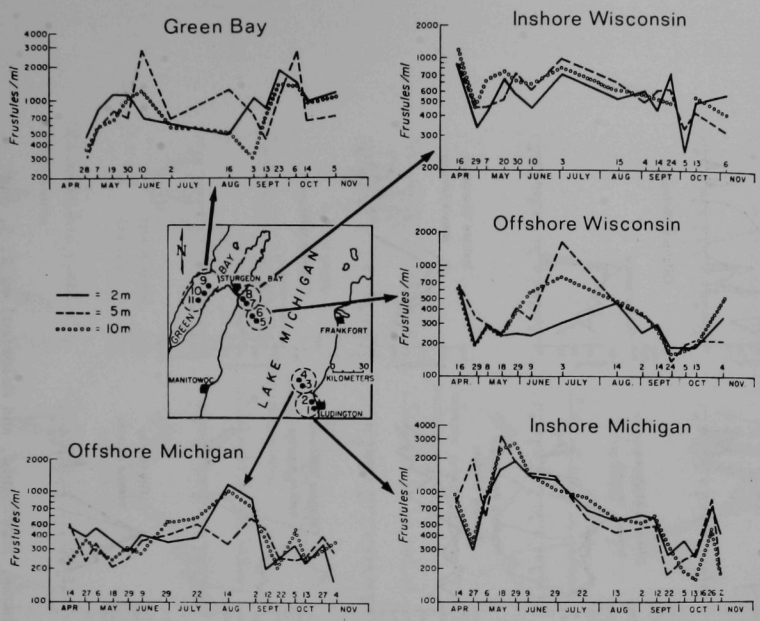

Fig. 22. Seasonal Abundance of Total Diatoms in Southern Green Bay and Lake Michigan, 1965. Sampling dates at each location are on the abscissa (Holland, 1969) (with permission, see credits).

abundance of *Cyclotella michiganiana*. In Green Bay, *Fragilaria crotonensis* and *S. tenuis* were major species in the spring peak, followed by *Fragilaria capucina* and *T. flocculosa* which dominated the summer community. *Melosira granulata* and *Melosira binderana* were restricted, occurring in high abundance only during late summer and early fall.

The third investigation was undertaken to detect differences in diatom abundance and dominant species over a transect extending from Milwaukee, Wisconsin, to Ludington, Michigan (Holland and Beeton, 1972). Five stations were established, including nearshore locations 4.8 km off Milwaukee and Ludington, one mid-lake station, and two stations located halfway between mid-lake and the inshore stations. Sampling was conducted at 10- to 14-day intervals from May 1970 to January 1971. Differences among the stations in concentrations of total and soluble phosphorus, dissolved silica, and nitrate-nitrogen are summarized in Table 11. Nutrient levels at the inshore station near Milwaukee were higher than at the other stations. The inshore station at Ludington, however, had nutrient levels similar to the offshore locations.

The abundance of dominant diatoms varied seasonally at each of the stations and with depth (*cf.* Fig. 25). In May, diatoms were more abundant at the inshore station than in the open Lake and were twice as abundant off Ludington as off Milwaukee. At this time, *Stephanodiscus hantzschii* was the major species off Ludington, and *Fragilaria crotonensis* and *Tabellaria flocculosa* were

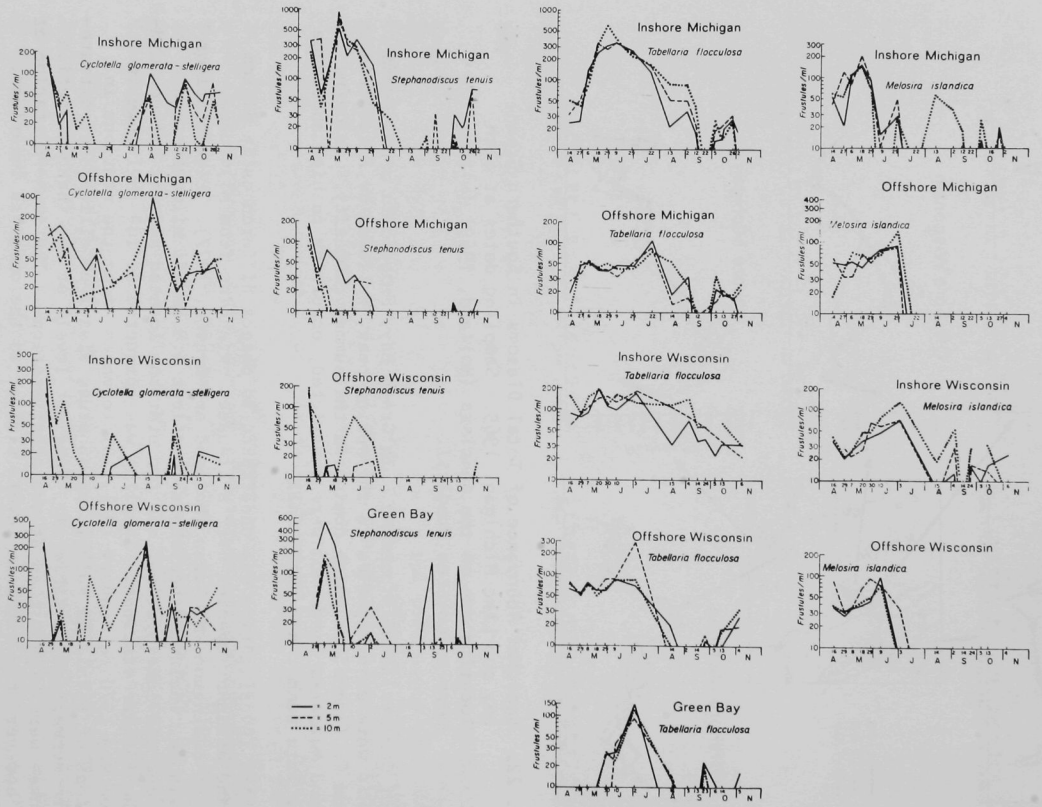

Fig. 23. Abundance of Diatoms (*Cyclotella*, *Stephanodiscus*, *Tabellaria*, and *Melosira*) at 2, 5, and 10 m at Sampling Stations in Lake Michigan and Green Bay, 1965. Collection from 10 m at inshore Wisconsin on 5 October was lost. Modified from Holland (1969) (with permission, see credits).

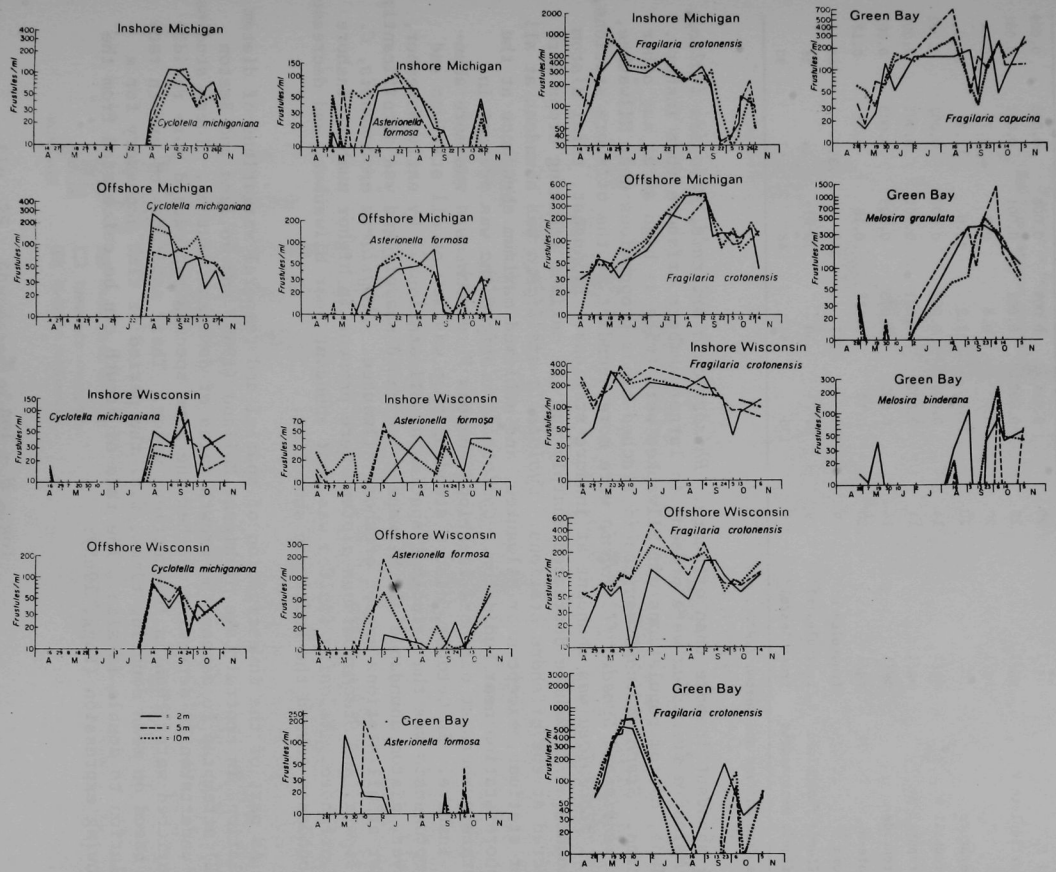

Fig. 24. Abundance of Diatoms (*Cyclotella*, *Asterionella*, *Fragilaria*, and *Melosira*) at 2, 5, and 10 m at Sampling Stations in Lake Michigan and Green Bay, 1965. Collection from 10 m at inshore Wisconsin on 5 October was lost. Modified from Holland (1969) (with permission, see credits).

Table 11. Average Values for Various Parameters from Milwaukee to Ludington, 1970-1971*

Parameter	Units	Number of Samples	Stations 1	2	3	4	5
Total P	mg/l	20	0.014	0.009	0.008	0.008	0.009
Nonparticulate P	mg/l	20	0.002	0.001	0.001	0.001	0.001
SiO_2	mg/l	20	0.7	0.8	0.8	0.7	0.6
Temperature	°C	20	11.8	12.2	12.0	12.3	14.0
Chlorophyll *a*	mg/l	14	0.004	0.002	0.002	0.002	0.002
Chlorophyll *c*	mg/l	14	0.002	0.001	0.001	0.001	0.001
Carotenoids	mg/l	14	0.005	0.003	0.003	0.003	0.003
Nitrate-N	mg/l	20	0.18	0.18	0.18	0.18	0.17
Diatoms	frustules/ml	9	753	345	362	353	445
Tabellaria flocculosa	frustules/ml	9	84	30	19	14	56
Fragilaria crotonensis	frustules/ml	9	138	84	48	47	90

*Data from Holland and Beeton (1972).

more abundant inshore than offshore. *Rhizosolenia eriensis*, *Melosira italica*, and *Melosira islandica* were present in larger numbers offshore than inshore. By June, diatom populations off Milwaukee were twice as high as at any other station. *Stephanodiscus hantzschii* reached bloom proportions near Milwaukee, *R. eriensis* and *Synedra filiformis* were more abundant at the offshore stations, and *T. flocculosa* was abundant at inshore stations. By August, total diatom abundance at Milwaukee decreased sharply and the maximum standing crops were detected at the offshore stations. *Cyclotella stelligera* was abundant at all other stations, except near Milwaukee, and achieved maximum abundance at the offshore station near Ludington. *Cyclotella michiganiana* was present in moderate numbers at offshore locations whereas *F. crotonensis* was more abundant inshore. In October, diatom standing crop was low at all stations and *F. crotonensis* was the principal species at all stations. By early November, however, diatom abundance off Milwaukee increased sharply and was significantly higher at all stations except offshore Milwaukee. *Fragilaria crotonensis*, *C. stelligera*, and *Stephanodiscus alpinus* were present in higher numbers inshore than offshore. *Melosira italica* was most abundant near Milwaukee, and decreased in abundance toward the Ludington shoreline.

As part of the investigation of spatial and temporal variations of diatom populations in central Lake Michigan, Holland (1969) and Holland and Beeton (1972) attempted to assess the growth rates of dominant diatoms. These studies were undertaken to determine whether the same species reproduced more rapidly in enriched water than in low-nutrient water. Their estimates of growth rate were based on mean doubling times, *i.e.* the period of time necessary for a population to double in size. The rate of growth can be calculated from the following expression (Fogg, 1965):

$$k = \frac{\log_{10} N - \log_{10} N_o}{t}, \qquad (3)$$

where k is the relative growth constant, N_o the number of cells at time zero, and N the size of the population at time t. The mean doubling time (which

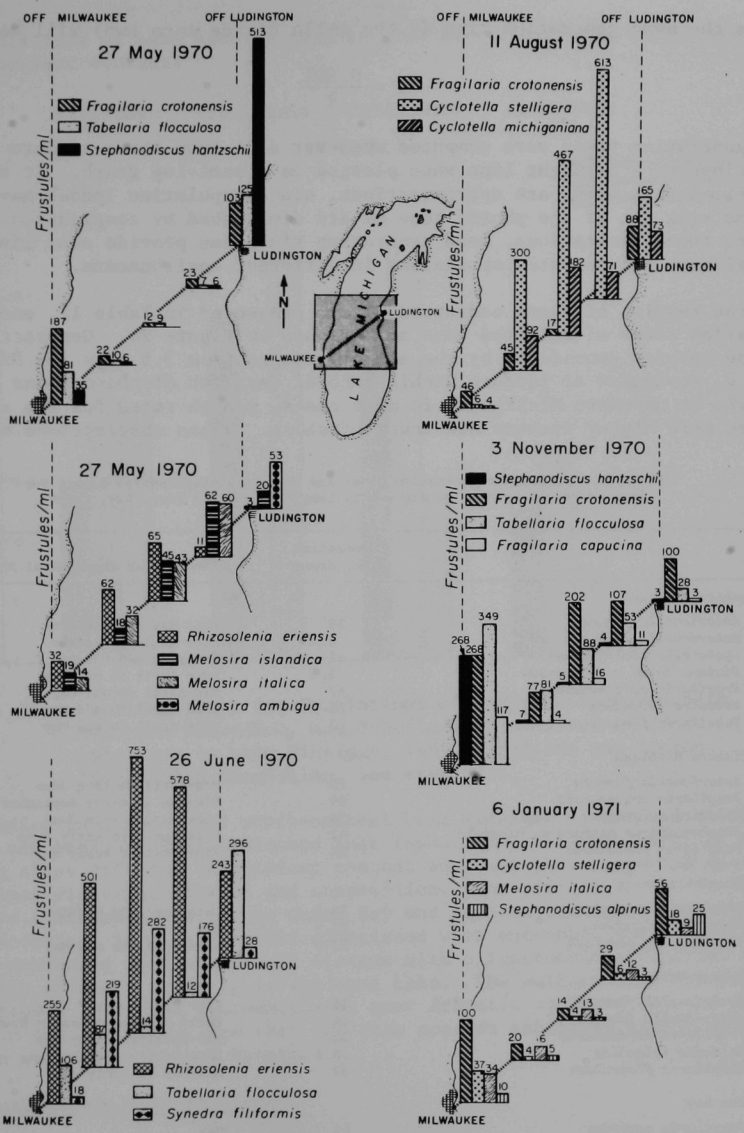

Fig. 25. Abundance of Predominant Diatom Species at Five Stations along the Milwaukee-Ludington Transect (Holland and Beeton, 1972) (with permission, see credits).

equals the mean generation time if the cells divide into two) will be:

$$G = \frac{0.301}{k} . \tag{4}$$

Mean generation times were computed whenever data from three or more samples were close to a straight line when plotted on a semi-log graph. It should be emphasized that these are approximations, since population losses may occur if diatoms sink out of the photic zone or are diminished by zooplankton grazing. Despite these limitations, mean generation times can provide some insight into the relative growth rates of diatoms in different environments.

The results of these computations are presented in Table 12, and the generation times of selected taxa are graphed in Figure 26. Generation times for the species considered by the authors ranged from 3.5 days for *Diatoma tenue* v. *elongatum* at inshore Michigan to 42 days for *Stephanodiscus astrea* v. *minutula* at offshore Michigan. In most cases, growth rates for the same species were higher inshore and lower offshore. These observations demonstrate

Table 12. Approximate Generation Times and Seasons of Exponential Growth for Some Principal Species of Diatoms in Lake Michigan and Green Bay, 1965*

	*Generation Time, days***	*Seasons of Exponential Phase*
Inshore Michigan		
Asterionella formosa	19	Late May to late June
Asterionella formosa	6.5	Mid- to late October
Cyclotella michiganiana	18	Early to mid-October
Diatoma tenue v. *elongatum*	3.5	Late April to mid-May
Fragilaria crotonensis	12	Mid-April to mid-May
Melosira islandica	16	Late April to mid-May
Tabellaria flocculosa	7	Late April to mid-May
Offshore Michigan		
Asterionella formosa	15	Mid-April to late June
Fragilaria crotonensis	29	Mid-May to early September
Melosira islandica	34	Late May to late June
Stephanodiscus astraea v. *minutula*	42	Late April to early June
Tabellaria flocculosa	13	Mid-April to early May
Inshore Wisconsin		
Fragilaria crotonensis	14.5	Late April to mid-May
Melosira islandica	21.5	May
Tabellaria flocculosa	20.5	Late April to mid-May
Offshore Wisconsin		
Asterionella formosa	11	Late May to early July
Asterionella formosa	14	Early October to early November
Fragilaria crotonensis	28	Mid-April to early May
Melosira islandica	28.5	Late April to early June
Tabellaria flocculosa	33	Mid-May to early July
Green Bay		
Fragilaria capucina	15	May
Fragilaria crotonensis	10.5	Late April to early June
Melosira ambigua	14	Late April to mid-May
Melosira granulata	19	Mid-August to early October
Stephanodiscus niagarae	34	Mid-August to late September
Tabellaria flocculosa	13	Late May to early July

*Data from Holland (1969).

**Average of values for 2, 5, and 10 m.

that populations of some species tend to grow more rapidly in areas with higher nutrient content.

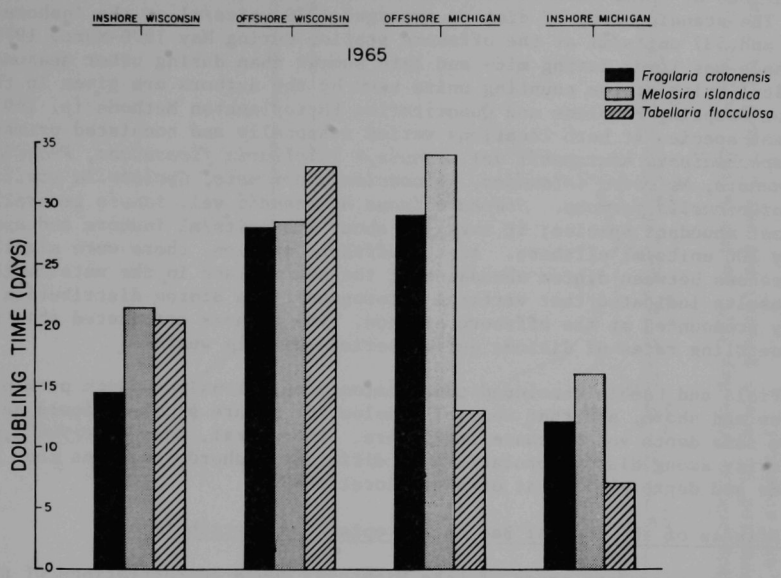

Fig. 26. Doubling Times for Populations of *Fragilaria crotonensis*, *Melosira islandica*, and *Tabellaria flocculosa* at Four Locations in Lake Michigan, 1965. (Holland and Beeton, 1972) (with permission, see credits).

Studies in central and north-central Lake Michigan by Holland (1969) and Holland and Beeton (1972) indicated that inshore and offshore water at the sampling sites differed in nutrient content and that they supported diatom assemblages differing in size and composition. The effects of nutrient enrichment were confined primarily to Green Bay and inshore stations, especially near Wisconsin. Species normally associated with eutrophic environments frequently dominated in these areas; diatoms with oligotrophic affinities were moderately abundant primarily in the open Lake. The authors also concluded that extremes in diatom abundance were more dramatic in Green Bay and inshore Wisconsin than offshore, and that the same species exhibited higher growth rates in nutrient-enriched waters.

Southwestern Lake Michigan

Information on seasonal variations of diatoms in southwestern Lake Michigan has been generated by the Nalco Chemical Company. These studies, conducted by Piala and Lamble (1971), Gulo and Lamble (1971), and Huh *et al.* (1972), were designed to monitor inshore and offshore water near the power plants at Waukegan and Zion, Illinois. Some of the data dealing specifically with diatoms is presented here; additional information on the phytoplankton is discussed below (see subsection on Southern Lake Michigan, p. 72).

The data of Piala and Lamble (1971) are of particular interest because they include detailed quantitative data on the seasonal variability of diatom populations at three inshore stations and at an offshore station (Figs. 27 and 28). The standing crop of diatoms averaged 1770 units/ml at the inshore stations and 537 units/ml at the offshore station during May 1970-March 1971. Abundance was lower during mid- and late summer than during other seasons. The numerical value of the counting units used by the authors are given in the section on Sampling Problems and Quantitative Phytoplankton Methods (p. 169). The dominant species at both locations varied seasonally and consisted primarily of *Stephanodiscus hantzschii* vel. *tenuis*,* *Tabellaria flocculosa*, *Fragilaria crotonensis*, *Melosira islandica*, *Rhizosolenia eriensis*, *Cyclotella stelligera*, and *Asterionella formosa*. *Stephanodiscus hantzschii* vel. *tenuis* generally was the most abundant species; it averaged about 700 units/ml inshore and approximately 100 units/ml offshore. At the offshore station, there were significant differences between diatom abundance at the surface and in the metalimnion. The results indicated that vertical heterogeneity in diatom distribution was highly pronounced at the offshore station. The authors attributed this to high settling rates of diatoms during periods of calm weather.

Piala and Lamble concluded that diatom populations vary with proximity to surface and shore, and that control samples for future studies should be taken at the same depth and distance from shore. In general, they observed a greater similarity among diatom populations at different inshore locations than between surface and depth samples at offshore locations.

Effects of the Thermal Bar on Phytoplankton Distribution

In some nearshore areas of Lake Michigan, dense concentrations of phytoplankton frequently discolor the water during spring and early summer. In certain areas this phenomenon is attributed to nutrients entering the Lake from streams and rivers. In other situations, however, the presence of a thermal bar (Rodgers, 1965) may contribute to the development of dense algal concentrations. A thermal bar can form in spring when shallow inshore water warms more rapidly than offshore water. Due to differences in density, mixing of the cold offshore water with the warmer inshore water may be markedly decreased. Nutrient loadings from tributaries and surface runoff during spring, therefore, are trapped landward of the thermal bar. The presence of elevated nutrient concentrations in rapidly warming inshore water promotes rapid phytoplankton growth (Stoermer and Kopczynska, 1967).

Stoermer (1968) conducted a preliminary investigation of the thermal bar effect near Grand Haven, Michigan. Phytoplankton samples were taken by vertical net tow on 28 and 29 April 1967. Visible differences in water color were supported by Secchi-disc measurements, and the location of the thermal bar was detected by measurements on surface-water temperature. Transparency was low nearshore and gradually increased offshore (Fig. 29a). Water temperature ranged from 8.0°C near shore to 3.0°C just beyond the bar (Fig. 29b).

**The nomenclatural term* vel. *is used to denote the fact that two morphologically distinct species were recorded in quantitative analysis as a single counting category. This is similar to the convention used by Holland (1969) (see p. 49 of this manuscript).*

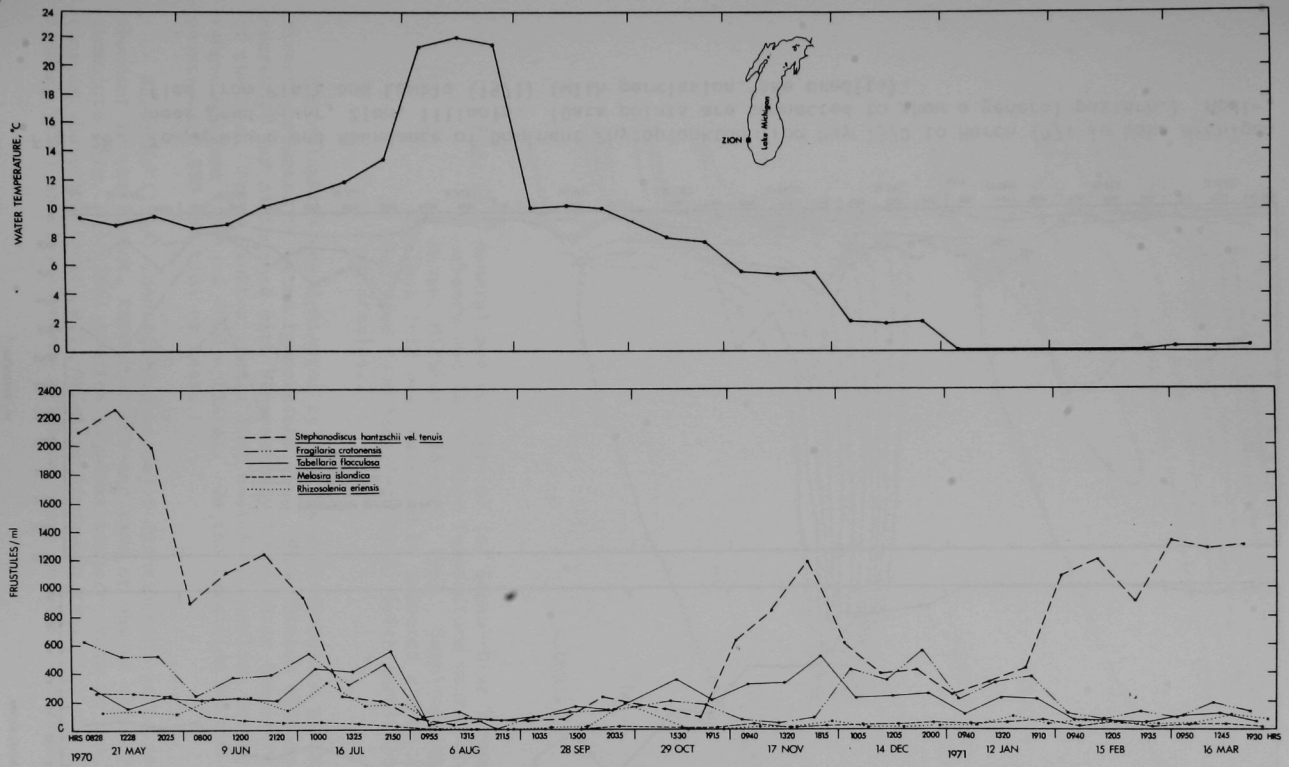

Fig. 27. Temperature and Abundance of Dominant Phytoplankton from May 1970 to March 1971 in Lake Michigan near Zion, Illinois. (Data points are connected to show a general pattern.) Modified from Piala and Lamble (1971) (with permission, see credits).

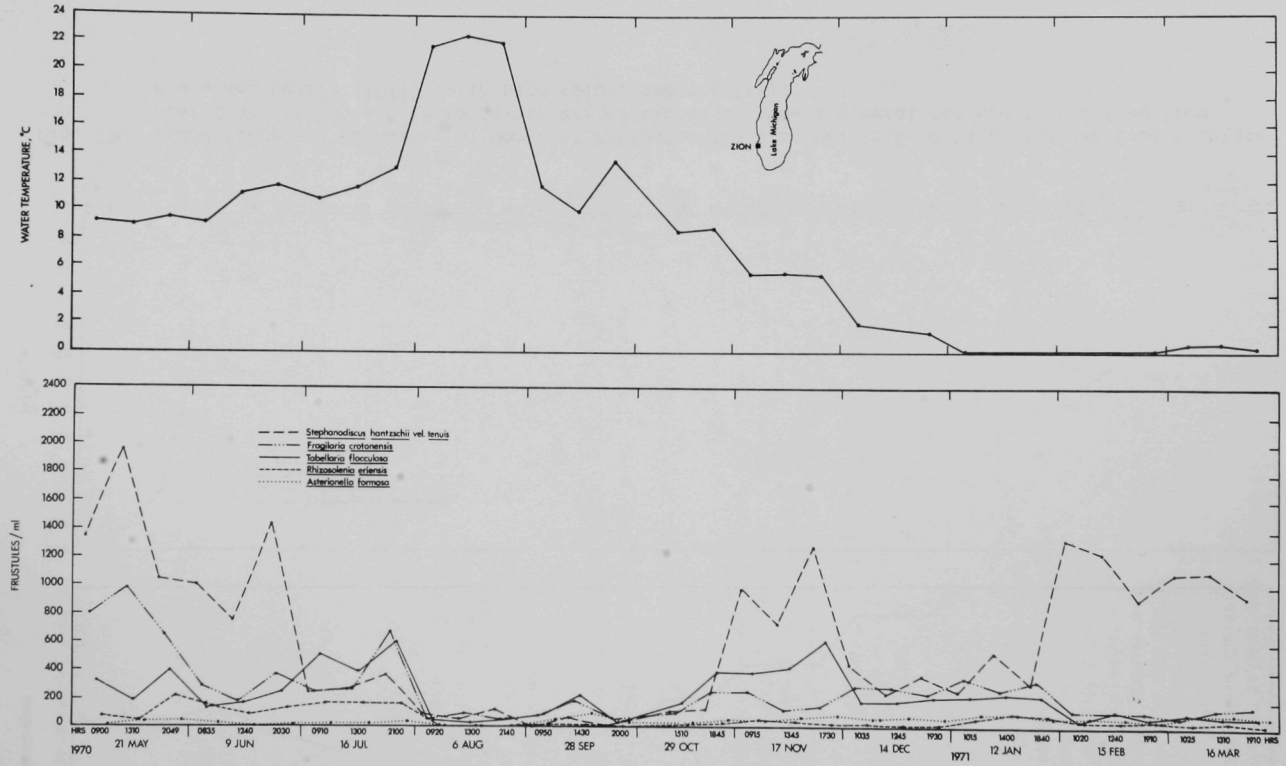

Fig. 28. Temperature and Abundance of Dominant Phytoplankton from May 1970 to March 1971 in Lake Michigan near Dead River, Zion, Illinois. (Data points are connected to show a general pattern.) Modified from Piala and Lamble (1971) (with permission, see credits).

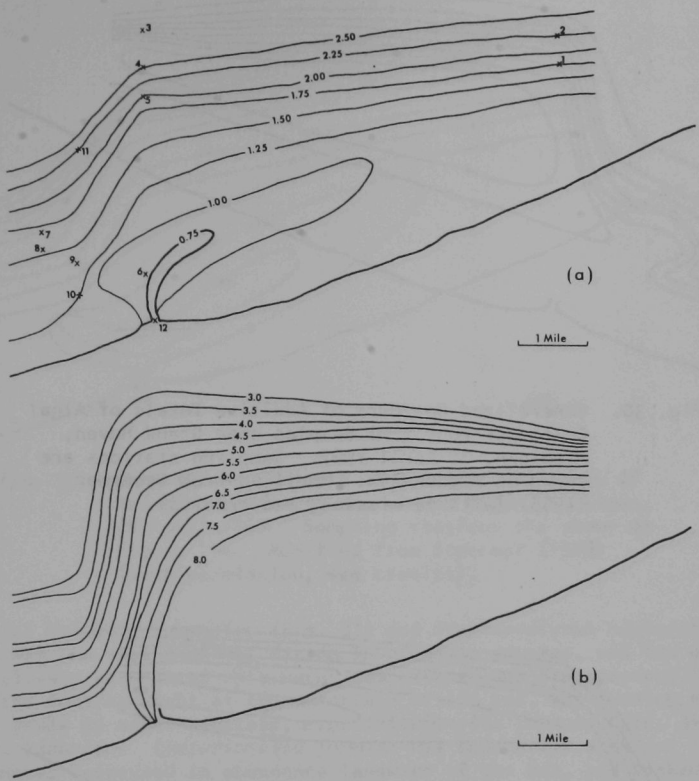

Fig. 29. Generalized Contours of (a) Secchi-Disc Transparency and (b) Surface Temperature near Grand Haven, Michigan, 28 April 1967. Sampling stations 1-12 are indicated by numbered *x's* on (a). Modified from Stoermer (1968) (with permission, see credits).

Phytoplankton was dominated by diatoms with abundance patterns that were directly related to water temperature (Fig. 30). Diatom abundance was greatest nearshore and diminished with successively lower water temperatures lakeward of the bar. Phytoplankton counts from nearshore sampling points generally ranged between 1500 and 2000 cells/ml. On the lake side of the bar, however, counts were 350 cells/ml or less.

Stoermer (1968) identified four major distribution patterns: (*i*) species abundant in the harbor, rare inshore, and rare or absent offshore, *e.g. Melosira granulata* (Fig. 31); (*ii*) species abundant inshore, rare in the harbor, and rare or absent offshore, *e.g. Melosira binderana* (Fig. 32) and *Stephanodiscus tenuis*; (*iii*) species abundant offshore, rare inshore, and absent in the

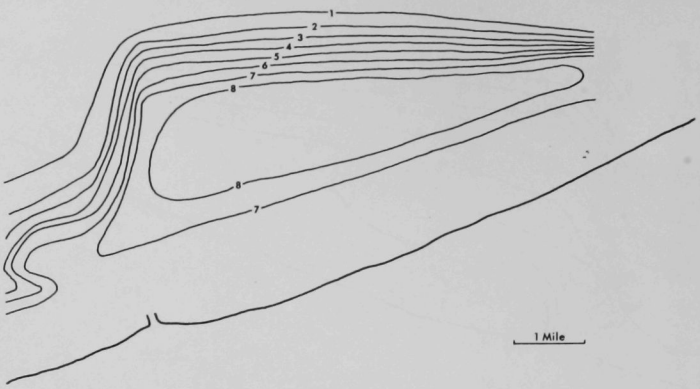

Fig. 30. Generalized Contours of Additive Totals of Algal Cells per Four 1-ml Samples near Grand Haven, Michigan, 28 April 1967. Sampling stations are shown on Figure 29a. Modified from Stoermer (1968) (with permission, see credits).

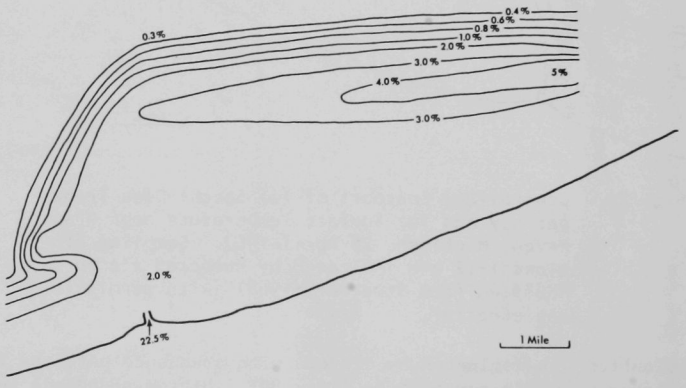

Fig. 31. Generalized Contours of Relative Abundance of *Melosira granulata* near Grand Haven, Michigan, 28 April 1967. Sampling stations are shown on Figure 29a. Modified from Stoermer (1968) (with permission, see credits).

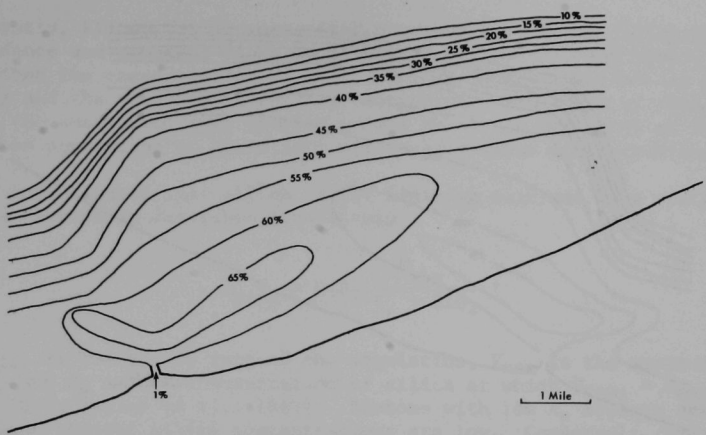

Fig. 32. Generalized Contours of Relative Abundance of *Melosira binderana* near Grand Haven, Michigan, 28 April 1967. Sampling stations are shown on Figure 29a. Modified from Stoermer (1968) (with permission, see credits).

harbor, *e.g. Melosira islandica* (Fig. 33) and *Stephanodiscus hantzschii*. (*M. islandica* was the most abundant diatom in offshore samples, and its distribution was closely correlated with water temperature and transparency.); and (*iv*) species most abundant at the interface of the bar, but showing secondary abundance peaks in other habitats, *e.g. Asterionella formosa* (Fig. 34) and *Fragilaria capucina*. (*Asterionella formosa* was moderately abundant in the river channel, decreased in abundance landward of the bar, and peaked at the interface. *Fragilaria capucina* showed a similar pattern but was less abundant than *A. formosa*.)

Although nutrient concentrations were not measured, Stoermer (1968) attributed species abundance patterns to entrapment of nutrient-rich water landward of the thermal bar, and suggested that temperature effects probably were of secondary importance. He also indicated that the thermal-bar environment is a dynamic system, and that more extensive studies on phytoplankton are needed before the phenomenon can be understood thoroughly. The reader is referred to Mortimer (1975; pp. 51-54) for further discussion of the thermal bar.

Ambient Concentrations of Silica and the Growth of Diatoms

Spatial and temporal variations of diatom abundance in Lake Michigan are undoubtedly controlled by numerous physical, chemical, and biological variables, including light intensity and temperature, concentrations of major and minor nutrients, and biotic interactions such as parasitism, grazing, and external metabolite secretions. It is highly unlikely that a single environmental variable controls or regulates spatial patterns or seasonal abundance of diatoms. Because diatoms, unlike other species of algae, have an absolute requirement for silica (Jørgensen, 1957; Lewin, 1962), it is pertinent to consider the importance of silica as a principal factor in determining seasonal abundance patterns and dominance in plankton communities.

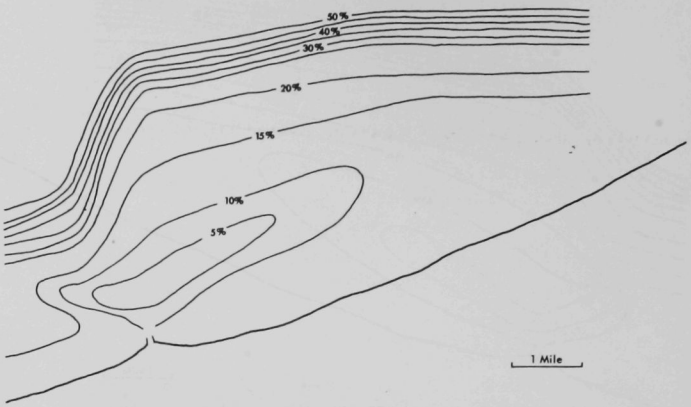

Fig. 33. Generalized Contours of Relative Abundance of *Melosira islandica* near Grand Haven, Michigan, 28 April 1967. Sampling stations are shown on Figure 29a. Modified from Stoermer (1968) (with permission, see credits).

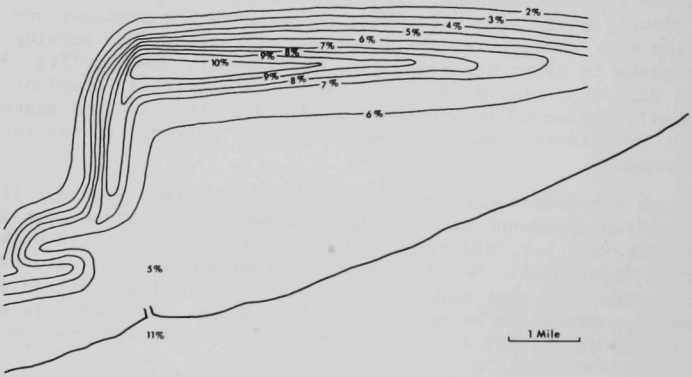

Fig. 34. Generalized Contours of Relative Abundance of *Asterionella formosa* near Grand Haven, Michigan, 28 April 1967. Sampling stations are shown on Figure 29a. Modified from Stoermer (1968) (with permission, see credits).

Recently, Kilham (1971) summarized numerous reports on diatom distribution and abundance and concentrations of dissolved silica in fresh water. He postulated that the concentration of silica may be highly important in determining dominance and the sequence of species succession. The basis of these arguments rests on the assumption that species growth rates are dependent on the ability of a diatom population to assimilate silica at various concentrations.

If it is assumed that silica is the limiting nutrient in a system, the following expression describes growth rate:

$$V_{SiO_2} = SiO_2 \frac{V_{max}}{K_s + SiO_2}, \qquad (5)$$

where V_{SiO_2} is the growth rate of the population, V_{max} is the maximum uptake velocity, and K_s is the concentration of silica at which $V_{SiO_2} = V_{max/2}$ (*cf.* Dugdale, 1967; Eppley *et al.*, 1969). Diatoms with low K_s replace species with high K_s when ambient silica concentrations are low. Conversely, species with high V_{max} would successfully compete with a species having a lower V_{max} value when silica concentrations are high. This equation has been successfully applied to studies on nutrient uptake and growth kinetics of several species of diatoms (*cf.* Paasche, 1973a, 1973b; Guillard *et al.*, 1973).

Schelske and Stoermer (1972) indicated that Kilham's scheme relating silica concentrations and diatom distribution is not directly applicable to the Great Lakes. Mean concentrations of silica as high as 13.4 mg SiO_2/l cited for *Melosira granulata* by Kilham do not occur in Lake Michigan. *Melosira granulata* and *M. granulata* v. *angustissima* do, however, occur as major species in the plankton of the Lake, but they are indicative of eutrophic water and not of incipient eutrophication as postulated by Kilham.

Kilham's scheme apparently does not apply directly to diatom distribution in the Lake; however, the hypothesis could be reinvestigated. Concentrations of dissolved silica in Lake Michigan normally are less than 3.0 mg/l, and frequently during summer are reduced to levels less than 0.05 mg/l inshore and in open water of the southern basin. It is necessary, therefore, to evaluate the large body of existing information on diatom abundance and silica concentrations in the Lake. Such a concerted effort has not been made yet. If it is found that certain diatoms achieve maximum abundance in eutrophic, low-silica environments, whereas others achieve maximum abundance in oligotrophic, high-silica environments, a basis would be provided for interpreting some aspects of spatial and temporal patterns of diatom abundance in Lake Michigan. This hypothesis and the importance of phosphorus and nitrogen are discussed in detail in a following section--Phosphorus, Silica, and Eutrophication (p. 114).

SPATIAL AND TEMPORAL VARIATIONS IN THE STANDING CROP AND COMPOSITION OF PHYTOPLANKTON

There has been a wide variety of investigations of total phytoplankton in Lake Michigan. The information presented here is divided arbitrarily into three sections: (*i*) a treatment of three early nearshore studies in southern Lake Michigan, (*ii*) a synopsis of long-term studies at the water treatment plants at Chicago and Milwaukee, and (*iii*) several independent studies arranged primarily by geographic location.

Early Studies in Southern Lake Michigan

The earliest quantitative studies of inshore phytoplankton, aside from those of Eddy (1927, 1934), were conducted at the breakwater near Northwestern University by Daily (1938) and Damann (1941). Daily's work was carried out in 1937 and 1938, and was continued by Damann during 1938 and 1939. The same site was studied again by Griffith (1955) in 1953 and 1954. The first two studies are of historical interest because they provide continuous data from a single station over a two-year period. They also illustrate the difficulties encountered when different methods are used to concentrate algae and to express quantitative data. Griffith's investigation is of particular interest because it was the first report indicating that a blue-green algal community dominated the plankton in Lake Michigan. The important results of each investigation are presented in the following text.

Daily (1938) examined samples taken at weekly intervals from the breakwater. Plankton was concentrated by drawing water through a sand filter, and was counted by the Sedgewick-Rafter method (APHA, 1960). Daily also recorded temperature of the surface water, hours of sunshine, turbidity, and bacterial counts.

The distribution of phytoplankton in 1937 and 1938 is shown in Figure 35. Variation in abundance ranged from a minimum of 152 individuals/ml in March to a maximum of 3688 individuals/ml in June. The plankton exhibited a pronounced bimodal curve with a large spring peak and a smaller fall maximum, and was dominated by diatoms. The peaks in spring and fall were composed of *Synedra* spp., with smaller maxima of the diatoms *Asterionella, Fragilaria, Melosira*, and *Tabellaria* occurring during the year. Golden-brown, blue-green and green algae, and dinoflagellates were present occasionally but in relatively small quantities.

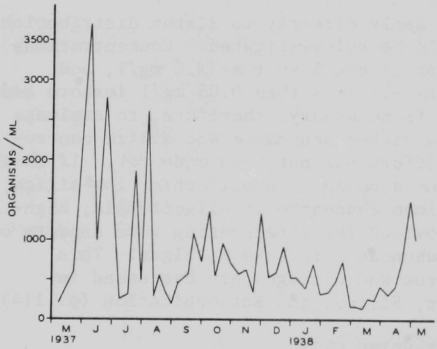

Fig. 35.

Seasonal Distribution of Phytoplankton in Lake Michigan at Evanston, Illinois, May 1937 to May 1938 (originally from Daily, 1938). From Davis (1966) (with permission, see credits).

Damann (1941) continued Daily's study on the assumption that seasonal fluctuations in plankton may vary from year to year, so that observations made in one year may not characterize the sampling site during the following year. Damann sampled the same breakwater at weekly intervals from 1 November 1938 through 1 November 1939. Plankton was concentrated and enumerated by methods similar but not identical to those of Daily. Damann observed two major abundance peaks. The spring maximum occurred on 9 May (1052 organisms/ml), and a

smaller fall peak developed in November. Standing crop was lowest on two days in March (81 organisms/ml). Diatoms dominated every collection, averaging 94% of the community. Golden-brown, blue-green and green algae, and dinoflagellates always were less than 5% of the assemblage. Diatom populations reached their maximum abundance at different times: *Asterionella* and *Cyclotella* in November, *Synedra* in May, and *Fragilaria* and *Tabellaria* in June and July.

A comparison of the investigations indicates that seasonal abundance trends were similar, but that average monthly values in 1937 and 1938 were about twice as large as those observed in 1938 and 1939 (Fig. 36). Damann attributed this discrepancy largely to a change in the annual abundance of *Synedra* between sucessive years. Although *Synedra* constituted a significant percentage of the plankton during the second year, monthly averages were only a fraction of those observed in 1937 and 1938. Based on these results, Damann concluded that the second year was a *deficient* one with respect to plankton production.

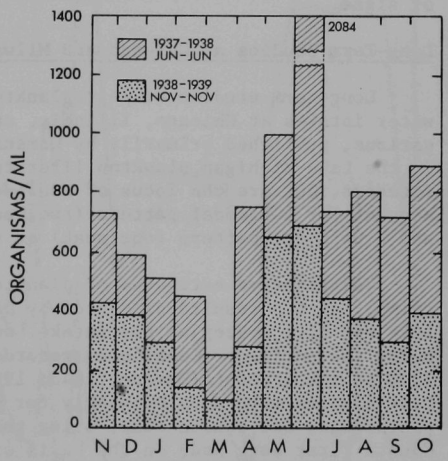

Fig. 36.

Comparison of Phytoplankton Abundance in 1937-1938 (Daily, 1938) with Phytoplankton Abundance in 1938-1939 (Damann, 1941), at Evanston, Illinois. Slightly modified from Damann (1941) (with permission, see credits).

Damann also speculated that methods of plankton concentration and enumeration could give rise to different values and, thus, account for part of the discrepancy. He investigated the effects of suction filtration versus natural settling on the quantitative recovery of plankton and found relatively good agreement between the methods. Standing crop estimates based on counts of unconcentrated samples were an order of magnitude higher than those derived from sand filtration. Damann concluded that if the counting methods gave similar results, each genus has years of high and low productivity, and that such variability has a pronounced effect on the total annual yield of phytoplankton. Both investigators concluded that temperature undoubtedly has a pronounced effect on plankton growth, but it is probably not the only factor controlling spatial and temporal variations in phytoplankton abundance.

Griffith's (1955) investigation was conducted from April 1953 to April 1954. Phytoplankton was concentrated by a Foerst continuous-flow centrifuge and counted by the Sedgewick-Rafter method (APHA, 1960). Counts were expressed by a unit method proposed by Wright and Tidd (1933) and are discussed in the

section on Sampling Problems and Quantitative Phytoplankton Methods (p. 169). Observations also were made on temperature, pH, turbidity, oxygen concentration, and bicarbonate and carbonate alkalinity.

The phytoplankton exhibited a single major peak in spring (4507 units/ml in June), followed by five minor peaks during the year. Minimum abundance was noted in January (Fig. 37). Sixty genera were identified in the study; the most important groups were blue-green, green, and golden-brown algae. The most significant observation, however, was that the plankton was dominated by blue-green algae. *Anacystis*,* a small coccoid alga, was present in nearly every sample and was dominant during most months (Fig. 37). Griffith encountered difficulties in correlating physical and chemical parameters with standing crop and with phylum yields of plankton. She noted an inverse relationship between turbidity and phytoplankton yield, and concluded that temperature cannot be directly correlated with seasonal variations in abundance of individual groups of algae.

Long-Term Studies at Chicago and Milwaukee

Long-term studies of phytoplankton abundance were conducted at municipal water intakes at Chicago, Illinois, and Milwaukee, Wisconsin. These investigations, published primarily by Damann (1945, 1960, 1966), are cited frequently in the Lake Michigan plankton literature. They not only are of historical interest, but are the focus of considerable discussion concerning factors that account for a bimodal pattern (two peaks) of plankton abundance at one location and a unimodal pattern (one peak) at the other.

Quantitative estimates of plankton at Chicago were made at several intake cribs, but the results presented by Damann are limited to Four Mile Crib. The Lake was 11.6 m deep at the intake, and water was drawn from a depth of 9.1 m below the surface. Continuous records on plankton abundance are available from 1928 to the present (Damann, 1945; 1960; 1966; 1975--personal communication). Five samples were counted weekly for green and blue-green algae, diatoms, protozoans, and crustaceans, using the Sedgewick-Rafter method (APHA, 1960). Counts first were made on the basis of *numbers* and later on *cell volume*.

At Milwaukee, water depth at the intake crib was approximately 20.4 m; water entered the crib from a point about 16.8 m below the surface. In 1958, workers at the plant adopted the method of clump count instead of continuing to use the areal standard unit; therefore, it is not possible to draw inferences about the absolute size of the standing crop at the two locations, but reasonably valid comparisons on a relative basis can be made.

Seasonal periodicity at monthly intervals between 1928 and 1945 at Chicago is shown in Figure 38. Plankton abundance follows a bimodal curve, with a spring maximum normally occurring in April, May, or June. The fall peak usually appears in October or November, but in some years it develops as late as December. The relative magnitude of the fall maximum generally tends to be

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**Species of Anacystis are small coccoid or ellipsoid cells ranging from 2 to 4 μm in greatest dimension. Although one or more species of this genus dominated the plankton numerically, it is unlikely that population biomass exceeded the combined total biomass of all other populations in the samples.*

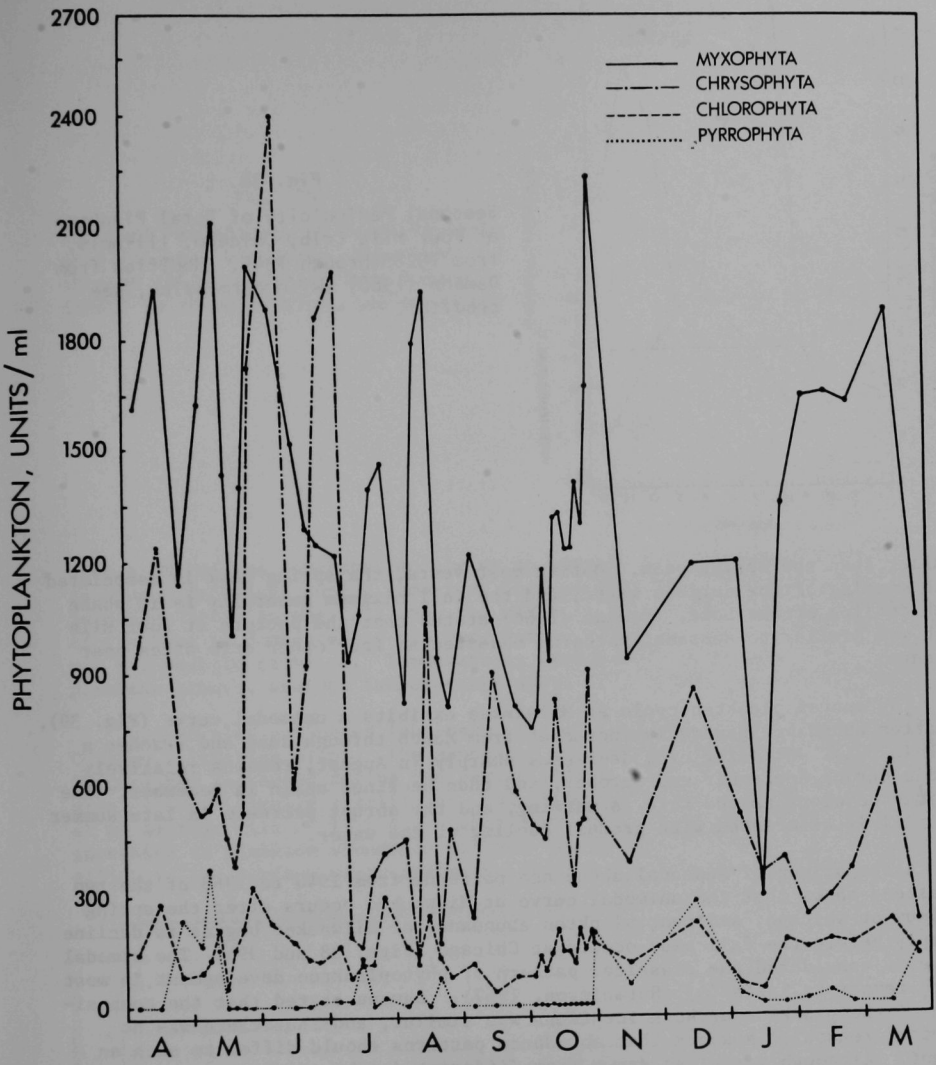

Fig. 37. Graphs Showing Phylum Yields for Each Collection. Modified from Griffith (1955) (with permission, see credits).

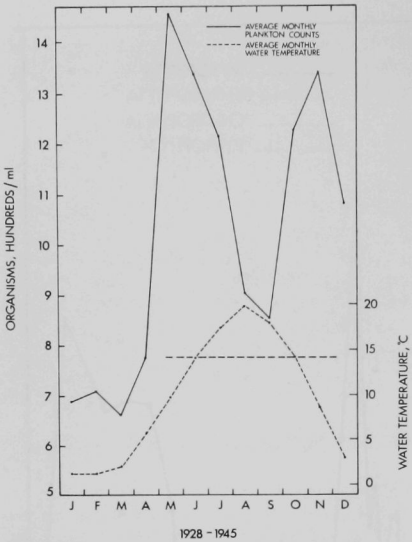

Fig. 38.

Seasonal Periodicity of Total Plankton at Four Mile Crib, Chicago, Illinois, from 1928 through 1945. Modified from Damann (1966) (with permission, see credits).

smaller than the spring peak. During most years, the spring peak is associated with warming of the surface water, and the fall maximum generally is in phase with cooling of the Lake. Damann (1966) stated that the pattern at Four Mile Crib was similar to seasonal patterns observed at four other crib sites near Chicago.

The annual plankton cycle at Milwaukee exhibits a unimodal curve (Fig. 39). Plankton abundance generally increases from March through June and reaches a peak in July. Standing crop decreases sharply in August, remains relatively stable during September and October, and then declines again in December. The maximum develops as the Lake is warming, and the abrupt decrease in late summer and fall is associated with gradual cooling of the water.

A comparison of seasonal abundance patterns from 1940 to 1963 at the two locations shows that the unimodal curve at Milwaukee occurs after the spring maximum at Chicago, and that plankton abundance at Milwaukee begins to decline sharply before the fall peak occurs at Chicago (Figs. 38 and 39). The bimodal curve is considered the classical pattern of phytoplankton development in most north-temperate lakes (*cf.* Hutchinson, 1967). Damann stated that the composition of the plankton at both locations was similar, and that there was no *a priori* reason to suspect that abundance patterns should differ to such an extent. Although water was drawn from different depths at the two stations, Damann believed that water temperature was a principal factor controlling plankton periodicity at both locations.

Water temperatures differ considerably at the two intakes. Summer maxima at both stations are reached in August, but the monthly average temperature at Chicago is 20°C, whereas it is only 12.5°C at Milwaukee. At Chicago, the spring maximum is reached in May at an average temperature of 10°C. The fall peak is reached when the average temperature is 8.7°C. Similarly, the summer

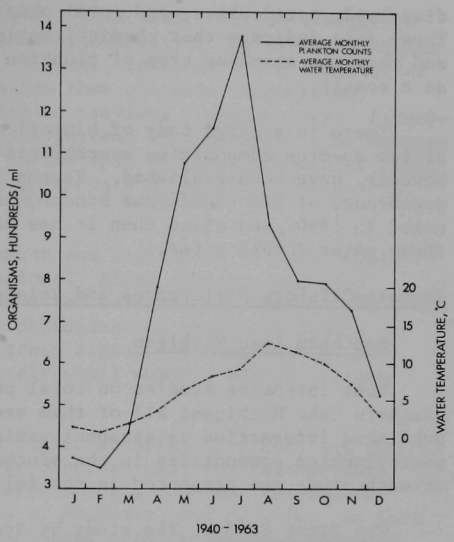

Fig. 39.

Seasonal Periodicity of Total Plankton at Milwaukee, Wisconsin, from 1940 through 1963. Modified from Damann (1966) (with permission, see credits).

peak at Milwaukee develops in July at an average temperature of 9.4°C. Plankton abundance decreases during summer at Chicago when temperatures exceed 10°C and increases again in the fall when the water cools to 10°C. Since the plankton of the Lake is dominated by diatoms, Damann claimed that a temperature of 10°C was a threshold stimulus. Temperatures approaching this value lead to rapid plankton growth, whereas temperatures above 10°C inhibit plankton growth.

Damann also evaluated long-term changes in plankton abundance at the Chicago filtration plant. The abundance of plankton in inshore water near Chicago has increased during the period 1926 to 1958 (Fig. 40). This regression is statistically significant, and indicates that plankton is increasing at an average rate of 13 ± 4.6 organisms/ml/yr. These trends of progressive increases in plankton abundance are associated with depletion of dissolved silica in the surface water and with increases in the concentration of

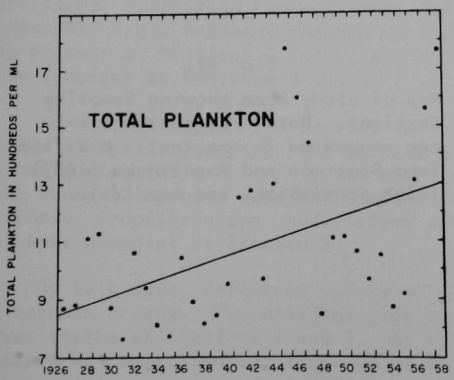

Fig. 40.

Regression of Annual Average Total Plankton Abundance against Year of Collection in Lake Michigan at Chicago, Illinois, from 1928 through 1958. The increase of total plankton with time was significant ($b = 13.06 \pm 4.6$, $t = 2.81$, $p < .01$). Slightly modified from Damann (1960) (with permission, see credits).

dissolved, particulate, and total phosphorus (*cf.* Powers and Ayers, 1967). These data indicate that chemical enrichment of inshore water has occurred, and that the standing crop of plankton apparently has increased significantly as a result.

There is a large body of historical information on qualitative changes in diatom species composition assemblages at the intakes. Few of these data, however, have been published. Vaughn (1961, 1962) has reported on the recent appearance of *Stephanodiscus binderanus*. This eutrophic diatom was first noted in 1960, and since then it has caused serious clogging of filters at these water intake sites.

Inshore-Offshore Differences and Related Phenomena

Southern Lake Michigan

Four intensive studies on total phytoplankton have been conducted in southern Lake Michigan; all of them are recent and represent most of the published information on seasonal variations in composition and size of phytoplankton communities in the southern basin. The salient observations of each study are presented in the following text.

The First Study. The study by Stoermer and Kopczynska (1967) was designed to yield detailed information on species composition, spatial and temporal patterns of phytoplankton abundance, and variations in depth distribution of phytoplankton populations. The results are based primarily on samples taken from 12 stations in the southern basin during August 1963, and from monthly collections along a series of stations extending from Chicago to just above Milwaukee. Several other sites were sampled less frequently (Fig. 41).

The flora consisted of several hundred taxa and included species from each of the five major algal Divisions. Diatoms constituted nearly one-half of the flora. The occurrence of most species was not restricted to particular stations;

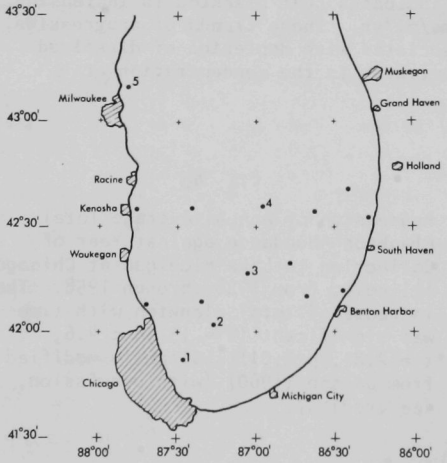

Fig. 41.

Map of Study Area Showing Sampling Stations. Data from stations 1-5 are presented in the text. Modified from Stoermer and Kopczynska (1967) (with permission, see credits).

in fact, most species were found at nearly all locations. The only significant exception was the diatom *Stephanodiscus hantzschii*; it occurred in higher frequency inshore. The authors observed, however, that nearshore communities tended to have a greater diversity of species than offshore communities. Their analysis also revealed that, contrary to previous findings, small flagellates of the Classes Cryptophyceae and Chrysophyceae were present. The authors did not identify many of these organisms to the species level because of their small size and because the presence of large amounts of detritus frequently obscured morphological details.

The standing crop of total phytoplankton and individual species populations exhibited pronounced seasonal variations. Algal abundance and the percentage composition by Division are shown for selected stations in Figures 42-46. Diatoms were the predominant phytoplankton component during spring, summer, and fall. Cryptomonads, green algae, dinoflagellates, and golden-brown algae were present in moderately small numbers during certain seasons.

In August, phytoplankton density was higher at offshore sites, and at most stations maximum abundance levels were observed near the thermocline. The predominant species were the diatoms *Asterionella formosa, Fragilaria crotonensis, Fragilaria* spp., *Synedra ulna* v. *chaseana*, and *S. ulna*. In late August, the phytoplankton standing crop increased significantly at three of the stations, but then decreased in September. During this period, phytoplankton abundance was uniform throughout the water column. By late October, total cell counts increased at all stations, especially in the offshore euphotic zone. This increase can be attributed primarily to increases in the abundance of several diatoms: *Asterionella formosa, Cyclotella comta, Cyclotella ocellata, Cyclotella stelligera, Cyclotella kuetzingiana, Cyclotella michiganiana, Fragilaria crotonensis, Melosira islandica*, and *Nitzschia holsatica*.

In April 1963, phytoplankton standing crop totaled 2477 cells/ml in the surface water at Station 1. This is a three-fold increase over abundance levels detected in October 1962 and early spring 1963. Phytoplankton density, however, was lower and remarkably uniform in the water column at Stations 2-5. Several diatoms accounted for the large standing crop: *Asterionella formosa, Cyclotella michiganiana, Fragilaria* spp., *Cyclotella ocellata, Cyclotella stelligera, Cyclotella kuetzingiana*, and *Nitzschia holsatica*. *Stephanodiscus hantzschii* was a dominant species at Station 1, *Diatoma tenue* v. *elongatum* was present at Stations 1 and 2, and *Synedra ulna* and *S. ulna* v. *chaseana* were abundant at Stations 3 and 4.

In May, phytoplankton density was higher at all stations and depths than it was in April, except at the surface at Station 1. The highest count in the investigation (2770 cells/ml) was obtained at mid-depth at Station 1. The most abundant species were the diatoms *Asterionella formosa, Rhizosolenia eriensis, Fragilaria* spp. and *Diatoma tenue* v. *elongatum*. The latter species was most abundant at Station 1.

By late June, different levels of abundance existed at some stations and at certain depths. The standing crop was smaller in the surface water than at lower depths at Stations 1 and 2. At offshore stations, however, phytoplankton density was approximately the same as in May and was remarkably uniform with

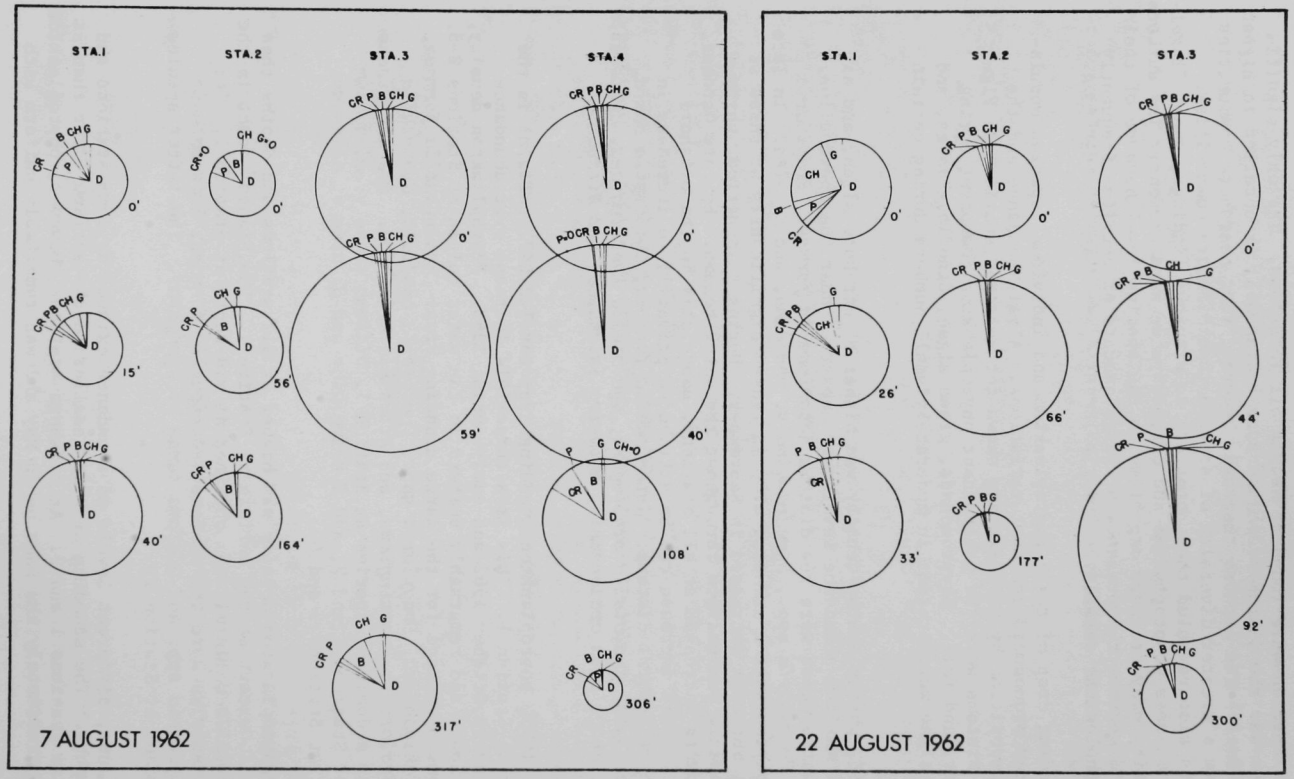

Fig. 42. Relative Abundance and Percentage Composition of Total Phytoplankton Populations at Stations 1-4 on 7 August 1962, and Stations 1-3 on 22 August 1962. Symbols: D, Bacillariophyta; G, Chlorophyta; CH, Chrysophyta; B, Cyanophyta; P, Pyrrophyta; CR, Euglenophyta, Cryptophyceae, and unidentified flagellates. Area of circles is proportional to total cell counts at depths sampled. Area of segments is proportional to contribution of major algal divisions. Number at lower right of circles gives depth (ft) from surface. Modified from Stoermer and Kopczynska (1967) (with permission, see credits).

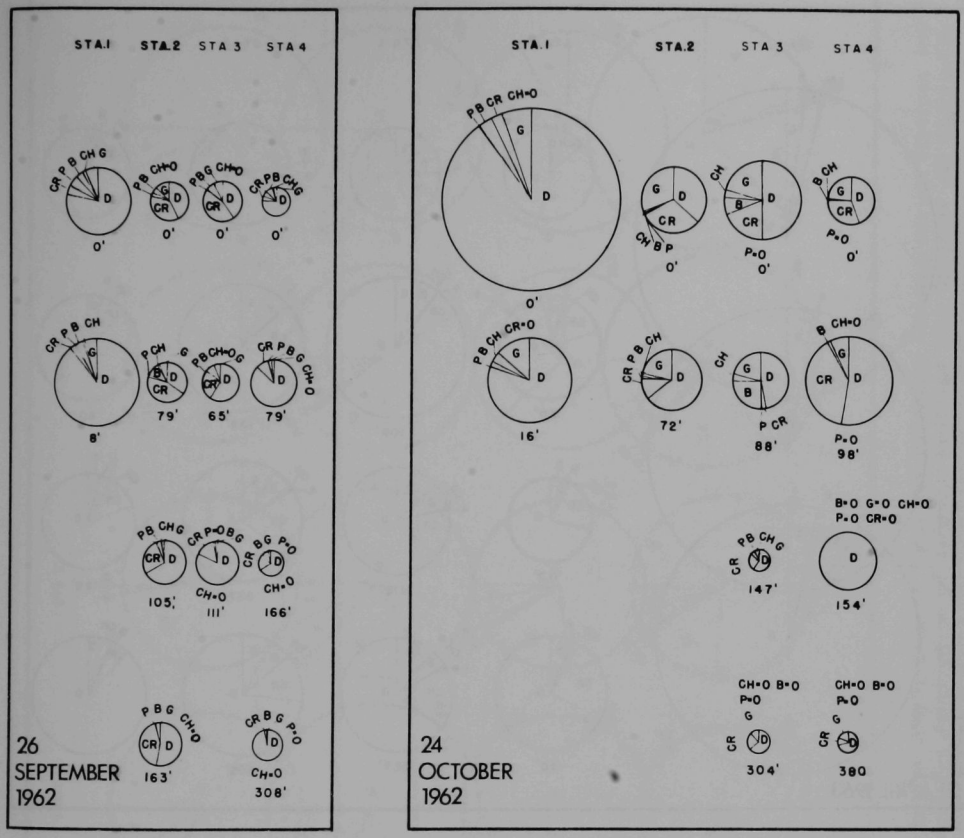

Fig. 43. Relative Abundance and Percentage Composition of Total Phytoplankton Populations at Stations 1-4 on 26 September and 24 October 1962. See Figure 42 for description of legend. Modified from Stoermer and Kopczynska (1967) with permission, see credits).

depth. Significant differences in species composition were observed at the stations. *Fragilaria crotonensis* was abundant at Stations 1 and 2, and *Melosira* spp. were prominent species at Stations 3 and 4 and in deep water at the inshore locations. *Rhizosolenia eriensis* was abundant at all locations except Station 1, and *Diatoma tenue* v. *elongatum* was recorded in relatively high numbers at all stations.

One of the significant observations of the study was the uniform distribution of phytoplankton in the water column. Although the abundance of some species varied with depth, total phytoplankton abundance was remarkably homogeneous. These observations indicate that active mixing occurs to an appreciable extent in the water column, especially during spring and early summer.

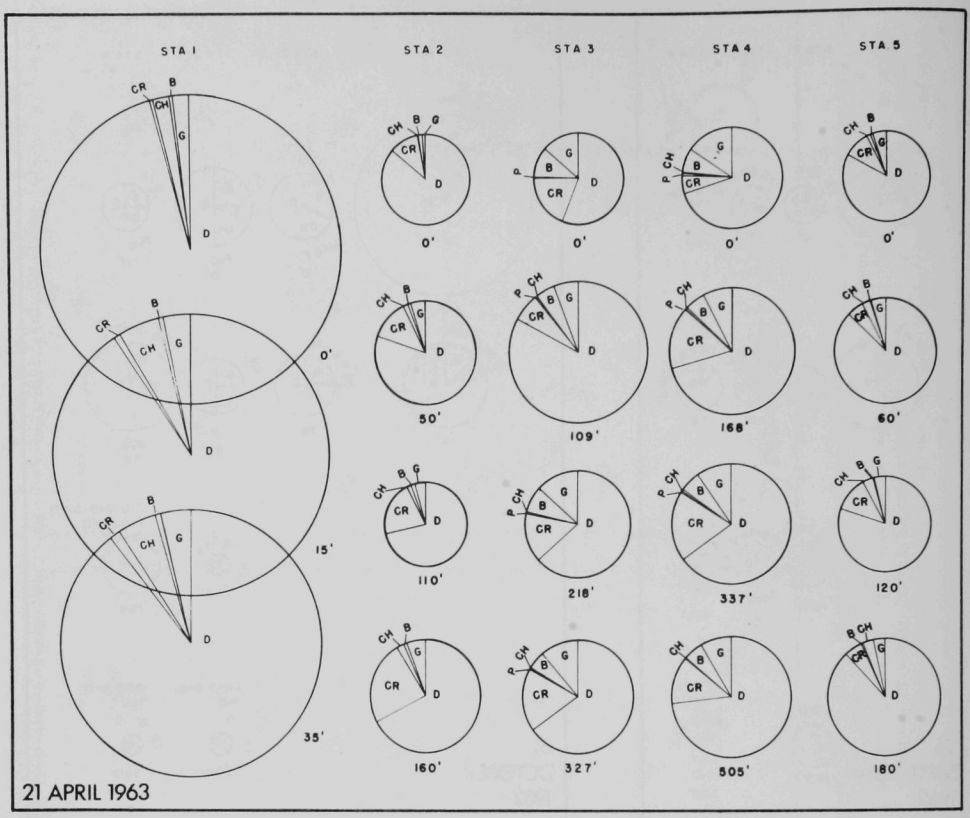

Fig. 44. Relative Abundance and Percentage Composition of Total Phytoplankton Populations at Stations 1-5 on 21 April 1963. See Figure 42 for description of legend. Modified from Stoermer and Kopczynska (1967) (with permission, see credits).

During fall, there is evidence that certain populations become concentrated at or near the thermocline. The authors attributed the presence of these metalimnetic populations to differential sinking rates of certain species and to the chrysophyte flagellates, cryptomonads, and blue-green algae which may have been living and actively reproducing at low light intensities in colder waters.

The Second Study. This study in southern Lake Michigan was conducted by Stoermer *et al.* (1972). It was designed to explore spatial and temporal variations in phytoplankton abundance in surface water. Samples were collected along two transects extending east to west and one transect extending north to south. The sampling sites were spaced geometrically with respect to distance from shore; sampling points were spaced more closely inshore than offshore.

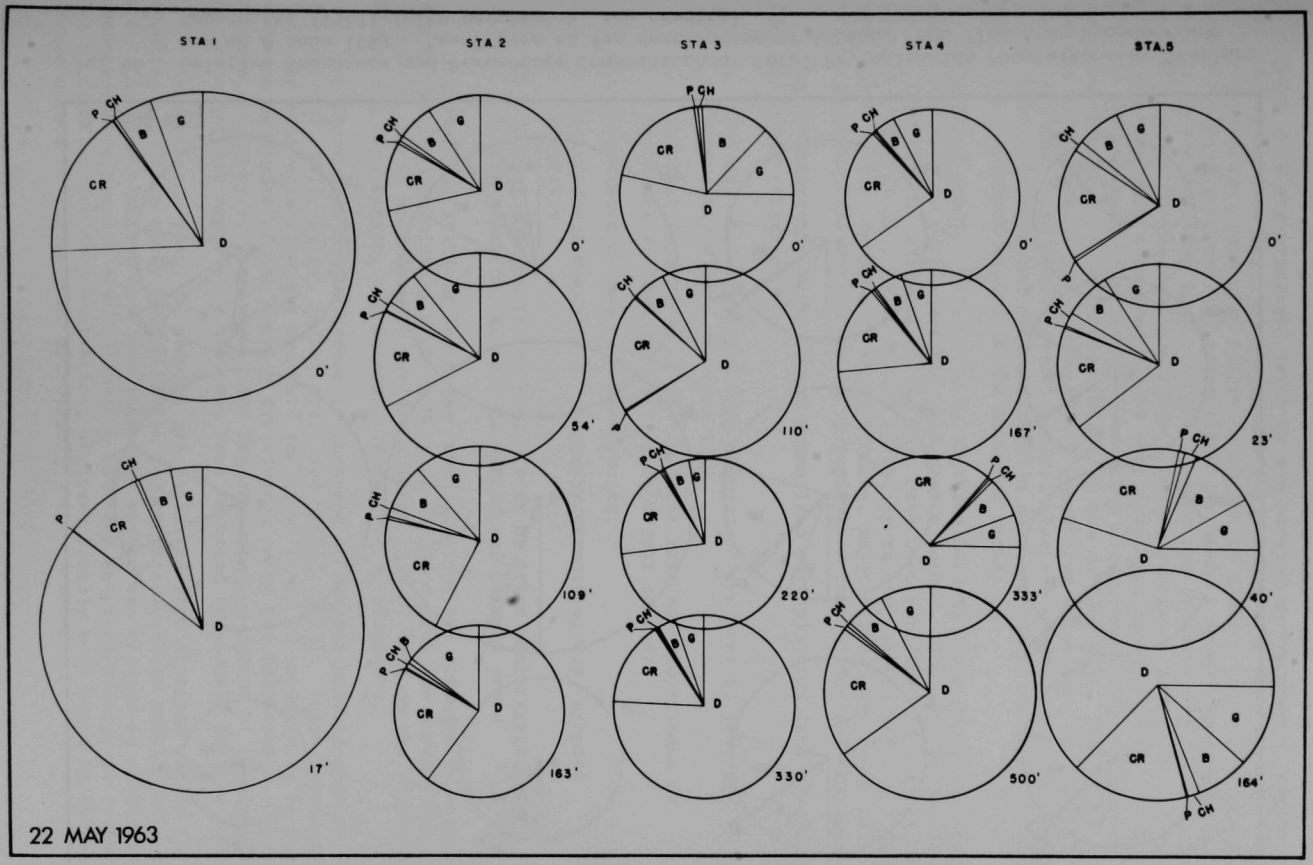

Fig. 45. Relative Abundance and Percentage Composition of Total Phytoplankton Populations at Stations 1-5 on 22 May 1963. See Figure 42 for description of legend. Modified from Stoermer and Kopczynska (1967) (with permission, see credits).

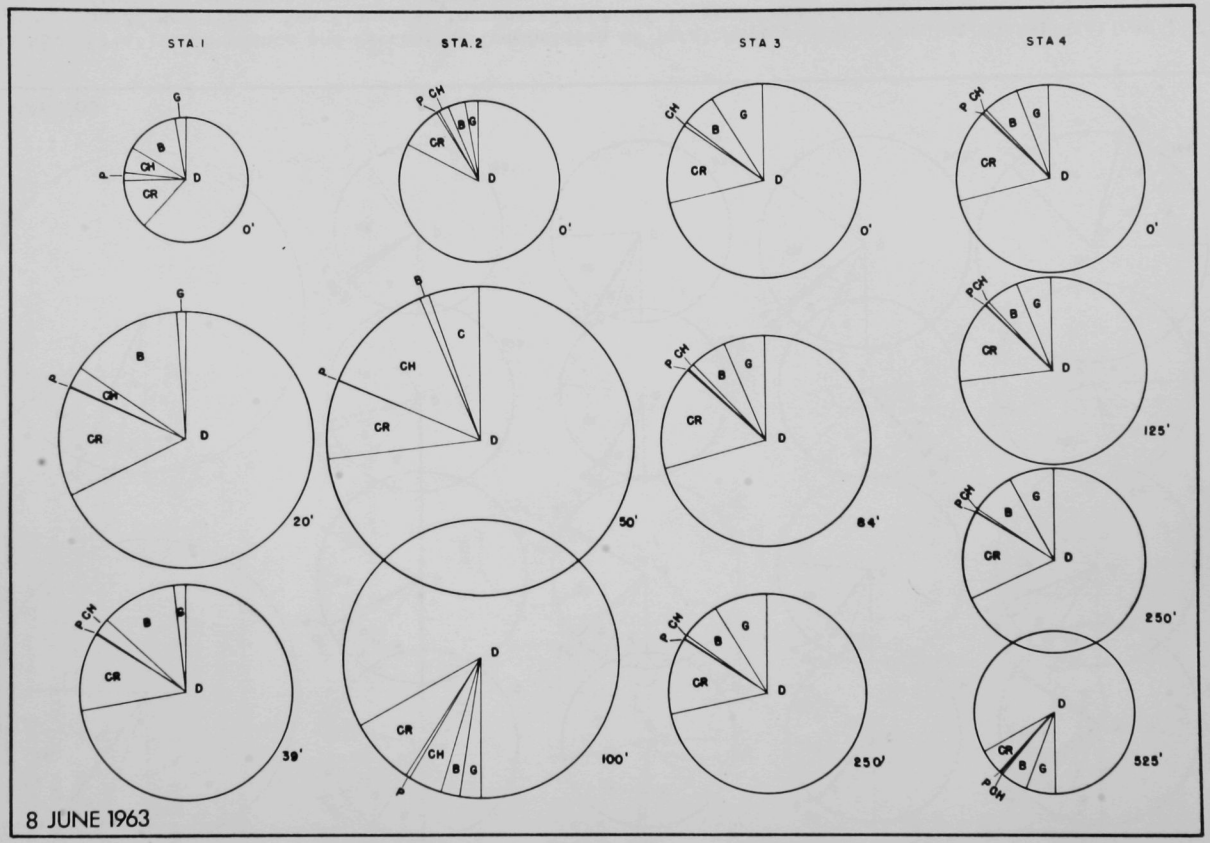

Fig. 46. Relative Abundance and Percentage Composition of Total Phytoplankton Populations at Stations 1-4 on 8 June 1963. See Figure 42 for description of legend. Modified from Stoermer and Kopczynska (1967) (with permission, see credits).

These data are presented later in the section on Phosphorus, Silica, and Eutrophication (see Figs. 55-62 and 68-75), because they form an integral part of the hypothesis concerning silica depletion by diatoms and the displacement of diatoms by blue-green and green algae during late summer and early fall. The results of the analyses indicate that diatoms are abundant and peak during spring or early summer in the southern basin. Diatom abundance diminishes by late summer, at a time when dissolved silica concentrations reach limiting levels, and diatoms are replaced by green and blue-green algae, including *Anabaena flos-aquae* and *Anacystis* spp. In October, cooling of the surface water and depression of the thermocline result in a resupply of phosphorus and silica to the euphotic zone. Although some diatom growth occurs, blue-green algae remain dominant. These authors interpreted this observation as a symptom of cultural eutrophication of the offshore region in the southern basin.

The Third Study. This study in southern Lake Michigan is being conducted near the Donald C. Cook power plant in Benton Harbor. The project was initiated in the late 1960's; portions of the data have been published in a series of reports (Ayers *et al.*, 1971, 1972a, 1972b; Ayers and Seibel, 1973; and Seibel and Ayers, 1974). As part of these studies, major efforts are being made to investigate seasonal variations in phytoplankton composition and abundance.

The investigators analyzed and summarized phytoplankton data according to five different criteria:

1. Variations in phytoplankton abundance from year to year and seasonally within the same year.
2. Seasonal variations of the dominant taxa and comparisons of abundance of dominant species from year to year.
3. Appearance of new dominant species.
4. Statistical measures of community structure, *e.g.* species diversity.
5. Unusual changes in the composition or other characteristics of the plankton, and trends within and between years.

The sampling stations for these investigations are arranged in a grid and are spaced logarithmically with respect to distance from the power plant. Collectively, these studies have yielded a large body of data on the phytoplankton flora, its composition, and seasonal variations in abundance.

The flora near Benton Harbor is composed of several hundred species (see Ayers *et al.* 1971, 1972a, 1972b; Ayers and Seibel, 1973). These inventories indicate that approximately one-half the known flora is represented by diatoms, with the remainder of the species distributed among the Chlorophyta, Chrysophyceae, Cyanophyta, Pyrrophyta, and Euglenophyta. A number of species listed by these authors apparently have not been reported previously for the Lake.

Three times a year, 52 samples are collected from stations within the sampling grid. In early phases of the investigation, these samples were taken with a metered plankton net, but later the method was changed to collection of unconcentrated samples and examination with the inverted-microscope technique. Due to difficulties in preservation, analyses finally were based on the settle-freeze method of Sandford *et al.* (1969).

An initial examination of these samples demonstrated that diatoms generally are the most abundant group of phytoplankton, that blue-green algae increase in numbers of species and abundance from spring into fall, and that green algae appear to reach maximum abundance in later summer. Small flagellates, however, are an important component of the community during all seasons. In more recent studies, Ayers and Seibel (1973) have shown that based on monthly collections from April through November 1972, diatoms clearly were the most abundant component of the phytoplankton, except in September. The authors observed, however, that the most abundant species rarely constituted more than 35% of the standing crop at any one time. The authors have published more recent and detailed information on spatial and temporal variations of phytoplankton abundance near the plant (Seibel and Ayers, 1974).

A phytoplankton survey conducted within the grid on 10 July 1970 is particularly informative (Ayers *et al.*, 1972a). Based on an analysis of 53 samples, the authors observed 59 dominant or co-dominant species, most of which were diatoms (*Melosira* sp., *Cyclotella* sp., *Tabellaria fenestrata*, and *Fragilaria crotonensis*). The data also were summarized for each station by tabulating the number of species and computing total standing crop and species diversity (Table 7). These data indicate that phytoplankton abundance and species diversity at closely spaced sites can differ greatly. Adjacent stations exhibit large differences in species number (32 to 42), large variations in abundance (630 to 13,274 individuals/ml), and dramatic differences in community structure (0.49 to 3.68 bits/individual).

From these and previous studies, the authors concluded that seasonal variations in phytoplankton abundance are highly significant and that small water masses, each with different characteristics, apparently move through the area of the Cook power plant. Survey studies clearly show that a high degree of patchiness exists in the distribution of phytoplankton in the sampling grid.

An effort also was made to assess the effects of the St. Joseph River on phytoplankton distribution near the Cook power plant. Data on phosphorus concentrations and flow rate show that the river adds large quantities of nutrients to the Lake near the power station; therefore, the immediate region is capable of supporting a river phytoplankton community (*cf.* Phosphorus, Silica, and Eutrophication, Table 27). Species characteristic of river phytoplankton in the area are listed by Ayers *et al.* (1972b) as *Amphora ovalis*, *Amphora* sp., *Cyclotella meneghiniana*, *Melosira granulata*, *M. granulata* v. *angustissima*, *Navicula capitata*, *Navicula costulata*, *Navicula decussis*, *Navicula gastrum*, *Navicula* spp., *Nitzschia acicularis*, *Nitzschia* sp., and *Synedra ulna*.

The composition of the flora on the 10 July 1970 survey indicates that a river phytoplankton community was present near the Cook power plant. The most prominent case of heavy dominance by a river plankter occurred at only one station, where *Melosira granulata* v. *angustissima* comprised about 20% of the community. The only general pattern detected by the authors was that river-associated phytoplankton occur primarily in shallow, nearshore water, close to the river's mouth.

The Fourth Study. The last investigation on phytoplankton in southern Lake Michigan is being conducted by Nalco Chemical Company. These studies are designed to assess biological and chemical conditions at the Zion power plant

site and to assess the effects of a thermal effluent from the power plant at Waukegan. The data on phytoplankton appear primarily in four reports: Piala and Lamble (1971); Gulo and Lamble (1971); Delinck and Lamble (1971); and Huh *et al.* (1972). Collectively, these investigations provide significant additions to information on the flora, and they document seasonal variations in phytoplankton composition and abundance in the southern basin. The results of two reports are presented here: Piala and Lamble (1971) and Gulo and Lamble (1971).

The study by Piala and Lamble (1971) was based on observations during 1970-1971 at four sampling sites near Zion. The inshore stations are situated one-half nautical mile offshore and two nautical miles apart; the offshore control station is six nautical miles off Zion. Duplicate samples were taken from both the inshore sites (at a depth of 2 m) and the control station (at a depth of 2 m and near the thermocline). Diatoms were identified and counted after being cleaned in nitric acid and filtered onto Millipore filters. Algae other than diatoms were sedimented with detergent (Mackenthun, 1969), placed on slides, and enumerated by strip count. Numerical counts were expressed by the unit method (see the section on Sampling Problems and Quantitative Phytoplankton Methods, p. 169, for a discussion of numerical values).

Monthly variations in phytoplankton abundance at the Zion plant are shown in Figure 47. The abundance of major algal groups varied seasonally; maximum total abundance (3600 units/ml) occurred in May, and minimum abundance (300 units/ml) was detected in August. Computations based on annual averages indicated that total standing crop was 1868 units/ml for the inshore stations and only 630 units/ml for the control station.

Diatoms were the most abundant component of the phytoplankton near Zion (Figs. 47 and 48). The abundance of this group averaged 1770 units/ml (95%) at inshore sites and 537 units/ml (85%) at the control station. Blue-green algae averaged 58 units/ml (3.0%) at inshore sites and 54 units/ml (9.0%) at the control station. *Coelosphaerium naegelianum* was the dominant blue-green alga during summer and early fall. *Anabaena flos-aquae*, another blue-green alga, reached maximum abundance in offshore water in August, and, together with several less abundant species, comprised 45% of the phytoplankton assemblage. Green algae of the genera *Ankistrodesmus*, *Scenedesmus*, and *Oocystis* were present in low numbers, averaging 20 units/ml (1.0%) inshore and 18 units/ml (3.0%) offshore. Golden-brown algae, consisting primarily of *Dinobryon* spp., represented only 1.0% of the standing crop inshore and 4.0% offshore. The most abundant species during the study were *Tabellaria flocculosa*, *Fragilaria capucina*, *Fragilaria crotonensis*, *Asterionella formosa*, *Cyclotella* spp., *Rhizosolenia eriensis*, *Melosira islandica*, and *Stephanodiscus hantzschii* vel. *tenuis*. The latter species frequently was dominant at nearshore stations.

The authors drew several conclusions from these observations. The seasonal abundance patterns of selected species and phytoplankton composition do not appear to be controlled by temperature. Nearshore populations were significantly larger than offshore populations, suggesting that nutrient levels are higher in inshore water. This speculation is at least partially supported by nearshore abundance patterns of *Stephanodiscus hantzschii* and *Stephanodiscus tenuis* as compared with smaller population sizes of these species at the offshore station. Individual species populations and total phytoplankton abundance generally varied with proximity to surface and shoreline. The authors stated

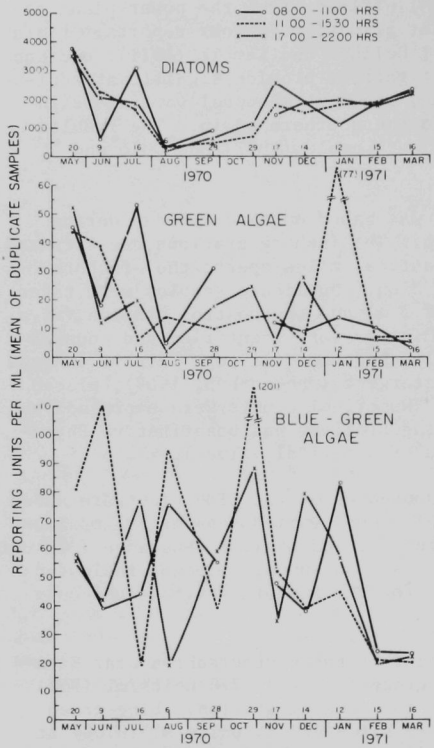

Fig. 47.

Major Lake Michigan Phytoplankton Groups near the Zion Nuclear Power Plant, Zion, Illinois (Piala and Lamble, 1971) (with permission, see credits).

that the best control samples for future studies, therefore, should be taken from the same depth and at the same distance from shore as the control samples.

The studies by Gulo and Lamble (1971) in southwestern Lake Michigan were designed to further investigate seasonal variations in species composition of the phytoplankton, and to determine the extent of species differences among inshore stations. As part of the analyses, an evaluation was made of the correlation between variations in phytoplankton abundance and water temperature. The sampling stations were near Zion and Waukegan. The inshore water near Zion was sampled at three closely spaced sites. A statistical analysis of data indicated that the results were similar, and, therefore, the data were pooled for comparative purposes. The other sites were at Kenosha and Chicago, with two sites near Waukegan (one was at the power plant intake and the other at the discharge). Water samples were taken at monthly intervals between May 1970 and March 1971. The procedures used to enumerate phytoplankton were similar to those of Piala and Lamble (1971).

Seasonal patterns in phytoplankton abundance for stations at Zion and Kenosha are shown in Figures 49 and 50. The highest monthly average for all sampling locations was 4650 units/ml in June 1970. A smaller, relatively less distinct maximum occurred in late fall and winter. A monthly low of 1063 units/ml for all stations occurred in October.

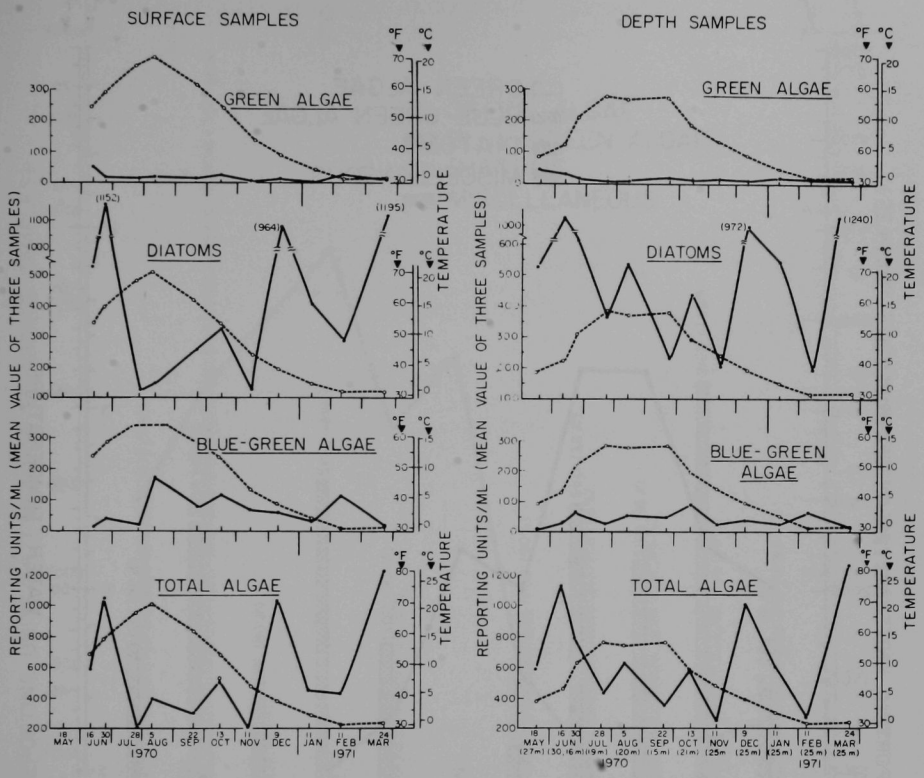

Fig. 48. Temperature (dotted line) and Abundance (solid line) of Offshore Phytoplankton near Zion, Illinois. Samples were collected at surface and mid-depth. Modified from Piala and Lamble (1971) (with permission, see credits).

The Waukegan stations supported larger standing crops of phytoplankton than did the other stations. This was due primarily to the presence of extremely large populations of the diatoms *Tabellaria flocculosa* and *Fragilaria crotonensis*. Higher abundance levels apparently resulted from higher nutrient levels in the intake and discharge canals than at locations in the vicinity of Waukegan. Previous observations by the Nalco Chemical Company indicated that the area is enriched with nutrients from nearby sewage effluents.

The phytoplankton at all stations was dominated by diatoms. The most abundant species were *Stephanodiscus hantzschii*, *Stephanodiscus tenuis*, *Cyclotella* spp., *Fragilaria crotonensis*, *Fragilaria capucina*, and *Tabellaria flocculosa*. Collectively, these species contributed between 42 and 98% of the phytoplankton assemblage during the year. Total numbers of diatoms ranged between 664 and 4112 units/ml; the low value occurred in October and the high value in June.

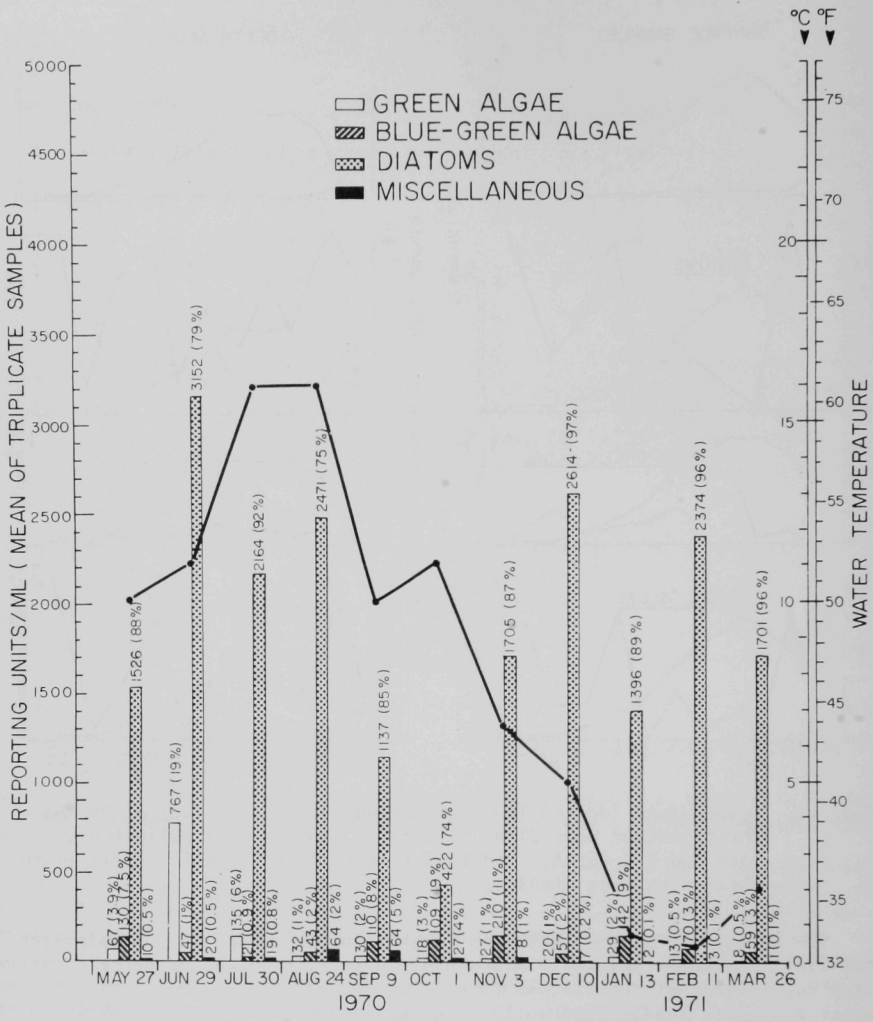

Fig. 49. Major Phytoplankton Groups and Corresponding Water Temperatures near Zion, Illinois (Gulo and Lamble, 1971) (with permission, see credits).

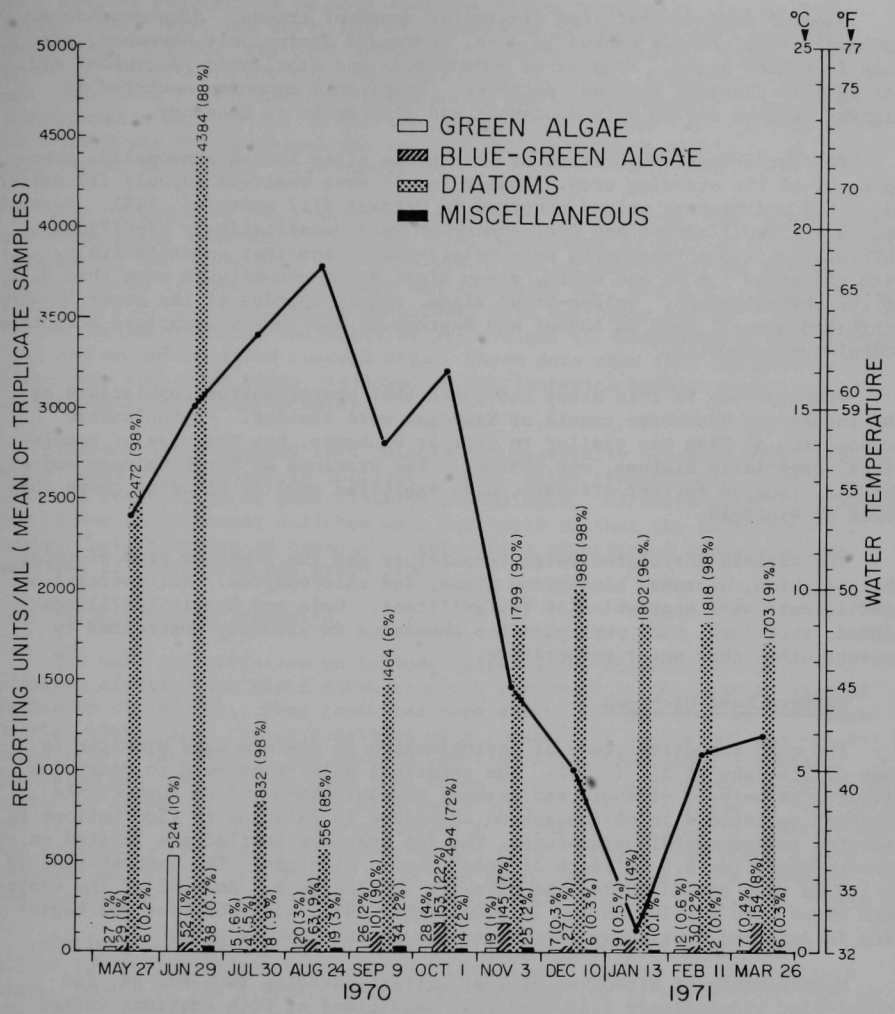

Fig. 50. Major Phytoplankton Groups and Corresponding Water Temperatures near Kenosha, Wisconsin (Gulo and Lamble, 1971) (with permission, see credits). (NOTE: The percentages 90% and 6% for 9 September 1970 appear to be reversed in this figure.)

Several diatoms exhibited dissimilar seasonal trends. *Stephanodiscus hantzschii* vel. *tenuis* peaked in June, decreased during July-November, and then increased again. *Fragilaria crotonensis* and *Tabellaria flocculosa* did not exhibit distinct seasonal patterns. *Fragilaria capucina* occurred in highest numbers during July-September and also again in December.

The percentage composition of blue-green algae varied seasonally, averaging 5% of the standing crop. Lowest levels were observed in July (17 units/ml, 0.8%) and highest values occurred in October (117 units/ml, 14%). Several species of *Oscillatoria* and *Coelosphaerium* were quantitatively significant. Chlorophytes and chrysophytes were relatively unimportant quantitatively. With the exception of one month, green algae never constituted more than 3.5% of the phytoplankton. Golden-brown algae, mainly species of the genus *Dinobryon*, exhibited a small peak in August and September, but rarely comprised more than 10% of the community.

Observations in this study indicated that phytoplankton populations at the intake and discharge canals at Waukegan were similar. Phytoplankton composition at Zion was similar to that at Waukegan, but the size of populations, especially diatoms, was smaller. The stations at North Chicago and at Kenosha, located further offshore, also exhibited smaller standing crops than those at Waukegan.

The authors correlated water temperature and the standing crop of total phytoplankton, diatoms, blue-green algae, and chlorophytes. All correlation coefficients were statistically insignificant. Gulo and Lamble (1971) concluded, therefore, that phytoplankton abundance is probably controlled by factors other than water temperature.

Eastern Lake Michigan

The only intensive study of phytoplankton in eastern Lake Michigan is that of Schelske *et al.* (1971). The principal objectives were to determine differences between offshore and inshore phytoplankton and to investigate seasonal variations in phytoplankton abundance in relation to fluctuations in selected environmental parameters. The two stations sampled are located on an east-to-west line 6.3 km south of Grand Haven, Michigan. The inshore station is 1.2 km west of the shore; the offshore station is 6.7 km west of the shore. Both sites were sampled during July-September 1971, with observations beginning in June and continuing into September at the inshore site.

Measurements of dissolved silica, nitrate-nitrogen (NO_3-N), pH, and Secchi-disc transparency indicated that conditions at both stations varied with time (Fig. 18). Transparency generally was greater at the offshore station. Concentrations of dissolved silica ranged between 0.1 and 1.14 mg SiO_2/l and generally were lower and less variable offshore. Very low silica concentrations (<0.4 mg/l) were detected offshore in July. Nitrate-nitrogen fluctuated dramatically at both stations, especially offshore. The pH ranged between 8.35 and 8.81 and generally was lower offshore. Upwelling of nutrient-rich bottom water appeared to occur in August and September nearshore.

Phytoplankton abundance fluctuated irregularly inshore except during September, when all counts were relatively low and moderately stable (Fig. 18b). Algal abundance offshore varied considerably in July, but appeared to stabilize at low levels during August and September.

Species populations at both stations varied seasonally (Tables 3-6). During June, July, and early August, nearshore populations were composed chiefly of diatoms. *Melosira granulata, Synedra filiformis, Rhizosolenia eriensis, Fragilaria crotonensis, Fragilaria capucina, Tabellaria fenestrata,* and *Cyclotella stelligera* were dominant or codominant species. The offshore phytoplankton was similar in species composition, except that *Cyclotella stelligera* was the principal diatom, and the chrysophyte *Dinobryon divergens* occurred in relatively large numbers.

One of the most important observations of the study was that blue-green and green algae constituted a significant percentage of the community during late August and September. The blue-green populations consisted of small coccoid forms (*Anacystis dimidiata* and *Anacystis* sp.) and a filamentous species (*Anabaena flos-aquae*) normally associated with eutrophic waters. The chlorophytes included several unidentified green algae (*Gloeocystis* sp. and *Oocystis* sp.) and an unidentified coccoid alga. These data show that populations of blue-green and green algae developed in nutrient-rich inshore water and also in nutrient-poor offshore water.

The authors concluded that inshore and especially offshore water exhibits significant fluctuations in nutrient levels, water transparency, and in the size and composition of phytoplankton assemblages. Offshore water apparently has become sufficiently enriched with nutrients so that the environment in eastern Lake Michigan is capable of supporting significant numbers and percentages of blue-green and green algae.

North-to-South Transects

The only investigation to include quantitative observations on phytoplankton distribution along north-to-south transects in the Lake is that of Parkos *et al.* (1969). They conducted four survey cruises from July through October 1969. Each cruise consisted of a consecutive southbound and northbound trip. Sampling of the surface water at all points along a transect generally was completed in less than three days. The approximate location of stations, along with estimates of primary productivity, is shown in Figures 51 and 52. Plankton samples were preserved in formalin, settled in Imhoff cones, and counted by the Sedgewick-Rafter method (APHA, 1960). The results were averaged and pooled by location, *i.e.* the northern, central, and southern regions of the Lake. Data from the early October cruise are given in Table 13.

Estimates of phytoplankton abundance in early October ranged from 1.37×10^6 to 1.78×10^6 organisms/l. Levels were highest in the southern basin, lowest in the northern basin, and intermediate in the central part of the Lake. The dominant species at all locations were blue-green algae, including one or more species of *Microcystis, Coelosphaerium, Lyngbya, Chroococcus,* and *Merismopedia*. Filamentous net plankton and nannoplankton also were significant components of the phytoplankton.

By the end of October, total phytoplankton counts in each area decreased significantly. Estimates ranged from 5.05×10^5 to 7.48×10^5 organisms/l. Once again, abundance was higher in the southern basin than in the northern basin. Although blue-green algae (*Coelosphaerium, Microcystis,* and *Chroococcus*) were dominant, the diatoms *Tabellaria* and *Asterionella* also were significant components of the plankton.

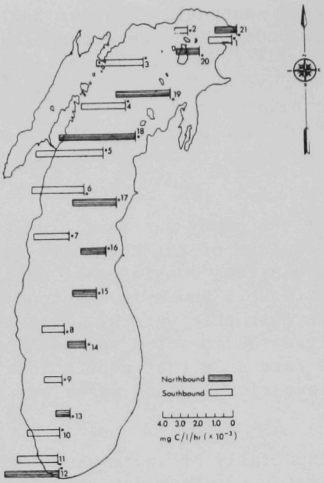

Fig. 51.

Productivity in Lake Michigan Surface Water, Trip 1, 1-3 July 1967. Values computed from 4-hr incubation, 15.6°C, 1000 foot-candles. Modified from Parkos *et al.* (1969) (with permission, see credits).

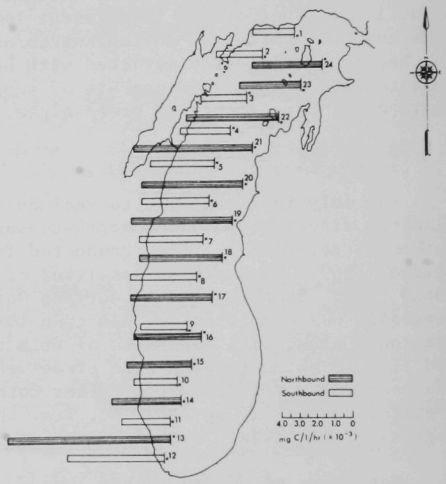

Fig. 52.

Productivity in Lake Michigan Surface Water, Trip 3, 6-8 October 1967. Values computed from 4-hr incubation, 15.6°C, 1000 foot-candles. Modified from Parkos *et al.* (1969) (with permission, see credits).

The information reported by these authors is of special interest. This was one of the first studies to provide evidence that blue-green algae are major components of open-water plankton. The basic conclusion drawn from these studies was that blue-green algae species normally associated with nutrient-enriched water do occur in the offshore regions of the Lake, and that phytoplankton abundance tends to be higher in the surface water of the southern basin than in the surface water of northern and central Lake Michigan.

Quadrat Monitoring by the U. S. Department of the Interior

Phytoplankton abundance was monitored in the early 1960's by the U. S. Department of the Interior (1968a) as part of its investigation on the water

Table 13. Lake Michigan Plankton (organisms/l), October 1967*

Northern Lake Region		*Central Lake Region*		*Southern Lake Region*	
		6-8 October			
Class Cyanophyceae		Class Cyanophyceae		Class Cyanophyceae	
Coelosphaerium	293,058	*Microcystis incerta*	630,276	*Microcystis incerta*	1,218,687
Microcystis incerta	223,665	*Coelosphaerium*	311,410	*Coelosphaerium*	176,064
Lyngbya contorta	186,387	*Merismopedia glauca*	27,528	*Chroococcus*	93,480
Chroococcus	18,925	*Chroococcus*	25,234	*Merismopedia glauca*	4,588
Merismopedia glauca	16,058	*Lyngbya contorta*	11,470		
Class Chrysophyceae		Class Chrysophyceae		Class Chrysophyceae	
Dinobryon	5,735	*Dinobryon*	8,029	*Dinobryon*	573
Class Bacillariophyceae		Class Bacillariophyceae		Class Bacillariophyceae	
Fragilaria crotonensis	4,014	*Cocconeis*	5,161	*Cocconeis*	2,294
Cyclotella	3,441	*Synedra acus*	3,441	*Cyclotella*	1,720
Ceratoneis	2,867	*Tabellaria flocculosa*	1,147	*Melosira*	1,147
Tabellaria flocculosa	2,294	*Cyclotella*	1,720	*Synedra acus*	573
Synedra acus	1,720	*Asterionella formosa*	573	*Tabellaria flocculosa*	573
Cocconeis	573	*Rhizosolenia*	573		
Stephanodiscus	573				
Class Chlorophyceae		Class Chlorophyceae		Class Chlorophyceae	
Cosmarium	573	*Scenedesmus*	2,867	*Scenedesmus*	573
Class Dinophyceae		Class Dinophyceae		Class Dinophyceae	
Ceratium hirundinella	573	*Ceratium hirundinella*	1,720	*Ceratium hirundinella*	1,147
Unidentified nannoplankton**	562,603	Unidentified nannoplankton**	292,485	Unidentified nannoplankton**	253,487
Unidentified net plankton†	48,741	Unidentified net plankton†	311,410	Unidentified net plankton†	29,248
Total Count	1,371,806	Total Count	1,496,257	Total Count	1,784,154
		25-26 October			
Class Cyanophyceae		Class Cyanophyceae		Class Cyanophyceae	
Coelosphaerium	155,992	*Microcystis incerta*	229,400	*Coelosphaerium*	129,037
Merismopedia glauca	9,176	*Coelosphaerium*	100,936	*Microcystis incerta*	83,157
Chroococcus	6,882	*Chroococcus*	26,381	*Chroococcus*	8,602
Class Chrysophyceae		Class Chrysophyceae			
Dinobryon	573	*Dinobryon*	573		
Class Bacillariophyceae		Class Bacillariophyceae		Class Bacillariophyceae	
Fragilaria crotonensis	2,867	*Tabellaria fenestrata*	9,176	*Tabellaria fenestrata*	17,205
Stephanodiscus	2,294	*Asterionella formosa*	8,602	*Melosira*	9,749
Synedra acus	2,294	*Synedra acus*	4,014	*Fragilaria capucina*	7,455
Tabellaria flocculosa	1,720	*Fragilaria capucina*	1,147	*Tabellaria flocculosa*	5,161
Cocconeis	573	*Melosira*	1,147	*Synedra acus*	4,588
		Tabellaria flocculosa	1,147	*Asterionella formosa*	4,014
		Cyclotella	573	*Fragilaria crotonensis*	1,147
				Stephanodiscus	573
				Class Dinophyceae	
				Ceratium hirundinella	573
Unidentified nannoplankton**	296,499	Unidentified nannoplankton**	278,721	Unidentified nannoplankton**	475,431
Unidentified net plankton†	20,072			Unidentified net plankton†	1,720
Total Count	505,251	Total Count	661,817	Total Count	748,412

*Data from Parkos et al. (1969).

**Nannoplankton: two forms only; presumed to be bacteria.

†Net plankton category based on size.

quality of Lake Michigan. Samples were taken routinely from rectangular areal quadrats at the surface and at depths of 5, 15, 30, 50, 75, and 100 m, at mid-depth, and near the bottom of the Lake. Phytoplankton counts were made using the Sedgewick-Rafter method (APHA, 1960) at a magnification of 200x.

Although there is danger in extrapolating the results of spot sampling within a quadrat to larger regions, the observations are extensive enough to provide a generalized picture of phytoplankton distribution and abundance in

the Lake. The range of values characterizing different conditions of water quality were set arbitrarily by the U. S. Department of the Interior at 0-300, 300-500, and over 500 organisms/ml. Algal concentrations less than 300/ml generally are regarded as indicating high water quality, whereas counts exceeding 500/ml are considered indicative of deteriorating water conditions or pollution. Records for spring, summer, and fall and selected data for 1963 are summarized in the following text.

Spring. In spring 1962, counts over 500 organisms/ml were observed at all inshore locations, except for the northernmost tip of the Lake and for the stretch of shore from Chicago to a point north of Milwaukee. Phytoplankton density generally was less than 200 organisms/ml at mid-lake locations, and ranged from 300 to 500 organisms/ml between mid-lake and the nearshore zone. Extremely high concentrations were observed in some nearshore regions. Counts greater than 1200 organisms/ml were detected in the areas of Manitowoc-Sheboygan and Chicago-Calumet, and densities were greater than 3000 organisms/ml off Benton Harbor. At the northern end of the Lake, phytoplankton density was 528 organisms/ml off Manistique, and was less than 300 organisms/ml offshore. During spring 1963, abundance levels also were high over most of the Lake. Concentrations of 6000 organisms/ml, for example, were observed near the mouth of the Milwaukee River and generally ranged between 1000 and 20,000 organisms/ml in the harbor itself.

Summer. In summer 1962, algal abundance over the Lake generally was much lower than during the previous spring, except for several nearshore areas. Counts above 300 organisms/ml were detected near Chicago, Milwaukee, and South Haven. Dense concentrations (>2000 organisms/ml) were observed only in a localized area near Grand Haven in eastern Lake Michigan. Phytoplankton abundance in Green Bay, however, generally was high during summer. In July 1963, concentrations as high as 20,000 organisms/ml were detected in Green Bay near the mouth of the Fox River. Phytoplankton concentrations decreased to levels between 5000 and 10,000 organisms/ml at a distance of 16 km out into the bay. Abundance along the eastern shore of the bay was lower, however, ranging from 500 to 5000 organisms/ml. Phytoplankton in the southern end of the bay consisted primarily of flagellates and coccoid forms of green algae and centric diatoms. Blue-green algae were present in relatively large numbers in many parts of the bay, ranging from 700 to 1500 organisms/ml. Algal concentrations near the mouth of the Oconto River usually exceeded 80,000 organisms/ml and consisted primarily of flagellated and coccoid green algae. These same species also were present in the general area of the Oconto River, ranging from 1000 to 20,000 organisms/ml.

Fall. In fall 1962, phytoplankton abundance was relatively low in the northern and central regions of the Lake. Nuisance concentrations were detected primarily in nearshore water of the southern basin. At Milwaukee, Wisconsin, concentrations as high as 1500 organisms/ml were observed in the harbor, but algal density decreased with increasing distance from shore. Inshore water near the harbor supported concentrations around 1000 organisms/ml, but values decreased to only 100 organisms/ml near mid-lake. The predominant organisms in the harbor and in nearshore water were the diatoms *Cyclotella*, *Stephanodiscus*, *Tabellaria*, and *Asterionella*. Near the Root River (Racine) area, however, dense concentrations of phytoplankton (>2000 organisms/ml) were detected. The predominant diatoms were the same genera as those observed near Milwaukee. Nuisance concentrations of phytoplankton (>600 organisms/ml) also were observed in quadrats near Grand Haven, Michigan.

The general conclusions drawn by U. S. Department of the Interior personnel were that phytoplankton distribution in the Lake was influenced by wind-driven water currents, and that nuisance concentrations of phytoplankton can be attributed to nutrients added to water along the shore from polluted rivers. Areas in which nuisance conditions develop are located near rivers that supply large quantities of phosphorus directly to the Lake [see the section on Phosphorus, Silica, and Eutrophication (Fig. 80 and Tables 27 and 31) and Zar, 1974].

Grand Traverse Bay

Grand Traverse Bay* is a narrow inlet of Lake Michigan that has attracted interest because of its fishery potential and its sheltered water. The southern portion of the bay is divided longitudinally by Old Mission Point into an east and west arm (Fig. 20). The Boardman River drains agricultural areas and receives treated sewage from Traverse City before it enters the southern end of the west arm. The Elk River, which is of high water quality, drains non-agricultural areas and flows through a series of lakes before it enters the east arm.

The water in the bay is considered oligotrophic and its quality compares favorably with high quality offshore water in northern Lake Michigan. Stoermer *et al.* (1972) assessed limnological conditions in the bay and determined the effects of nutrient input from the Boardman River on phytoplankton abundance, species composition, and primary productivity. Twelve stations were established in the bay and were sampled in May and again in June 1970 (Fig. 20). In May, all samples were taken at a depth of 5 m, but in June, chemical determinations were made at 5 m and at 1 m above the bottom. Phytoplankton samples were prepared by aldehyde fixation followed by filtration onto Millipore filters.

Measurements of water transparency, particulate phosphorus, nitrate-nitrogen, dissolved silica, phytoplankton abundance, and primary productivity are presented in Table 9. In May, phytoplankton abundance ranged from 1455 cells/ml (Station 4) to 3355 cells/ml (Station 10). The largest standing crop values were detected in the lower portions of the west arm, and the smallest values were observed in the upper region of the east arm.

In June, phytoplankton abundance increased significantly over May levels. Values ranged from a low of 2500 cells/ml (Station 6) to a high of 6469 cells/ml (Station 10). Phytoplankton abundance was highest again at stations near the Boardman River and lowest in the upper region of the east arm. Secchi-disc transparency and chemical measurements also indicate that production rates were highest in the west arm, especially close to the mouth of the Boardman River, and lowest in the upper portion of the east arm. These results indicate that nutrient loadings from the river have resulted in partial eutrophication of the west arm. Phytoplankton abundance levels appear to be intermediate between those of inshore and offshore water in the open Lake.

The algal flora of the bay was dominated by diatoms (Tables 5, 8 and 14). Although there was a noticeable effect of localized nutrient enrichment on the standing crop, the composition of the phytoplankton appeared to be unaffected.

**Recent studies on the limnology of Grand Traverse Bay by Auer et al. (1976a, 1976b) include seasonal data on phytoplankton composition and abundance for 1971.*

Table 14. Relative Frequency of Pollution-Tolerant Taxa in Samples Collected at 5-m Depth from Grand Traverse Bay, Lake Michigan, 18 May and 20 June 1970*

Diatom Species	Stations											
	1	2	3	4	5	6	7	8	9	10	11	12
						18 May						
Stephanodiscus binderanus (Kütz.) Krieger	0	0	0	0	0	0	0	0	0	0	0	0
Stephanodiscus subtilis (Van Goor) A. Cl.	0	0	0	0	0	0	0	0	0	0	0	0
Diatoma tenue Ag.	0.1	0	0	0.2	0.1	0	0.2	0.5	0.4	0.1	0.2	0.3
Diatoma tenue var. *elongatum* Lyngb.	0.2	0.3	0.3	0.2	0.07	0.1	0.03	0	0	0	0	0.03
Cyclotella meneghiniana fo. *plana* Fricke	0.1	0	0	0	0	0	0	0	0	0	0	0
Stephanodiscus tenuis Hust.	0.03	0.08	0	0	0.03	0	0.03	0	0	0	0	0.03
Fragilaria capucina Desm.	0.07	0.2	0.04	0	0	0.07	0	0.02	0.02	0.02	0.03	0
Percentage of assembly	0.5	0.6	0.3	0.4	0.2	0.2	0.3	0.5	0.4	0.2	0.2	0.4
						20 June						
Stephanodiscus binderanus (Kütz.) Krieger	0.02	0.03	0	0	0.03	0.03	0.01	0	0	0.01	0	0
Stephanodiscus subtilis (Van Goor) A. Cl.	0	0	0	0	0	0	0	0.08	0	0	0	0
Diatoma tenue Ag.	0.3	0.1	0.4	0.9	0.6	0.9	0.6	0.7	0.5	0.5	0.3	0.2
Diatoma tenue var. *elongatum* Lyngb.	0.06	0.2	0	0.04	0.5	0.5	0.01	0.03	0.01	0	0.06	3.0
Cyclotella meneghiniana fo. *plana* Fricke	0	0	0	0	0	0	0	0	0	0	0	0
Stephanodiscus tenuis Hust.	0	0	0	0.02	0.05	0.08	0.01	0.01	0.02	0	0	0.9
Fragilaria capucina Desm.	0.02	0.09	0.02	0.06	0.01	0	0.04	1	0.1	0.01	0.1	0.5
Percentage of assembly	0.4	0.4	0.4	1.0	1.2	1.5	0.7	1.8	0.6	0.5	0.5	4.6

*Data from Stoermer *et al.* (1972).

Diatoms normally associated with eutrophic conditions in the Lake were as abundant in the upper east arm as they were in the west arm near the effluent of the Boardman River. The cause of this response is not clearly understood. The authors speculated that either of two mechanisms may account for the similarities in floral composition. It is possible that phytoplankton assemblages have the capacity to accommodate increases in nutrient levels without exhibiting significant changes in composition until a threshold level is reached and surpassed. If this mechanism is operative in the bay, it can be assumed that nutrient enrichment has not yet reached this critical level. Another mechanism that may account for this phenomenon is the response of populations to changes in the balance of conservative elements or trace metals or other coincidental factors that normally are associated with nutrient enrichment.

CONCLUSIONS AND DISCUSSION

The information presented in this section indicates that considerable data exists on characteristics of diatom and total phytoplankton communities in Lake Michigan. A number of significant and controversial issues are summarized here.

Species Composition of the Flora

The flora of the Lake appears to be relatively large and diverse (more than 2000 taxa) and should be regarded as incompletely known. Future research could add significantly to the existing data on species composition if the following four areas are investigated:

1. Very few observations have been made in the Lake during winter. It is expected that a winter flora, *i.e.* organisms adapted to low temperature and illumination, exists in the Lake.

2. It is possible that nutrient enrichment has altered the environment directly or indirectly to produce modified habitats that can be occupied by species which are not part of the native flora. Evidence substantiating this has been presented by Stoermer (1967) and Stoermer and Yang (1969, 1970). It also is possible that heated effluents produce localized alterations in nearshore habitats and provide conditions suitable for the growth of species not normally found in the Lake.

3. There are numerous unresolved taxonomic problems, particularly within the diatoms as a group (*cf.* Holland, 1969; Stoermer and Yang, 1969; and Holland and Beeton, 1972). Problems of species identification exist within many of the genera, especially planktonic species of *Cyclotella, Stephanodiscus, Fragilaria, Synedra,* and *Melosira*, and with many species of littoral and benthic diatoms found in nearshore water and in the open water of the southern basin. It is plausible that the planktonic environment of the Great Lakes differs from smaller north-temperate lakes (Stoermer, 1967; Stoermer and Yang, 1969, 1970); consequently, new species, varieties, and forms may be encountered, or the taxonomic limits of many taxa in the Lake may not be in agreement with monographic treatments and other literature. It is expected that intraspecific variability of some species and the morphologic limits of other problematic taxa will be resolved through careful study using light, phase, or electron microscopy and through laboratory culture investigations.

4. Many of the taxa reported from the Lake are observed only if very large samples are examined. Stoermer (1967), for example, encountered single specimens of some species only when 40,000 to 50,000 individuals in a sample were examined. Thus, there undoubtedly are many unreported taxa in the Lake, but they are present in such low abundance that they escape detection in routine analyses. In addition, it is known that nannoplankton, particularly small flagellates in the genera *Ochromonas, Chromulina, Cryptomonas, Chrysochromulina, Chroomonas*, and *Rhodomonas*, often constitute a significant percentage of the standing crop of phytoplankton in freshwater lakes (*cf.* Schindler and Holmgren, 1971; Kristiansen, 1971; Pavoni, 1963; Tarapchak, 1973; Rodhe *et al.*, 1958). Similar results also have been reported for Lakes Superior and Ontario (Tarapchak, 1973; Munawar and Nauwerck, 1971). Many studies, however, have failed to detect these populations in Lake Michigan, and it is suspected that techniques of preservation, concentration, and enumeration used by many investigators are not suitable for the detection of such species. Stoermer and Kopczynska (1967) already have observed a relatively diverse nannoplankton flora in southern Lake Michigan. Although the organisms were not treated systematically in their studies, the principal genera were in the Chrysophyceae and Cryptophyceae and were species of the genera *Cryptomonas, Chroomonas, Ochromonas*, and *Chromulina*. Recently, Munawar and Munawar (1975) examined samples from southern Lake Michigan using the inverted-microscope technique and observed a relatively rich flora of cryptomonads and golden-brown algae in some samples.

Recent Numerical Changes in the Flora

The observation that the phytoplankton flora of the Lake is now more diverse than in the early 1930's is in direct contrast to the general theory that numbers of species decrease rather than increase with eutrophication in north-temperate lakes (*cf.* Hutchinson, 1967; Margalef, 1968). Stoermer (1968) and Stoermer and Yang (1969) contended that Lake Michigan, and perhaps the Great Lakes in general, may be unique aquatic systems in this regard. Whether this contention is true or not, the authors have demonstrated that littoral and benthic algal populations exist in the open-water regions of the southern basin. This phenomenon can be viewed as circumstantial evidence indicating that nutrient enrichment of offshore water has occurred.

Response of Species and Community Structure to Nutrient Enrichment, Indicator Species, and Species Diversity

All available evidence indicates that indicator species exist in Lake Michigan (Table 2), and that their distribution and abundance generally can be correlated with water of differing nutrient content. The data generated on indicator species in Lake Michigan closely parallel some of the findings in Lake Erie. Hohn (1968--unpublished, 1969), for example, observed changes in the abundance of certain planktonic diatoms in Lake Erie which are similar to trends observed in Lake Michigan. *Cyclotella stelligera* and *Rhizosolenia eriensis*, diatoms characteristic of oligotrophic environments, have decreased in Lake Erie since 1938. *Fragilaria capucina* and *Melosira ambigua*, species favored by nutrient enrichment, have increased significantly in abundance over the last 30 years in Lake Erie. *Stephanodiscus alpinus*, an abundant alga in some highly eutrophic lakes, has become a predominant diatom in western Lake Erie recently.

It is apparent that the planktonic diatom flora of Lake Michigan contains species associated with advanced stages of eutrophication and increased salinity. Although many of them are abundant in polluted harbors, they are present in lower abundance offshore. *Stephanodiscus binderanus*, *Stephanodiscus tenuis*, *Coscinodiscus subsalsus*, and *Thalassiosira* spp. are notable examples. *Stephanodiscus binderanus*, apparently introduced into the Lake in the early 1930's, has caused clogging problems at the Chicago water filtration plant. It is abundant now in polluted harbors and nearshore water, and its abundance appears to be increasing offshore.

It is expected that future studies will more clearly delineate the trophic preference of many phytoplankton species. Most studies thus far have been based on relatively subjective forms of data analyses. The future use of multivariate and related statistical procedures, *e.g.* cluster analysis, ordination and factor analysis, time series analysis, canonical analysis, and various types of association analyses may provide more accurate determinations of indicator species and especially associations of indicator species (*cf.* Allen, 1971; Allen and Skagen, 1973; Levandowsky, 1972; McIntire, 1973; Fager, 1963). A recent study by Holland and Claflin (1975) is especially instructive in this regard. They utilized several multivariate statistical techniques to detect associations of planktonic diatoms in Green Bay. Principal component analyses revealed the presence of two major species groupings in the bay, one consisting of *Melosira granulata*, *Stephanodiscus* spp., *Cyclotella meneghiniana*, and *Stephanodiscus niagarae*, and another consisting of *Fragilaria crotonensis*, *Asterionella formosa*, *Tabellaria flocculosa*, and *Cyclotella comta*. Cluster

analysis, based on diatom distribution over 68 stations, clearly divided the bay into three basic geographic areas, and also revealed the presence of three primary diatom assemblages, one of which is localized in the extreme southern part of the bay near the discharge of the Fox River. Such analyses, especially if coupled with seasonal observations on nutrient concentrations and variations in physical parameters, could provide better insights into the factors that regulate the distribution and abundance of diatoms and other algal populations.

Data on the diversity of diatom and total phytoplankton assemblages do not support the contention that species diversity is higher in oligotrophic than in eutrophic water. On the basis of current information, measurements of phytoplankton community structure appear to be of limited value as indicators of trophic state and as a means of comparing and contrasting algal assemblages in different regions of the Lake. Tarapchak (1975--unpublished) recently evaluated data on species diversity from Lakes Superior, Michigan, and Ontario. He found that mean diversity values for Lakes Superior and Ontario were statistically different, but that some data sets from Lake Michigan did not differ from diversity measurements in Lakes Ontario and Superior. Further studies and the use of appropriate statistical analyses, however, are necessary to validate or to reject the utility of diversity measurements in Lake Michigan.

Spatial and Temporal Variations in the Standing Crop and Composition of Diatoms and Phytoplankton

Quantitative studies on diatom assemblages and total phytoplankton communities demonstrate that algal abundance varies seasonally and appears to be less stable inshore than offshore. Regions of the Lake supporting dense populations generally are those receiving nutrient inputs from polluted rivers. Precise comparisons of the results of different studies are nearly impossible to make because investigators have used different methods to collect, concentrate, and express quantitative data. (See the section on Sampling Problems and Quantitative Phytoplankton Methods, p. 169.) A summary of phytoplankton abundance levels in Lake Michigan is given in Table 15.

One of the current controversies concerning phytoplankton growth in Lake Michigan is based on the importance of temperature as a factor leading to the development of a unimodal maximum at the water filtration plant at Milwaukee and a bimodal pattern of abundance at Chicago (Damann, 1960, 1966). It should be pointed out that although the data presented by Damann provide strong circumstantial evidence implicating water temperature as a critical variable in plankton growth, Holland (1969) observed that maximal sizes of diatom populations do not always develop at an optimum temperature of 10°C. Her data indicate that planktonic diatoms were most numerous at inshore Michigan stations in late May when the water temperature was 10.2°C and at offshore Wisconsin stations in early July when the temperature was 10.6°C. Maximum diatom abundance occurred at temperatures of 18.2°C in August at offshore stations in Lake Michigan. Observations of water temperature and diatom abundance show maxima in June and October at 14.7°C and 12.1°C in Green Bay, and maxima on 16 April at 1.3°C near inshore Wisconsin.

In contrast, Stoermer and Kopczynska (1967) and Stoermer (1974) provided previously unavailable information on the apparent importance of temperature in (*i*) the initiation of spring diatom peaks, (*ii*) the seasonal patterns of regional distribution of phytoplankton, and (*iii*) the occurrence of unimodal

versus bimodal maxima in the Lake. These authors observed that phytoplankton pulses are initiated inshore and follow the advance of thermal contours out into offshore water. Apparently, warming water that is moderately high in nutrients is conducive to the rapid growth of phytoplankton. As the water warms gradually and moves progressively farther out into the basin, pulses of diatoms develop. These trends are suggested in Figures 42-46 and are illustrated dramatically in a later section (Phosphorus, Silica, and Eutrophication, Figs. 55-62 and 68-75). It can be pointed out that a related phenomenon also occurs near Grand Haven, Michigan. Stoermer (1968) demonstrated that dense concentrations of phytoplankton develop between the thermal bar and the shoreline, and that the phenomenon is largely attributable to high concentrations of nutrients trapped in rapidly warming nearshore water.

Table 15. A Summary of Diatom and Total Phytoplankton Abundance Measurements for Lake Michigan

Location	*No. of Stations*	*Range*	*Mean*	*Comments*	*Reference*
				Diatoms	
Central region				Average standing crop of *Melosira* spp., April-November 1965. Based on 219 samples taken at 2, 5, 10 m from 4 regions in Lake Michigan and 1 location in southern Green Bay. Counting unit: diatom frustules/ml and biomass in µg/l (in parentheses).	Holland, 1968
Inshore Michigan	2	ID	813 (0.5)		
Offshore Michigan	2	ID	390 (0.23)		
Offshore Wisconsin	2	ID	350 (0.17)		
Inshore Wisconsin	2	ID	514 (0.23)		
Green Bay	3	ID	944 (2.24)		
Inshore Michigan	2	ID	754	Average diatom standing crop, April-November 1965. Based on 219 samples taken at 2, 5, 10 m from 4 regions in Lake Michigan and 1 location in southern Green Bay. Counting unit: diatom frustules/ml.	Holland, 1969
Offshore Michigan	2	ID	416		
Inshore Wisconsin	2	ID	480		
Offshore Wisconsin	2	ID	281		
Green Bay	3	ID	976		
Inshore Wisconsin	1	ID	753	Average diatom standing crop, May 1970-January 1971. Samples taken at 4 m from 5 stations along a Milwaukee-Ludington transect. Counting unit: diatom frustules/ml.	Holland and Beeton, 1972
Offshore Wisconsin	1	ID	345		
Mid-Lake	1	ID	362		
Offshore Michigan	1	ID	353		
Inshore Michigan	1	ID	445		
Green Bay				Standing crop of diatoms based on samples taken at 2 m, mid-July 1970. Counting unit: frustules/ml.	Holland and Claflin, 1975
Southern (extreme)	25	650-5926	3342		
Northern and western	17	325-1086	607		
Southern and eastern	26	0.5-832	146		
Waukegan/Zion, Ill.				Monthly surface samples from each location, May 1970-March 1971. Counting unit: units/ml.	Piala and Lamble, 1971
Waukegan	1	205-2600	1688		
Dead River	1	226-3723	1673		
Zion	1	299-3742	1706		
Offshore	1	129-1195	493		
Waukegan/Zion, Ill.				Monthly near-surface samples from each location, May 1970-March 1971. Counting unit: units/ml	Gulo and Lamble, 1971
Waukegan intake	1	331-4946	2498		
Waukegan discharge	1	562-4887	2528		
Zion	1	422-3152	1878		
North Chicago	1	589-3191	1673		
Kenosha	1	494-4384	1756		
Waukegan/Zion, Ill.				Monthly samples at 1 m from 3 stations at each location, April 1971-March 1972. Counting unit: units/ml.	Huh *et al.*, 1972
Zion	3	89-4889	2388		
Dead River	3	138-5519	2286		
Waukegan	3	284-5877	2568		
Benton Harbor, Mich.	Sampling grid	94-2028	455	Surface samples from 53 stations near the Cook Power Plant, 10 July 1970. Counting unit: cells/ml.	Ayers *et al.* 1972a
				Total Phytoplankton	
Synoptic survey				Surface-water samples pooled by location, October 1967. Phytoplankton settled in Imhoff cones and counted by Sedgewick-Rafter method. Counting unit: organisms/ml. Overall mean: 1550 organisms/ml (early October) and 640 organisms/ml (late October).	Parkos *et al.*, 1969
Northern region					
Early October	ID	ID	1370		
Late October	ID	ID	510		
Central region					
Early October	ID	ID	1490		
Late October	ID	ID	660		
Southern region					
Early October	ID	ID	1780		
Late October	ID	ID	750		
Synoptic survey				Lake-wide samples collected at intervals of 0, 15, 30, 50, 75, and 100 m from the surface and at surface, mid-depth, and near bottom, 1962-1963. Counting unit: organisms/ml. Overall mean: 1966 organisms/ml.	USDOI, 1968a
Spring 1962	45	165-3696	730		
Summer 1962	38	28-1067	310		
Fall 1962	34	66-2229	505		
Spring 1963	29	357-6310	1731		
Summer 1963	15	352-60,088	6552		

Table 15. (contd.)

Location	No. of Stations	Range	Mean	Comments	Reference
Michigan City, Ind.-Sawyer, Mich.				Two or three samples per location, 1926-1927. Quantitative surface tows taken near the shore using a silk plankton net. Counting unit: organisms/ml. Overall mean: 6.2 organisms/ml.	Eddy, 1927
Dunes Park, Ind. (October 1926)	1	ID	2.6		
Michigan City, Ind. (October 1926)	1	ID	2.0		
Sawyer, Mich. (October 1926)	1	ID	0.5		
Gary, Ind. (May 1927)	1	ID	8.9		
Dunes Park, Ind. (May 1927)	1	ID	6.2		
Dunes Park, Ind. (May 1927)	1	ID	5.7		
Chicago, Ill. (July 1927)	1	ID	17.7		
Evanston, Ill.	1	687-4507	2169	49 surface-water samples analyzed, April 1953-April 1954. Counting unit: units/ml.	Griffith, 1955
Evanston, Ill.	1	250-2084	760	Weekly surface-water samples analyzed, May 1937-May 1938. Counting unit: organisms/ml.	Daily, 1938
Evanston, Ill.	1	96-687	367	Weekly surface-water samples analyzed, November 1938-November 1939. Counting unit: organisms/ml.	Damann, 1941
Chicago, Ill.				Long-term yearly average plankton standing crops at the Chicago Water Filtration Plant. Counting unit: organisms/ml.	Damann, 1960
1926-1942	1	760-1277	957		
1926-1958	1	-	1086		
1943-1958	1	772-1778	1222		
Milwaukee, Wis.	1	353-1381	779	Long-term average plankton standing crops at the Milwaukee Water Filtration Plant based on monthly averages, 1940-1963. Counting unit: organisms/ml.	Damann, 1966
Benton Harbor, Mich.	9	186-1262	844	Monthly samples from 9 stations near the Cook Power Plant, April-November 1972. Counting unit: cells/ml.	Ayers and Seibel, 1973
Benton Harbor, Mich.	53	140-13,000	1300	Surface-water samples from 53 stations near the Cook Power Plant, 10 July 1970. Counting unit: cells/ml.	Ayers *et al.*, 1972a
Benton Harbor, Mich.	9	977-2062	1537	Monthly samples from 9 stations near the Cook Power Plant, April-October 1973. Counting unit: cells/ml.	Seibel and Ayers, 1974
Waukegan/Zion, Ill.				Monthly samples at 1 m from 3 stations at each location, April 1971-March 1972. Counting unit: units/ml.	Huh *et al.*, 1972
Zion	3	180-8000	2300		
Dead River	3	110-8900	2500		
Waukegan	3	510-8700	2700		
Waukegan/Zion, Ill.				Monthly samples at 2 m from each location, May 1970-March 1971. Counting unit: units/ml.	Piala and Lamble, 1971
Waukegan	1	275-2714	1809		
Dead River	1	290-3831	1762		
Zion	1	410-3908	1737		
Offshore	1	202-1240	602		
Waukegan/Zion, Ill.				Monthly near-surface samples from each location, May 1970-March 1971. Intake and discharge canals located at Waukegan Power Station. Counting unit: units/ml.	Gulo and Lamble, 1971
Waukegan intake	1	750-5100	2677		
Waukegan discharge	1	750-5200	2840		
Zion	1	600-6000	2091		
North Chicago	1	750-3400	1827		
Kenosha	1	650-5000	1891		
Grand Haven, Mich.				Samples at 7 m from inshore (18) and offshore (8) stations, July-September 1969. Counting unit: cells/ml.	Schelske *et al.*, 1971
Inshore	1	420-2100	1000		
Offshore	1	290-1300	680		
Grand Traverse Bay				Samples from east arm, west arm, and open bay at 5-m depth, May-June 1970. Counting unit: cells/ml.	Stoermer *et al.*, 1972
May	12	1500-3400	2100		
June	12	2500-6500	4300		

Symbols: ID = Insufficient data to identify range values; USDOI = U. S. Department of the Interior.

Data provided by Stoermer (1974) and Stoermer and Kopczynska (1967) also provide evidence that the unimodal curve, evidenced in nearshore water at Milwaukee, may be more characteristic of the main water mass of the Lake than the bimodal curve observed at Chicago. Holland (1969) also expressed the same view. It can be observed from Stoermer's (1974) data that from April through mid-July, phytoplankton abundance at mid-lake on a line between Waukegan and South Haven was very low. From late August through early October, standing crop levels increased gradually and reached an apparent maximum in late October (see Figs. 55-62). Similarly, seasonal variations in abundance at Station 5 (Figs. 41-46) suggest that a single maximum occurred in mid-lake.

Both of the above data sets and the observations of Holland (1969) and Holland and Beeton (1972) suggest that a bimodal curve similar to the one at the water intake at Chicago occurs in nearshore water in southern Lake Michigan and offshore in the extreme southern portion of the Lake. It is entirely possible that a bimodal curve develops in water of higher nutrient content.

Such conditions are present in the southern region of the Lake, but nutrient levels are probably not as high in the main water mass of central and northern Lake Michigan where a unimodal curve apparently develops.

An alternative explanation for the occurrence of the spring bloom (especially sudden, dramatic population increases) in the southern basin is based on thermocline formation and critical depth of mixing. As the water warms rapidly in relatively shallow areas, a thermocline develops and thus stabilizes the water column. Phytoplankton populations are no longer carried below the euphotic zone where light limits growth. Instead, they are concentrated in relatively warm, well-lighted water where nutrient concentrations are high, especially in the spring.

A further discussion of the factors that affect the growth of phytoplankton in Lake Michigan, especially interactions between limiting concentrations of phosphorus, nitrogen, and silica, is presented in the section on Phosphorus, Silica, and Eutrophication (p. 114), and the section on Phytoplankton Ecology in Green Bay (p. 160).

PRIMARY PRODUCTIVITY

Primary productivity is a unifying concept in modern aquatic research (*cf.* Likens, 1972; Goldman, 1965; Saunders, 1963). The rate and amount of carbon fixed at the primary producer level can determine the amount of matter and energy available for transfer and use at higher trophic levels. Despite the obvious importance of primary productivity of Lake Michigan phytoplankton, investigations have been restricted to a few studies until recently because of logistical problems, economic factors, and inadequate or unsuitable analytical techniques. During the last ten years, however, several significant studies have been executed. The information presented in this section is divided into four major subsections. The first treats methodology, the application of the radiocarbon technique to Lake Michigan, and the use of the radiocarbon method in nutrient-enrichment experiments. The second presents the results of seasonal studies carried out at *fixed* stations. Investigations of regional differences in primary production are summarized in the third subsection. A synopsis of this information is presented in the last subsection.

METHODOLOGY OF MEASURING PHYTOPLANKTON PHOTOSYNTHESIS

Several methods can be used to estimate phytoplankton photosynthesis. A detailed treatment of methods is beyond the scope and intent of the present report. Principles and limitations of the techniques can be found in Strickland (1960), Strickland and Parsons (1968, 1972), Ryther and Yentsch (1969), Vollenweider (1969, 1974), and Steemann-Nielsen *et al.* (1974).

In Lake Michigan, nearly all investigations on primary productivity are based on the radiocarbon technique. This procedure involves the addition of radiocarbon, usually in the form of ^{14}C-labeled $NaHCO_3$, to samples of lake water. The samples are placed in light and dark bottles *in situ* or *in vitro* and put in an incubator for a period of hours up to a day. After incubation, samples are filtered through filters, and the radiocarbon content of the particulate material is assayed by any one of several instruments that detect β radiation. Both Geiger-Müller planchet counters and liquid scintillation spectrometers are commonly used.

Since the introduction of the radiocarbon method by Steemann-Nielsen (1952), this procedure has been modified and refined through continuous use. It is believed that measurements using the technique approximate net primary productivity. The method is sensitive and relatively easy to use, but it is moderately expensive. Despite widespread use of the method in fresh and marine water, a number of errors can affect its accuracy and precision. Four errors can introduce a significant bias into estimates of photosynthesis: (*i*) leakage of labeled carbon from algal cells due to preservation and filtration procedures, (*ii*) failure to extrapolate radiocarbon counts to infinite thinness in planchet counting, (*iii*) non-biological or non-photosynthetic *fixation* of radiocarbon, and (*iv*) release of ^{14}C-labeled extracellular metabolites and significant uptake of carbon in dark bottle controls by photosynthesizing populations. These and related analytical problems are discussed by numerous authors, including Arthur and Rigler (1967), Wetzel (1965), Schindler and Holmgren (1971), Nalewajko (1966), and recently by Eppley and Sharp (1975), and Vollenweider (1974).

Application of the Radiocarbon Technique and Experimental and Theoretical Procedures for Estimating Primary Productivity in Lake Michigan

Two major studies have been undertaken to investigate experimental and theoretical procedures for estimating primary productivity in Lake Michigan. The first was by Saunders *et al.* (1962) in Grand Traverse Bay and in Douglas Lake, Michigan. They attempted to evaluate several calculative and theoretical procedures proposed by Sorokin (1956) and Ryther and Yentsch (1957) for determining integral* photosynthesis. Measurements of *in situ* primary productivity were compared with estimates from an incubator on board the vessel and with estimates derived by various theoretical formulae (Table 16). The procedures and a statistical treatment of data are presented in detail by the authors. The results indicate that the calculative methods of Sorokin can be used to predict integral photosynthesis at different locations in the Lake, and they can be regarded as useful tools for general survey work. The empirical formulae of Ryther and Yentsch (1957) and Rodhe *et al.* (1958) also yield estimates of primary productivity that provide first-order approximations of true photosynthetic rates.

Recently, Fee (1969, 1973a) developed a computer-based model and experimental technique for determining integral primary productivity in phytoplankton communities. Fee, among others, contended that hourly variations in photosynthesis often are extremely large; therefore, daily estimates are needed to provide reliable estimates of seasonal or annual production rates. Obviously, daily *in situ* estimates are impractical on a large scale because of logistics and cost factors.

The model developed by Fee (1973a) is based on four assumptions: (*i*) uniform distribution of phytoplankton in an isothermal and optically homogeneous euphotic zone, (*ii*) constant physiologic properties of phytoplankton from sunrise to sunset, (*iii*) requisite parameters which can be measured experimentally in the lake or predicted with a reasonably high degree of accuracy,

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**Integral photosynthetic rate refers to the amount of carbon fixed by phytoplankton in a vertical water column. It is common practice to calculate primary productivity beneath a square meter of lake surface.*

and (*iv*) utilization of a single extinction coefficient to characterize light penetration. A detailed description of the methods and the equations are presented by Fee (1973a, 1973b).

Fee tested the model predictions by performing two sets of *in situ* experiments in Lake Michigan. On 19 October and 20 November 1970, integral photosynthesis was measured *in situ* at a station 16 km off the Wisconsin shore at Milwaukee. The agreement between actual *in situ* estimates and those based on the model and experimental techniques was extremely good for both dates.

The experimental data necessary to relate solar radiation to photosynthetic rates in Fee's model are generated by performing primary productivity experiments in a specially designed incubator. The procedure is similar to

Table 16. A Summary of Primary Productivity Measurements Made in Lake Michigan

		Productivity/Unit Volume/Hour, mg C/m^3/hr			
Location	*No. of Measurements*	*Range*	*Mean*	*Comments*	*Reference*
Northern basin	13	0.86-3.09	2.40	Estimates from 4 stations on 2 cruises, July 1968; surface water incubated on board using methods of Schelske and Callender (1970).	Schelske and Roth, 1973
Synoptic survey				Two synoptic cruises (39 stations), July-August 1969; water from 2, 5, or 10 m placed in shipboard plexiglass incubator, light reduced by 53 and 68%, 4- to 6-hr incubations at ambient lake temperatures.	Schelske and Callender, 1970
Northern basin					
S. Green Bay	3	18.2-45.9	27.9		
N. Green Bay	6	3.34-5.49	4.41		
Lake stations	16	1.77-5.85	3.06		
Southern basin	14	1.04-9.79	3.55		
Total (excluding Green Bay)	30	1.04-9.79	3.17		
Synoptic survey				Northbound and southbound cruises (17 to 24 samples), 1967; surface water incubated at 15.5°C for 4 hr at 1000 footcandles.	Parkos *et al.*, 1969
1-3 July	21	0.73-4.33	2.10		
17-19 July	17	0.70-4.37	2.03		
6-8 October	24	2.35-9.28	4.13		
23-26 October	24	1.03-8.30	4.39		
Total	86	0.70-9.28	3.14		
Central region				Optimum photosynthetic rate [highest rate observed in Fee's (1973a) incubator], May 1970-October 1971; surface water from 5 stations incubated for 4 hr at ambient lake temperatures at 8- to 21-day intervals.	Rousar, 1973
Inshore Wisconsin	32	3.1-31.0	8.60		
Offshore Wisconsin	32	0.9-5.2	2.70		
Mid-Lake	32	0.6-5.2	2.30		
Offshore Michigan	32	0.8-5.3	2.50		
Inshore Michigan	32	1.0-10.6	3.40		
Grand Traverse Bay				Triplicate samples at 5 m from 12 stations, May-June 1970; incubated by methods of Schelske and Callender (1970).	Stoermer *et al.*, 1972
May	12	4.5-8.63	5.51		
June	12	2.74-13.44	5.88		
Grand Traverse Bay	11	1.43-5.78[a]	3.46[a]	Quadruplicate samples collected July and August 1959; incubated *in situ* at 5 m for 24 hr.	Saunders *et al.*, 1962
Grand Haven				Samples collected July-September 1969; incubated by methods of Schelske and Callender (1970).	Schelske *et al.*, 1971
Inshore	14	4.0-12.5	6.49		
Offshore	8	3.0-8.5	4.90		
Grand Haven				Photosynthetic rates measured by CO_2 change indicated by Δ pH.	Verduin, 1972
Inshore	ID	ID	31.0		
Offshore	ID	ID	4.8		
Kenosha	9	0.15-2.23	0.75	Monthly triplicate samples collected August 1970-April 1971; incubated at 500 footcandles for 4 hr at ambient lake temperatures.	Delinck and Lamble, 1971

Table 16. (contd.)

Location	No. of Measurements	Productivity/Unit Lake Surface/Day, mg C/m^2/day Range	Mean	Comments	Reference
Grand Traverse Bay Experimental*					Saunders *et al.*, 1962
In situ	11	295-536	456	Quadruplicate samples from 5, 10, 15, 20, 25 m, July-August 1959.	
Calc. ^{14}C	11	265-551	441	Constant light and optimum-depth photosynthesis.	
Calc. chlorophyll	11	267-679	438	Chlorophyll *a* and optimum-depth photosynthesis.	
Day ^{14}C	11	220-726	436	Constant light and daylight aquarium photosynthesis.	
Day chlorophyll	11	228-696	411	Chlorophyll *a* and daylight aquarium photosynthesis.	
Calc. transparency	11	246-554	411	Optimum-depth photosynthesis (absolute photosynthesis as reference).	
Calc. ^{14}C relative to 0 m	11	252-513	372	^{14}C calc. (surface photosynthesis as reference)	
Theoretical**					
Average chlorophyll	11	180-531	332	Ryther and Yentsch (1957): radiation, transparency, chlorophyll.	
Specific chlorophyll *a*	11	191-434	272	Ryther and Yentsch (1957): relative photosynthesis and chlorophyll.	
Photosynthesis light sat.	11	211-509	381	Ryther and Yentsch (1957): gross photosynthesis of unit population of phytoplankton.	
Optimal *in situ* photosynthesis	11	242-530	380	Rodhe *et al.* (1958): carbon assimilation in optimal photosynthetic layer and light extinction.	
Central region				22 *in situ* estimates based on experimental incubation of surface water and a computer-based model, May 1970-February 1971.	Fee, 1973a
Station 1	22	∿100-1600	∿670		
Station 2	22	∿100-900	∿380		
Station 3	22	∿100-700	∿331		
Station 4	22	∿175-1100	∿381		
Station 5	22	∿175-1400	∿512		

[a]*Hourly rate assuming a 12-hr day.*

**Calculative methods, computations, and statistical analyses are given in detail by Saunders et al. (1962).*

***Theoretical methods, computations, and statistical analyses are given in detail by Saunders et al. (1962).*

Symbol: ID = insufficient data in publication to determine number of measurements or range and mean values.

the one proposed by Steemann-Nielsen (1952). Samples of lake water from a depth of 4.0 m were placed in 300-ml BOD bottles and mounted on four rotating discs; each sample bottle received a different light intensity. The amount of visible light striking the bottles was measured directly with a spectroradiometer. Using these data and the model equation, Fee estimated seasonal patterns and annual rates of primary production in the Lake. The results are described in a later section.

Nutrient-Enrichment Experiments

One of the current uses of the radiocarbon technique is in nutrient-enrichment or *perturbation* experiments, where one or more nutrients are added to a sample of lake water and the response of phytoplankton is measured by an increase or decrease in photosynthetic rate. This technique has been used widely in north-temperate lakes (*cf.* Likens, 1972; Goldman, 1965) to determine which nutrient or nutrients limit phytoplankton growth in Lake Michigan (*cf.* Schelske and Stoermer, 1971, 1972; Stoermer *et al.*, 1971).

A number of criticisms have been leveled at nutrient-enrichment techniques and at the interpretation of experimental data (*cf.* Schindler *et al.*, 1973). A major criticism is that a stimulation of photosynthetic rate may be a transient or temporary phenomenon, *i.e.* a nutrient may increase the rate of carbon fixation, but it may not result in an actual increase in algal biomass over the course of several generations. It also is argued that samples enclosed in bottles or similar containers may respond differently to nutrient additions than populations in open water. This can occur through a variety of *bottle* effects, such as alteration in light climate, enhanced bacterial growth, alterations in regeneration rates of nutrients, or changes in turbulence (*cf.* Strickland, 1960). Despite inherent limitations, the technique provides some insight into nutrient limitation in phytoplankton communities, and it can be used to investigate some physiological properties of phytoplankton.

Design of Experiments

Schelske and Stoermer (1971, 1972) and Stoermer *et al.* (1971) have used radiocarbon as a tracer in enrichment experiments to identify nutrients limiting phytoplankton growth in Lake Michigan. The design of their experiments and the types of phytoplankton responses are discussed below as general background information. The experimental results are presented in detail in the section on Phosphorus, Silica, and Eutrophication (p. 114).

In most nutrient-enrichment experiments, investigators use small containers, *e.g.* BOD bottles or glass flasks. The procedures employed in Lake Michigan, however, differ substantially from conventional methods. The authors used 4-mil polyethylene plastic bags (1000- or 4000-l capacity). The bags are filled with lake water, using nonmetallic pumps. Phytoplankton samples and water for chemical analyses are taken from the bags by scuba divers who insert a sampling hose and obtain water with submersible pumps.

The use of large plastic bags has several advantages over other incubation techniques. First, phytoplankton are exposed only briefly to high light intensities, and thermal *shocks* are essentially avoided. Second, the surface-to-volume ratio of the bags is less favorable for bacterial growth than that of small containers. Third, sufficient volumes of lake water are available for chemical and biological analyses over the course of several weeks. This allows continous monitoring of changes in phytoplankton composition and abundance over extended periods of time. In long-term experiments, the authors failed to detect the growth of bacteria and algae on the outer surface of the bags, so they assumed that the light climate was not significantly different than that in open water.

The technique, however, has at least one disadvantage. The bags occasionally cannot withstand high turbulence over the period of the experiment. When rupturing of the bags resulted in leakage equivalent to one-fourth of the original volume, the authors discarded the results of an experiment.

Type Responses

In enrichment experiments on Lake Michigan, Schelske and Stoermer (1971, 1972) and Stoermer *et al.* (1971) attempted to detect the effects of phosphorus, nitrogen, and silica on phytoplankton photosynthesis and to evaluate the effects of these nutrient additions on phytoplankton species composition and abundance. Three basic types of response were observed.

The first was no response to any nutrient addition. The authors speculated that an inhibitory or toxic substance may have been present. *Anabaena flos-aquae* was in the phytoplankton, and it is possible that external metabolites or toxic products liberated by cell lysis of this blue-green alga inhibited the growth of other species (*cf.* Hartman, 1960; Fogg, 1962, 1966; Gorham, 1964; Gorham *et al.*, 1964; Vance, 1965). It also is possible that nutrients other than those added at the time of the experiment were limiting growth. This type of response was first observed in July near the mouth of the Grand River.

The second type of response was characterized by a stimulation of photosynthesis and by increases in phytoplankton abundance in bags receiving nutrient additions. The experiments were invalidated, however, because the control bags also showed comparable increases in primary productivity and cell numbers. Since the control bags did not receive nutrient additions, the authors speculated that the lake water was high in nutrients at the onset of the experiment and, therefore, phytoplankton was unaffected by further elevation of nutrient concentration.

The third type of response was characterized by control bags that exhibited a minimal response to enclosure and by increases in cell numbers and primary productivity in bags receiving nutrient additions. This type of response was detected most frequently by the authors. They have used these experimental data to explain relationships between phosphorus and silica limitation in Lake Michigan. The results and their interpretations are presented in the section on Phosphorus, Silica and Eutrophication (p. 114).

SEASONAL VARIATIONS IN PRIMARY PRODUCTIVITY AT FIXED STATIONS

There have been three studies on seasonal variations in primary productivity at fixed stations. Recent studies by Fee (1973a) and Rousar (1973) also provide data on primary productivity at several fixed stations. Their results, which include comparative information on production rates for inshore and offshore stations, are presented in the following subsection on Regional Variations in Primary Productivity (p. 106).

Grand Haven Area

Studies by Schelske *et al.* (1971) near Grand Haven, Michigan, provide baseline information on seasonal variations in primary productivity at an inshore and an offshore station in the eastern region of the Lake. These studies were carried out July to September 1969, in conjunction with observations of fluctuations in water chemistry and phytoplankton composition and abundance (Fig. 18, Tables 3-6). Water samples were collected at 7 m, dispensed into Pyrex glass-stoppered bottles, and taken to the R/V Inland Seas for on-board incubation. The flasks were wrapped in plastic window screen, reducing light intensity by 50%.

Rates of photosynthesis during the period ranged between 3.1 mg $C/m^3/hr$* (offshore) and 12.3 mg $C/m^3/hr$ (inshore) (Fig. 53). On each day, higher

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**Notation of rate function expressed as quantity y/unit volume or weight/unit time is employed for editorial convenience, and means the same as quantity y (unit volume or weight)$^{-1}$ (unit time)$^{-1}$ (e.g. 3.1 mg C m^{-3} hr^{-1}).*

production rates were obtained at the inshore station; however, there was considerable variation at both stations on successive sampling dates. The only periods of relatively constant primary productivity were in July at the offshore station (∿4.0 mg C/m^3/hr) and in mid- to late September at the inshore station (5.5-6.5 mg C/m^3/hr).

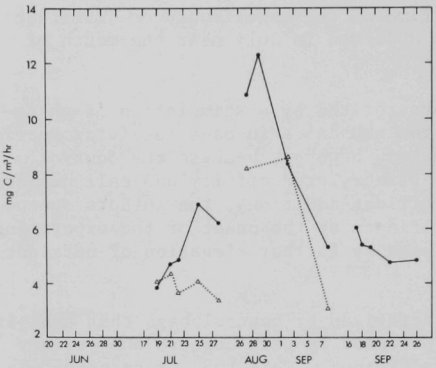

Fig. 53.

Rates of Carbon Fixation Determined by ^{14}C Method at Inshore (solid circles) and Offshore (open triangles) Stations. Redrawn from Schelske *et al.* (1971) (with permission, see credits).

The highest photosynthetic rates at the inshore station were observed during a period of upwelling of nutrient-rich bottom water. According to the authors, the higher rates can be attributed largely to a sudden elevation in nutrient concentration in the euphotic zone and to a large standing crop of phytoplankton. The peak in primary productivity at the nearshore station coincides with an increase in phytoplankton abundance.

Waukegan-Zion Area

As part of a monitoring program near the Waukegan Generating Station in southwestern Lake Michigan, Nalco Chemical Company initiated studies on primary productivity. Delinck and Lamble (1971) attempted to determine the effects of elevated water temperatures on photosynthetic rates. The investigations are of particular interest because they appear to represent the only experimental data on the effects of temperature on photosynthetic rates of Lake Michigan phytoplankton.

Investigations were carried out at an inshore station near Kenosha, Wisconsin, and at the water intake at the water treatment plant. Lake water was withdrawn 1370 m offshore at 9.1 m. Monthly sampling was carried out from August 1970 to April 1971. Primary productivity was measured by the techniques of Wetzel (1964). In addition, chlorophyll *a*, *b*, and *c* were determined (Richards and Thompson, 1952), phytoplankton species were identified and counted, and temperature, nitrate-nitrogen, dissolved silica, and total phosphorus were measured.

The phytoplankton generally was dominated by diatoms (*Stephanodiscus hantzschii* vel. *tenuis*, *Fragilaria crotonensis*, and *Tabellaria flocculosa*), although blue-green algae (*Gomphosphaeria aponina* and *Coelosphaerium naegelianum*) were moderately abundant during some months. The period of maximum abundance occurred between November 1970 and March 1971 (1861-2028 reporting units/ml), and minimum standing crop levels were detected from

August through October (660-1662 reporting units/ml). The numerical values of reporting units are presented in the section on Sampling Problems and Quantitative Phytoplankton Methods (p. 169).

Chlorophyll *a* concentrations were less variable than levels of chlorophyll *b* and *c*, and were reasonably well correlated with phytoplankton abundance. Chlorophyll *a* concentrations were relatively low from August to October 1970 (2.80-3.76 mg/m^3), and high during November, December, February, and April (4.79-6.09 mg/m^3). The periods of low primary productivity occurred during August-November and in April (0.15-0.21 mg $C/m^3/hr$). High productivity occurred during December-March (0.91-2.23 mg $C/m^3/hr$).

The authors performed correlation and regression analyses to determine whether significant relationships existed between primary productivity and population density. Because of the observed periods of low and high productivity, analyses were conducted separately. The results indicated that the correlation between primary productivity and phytoplankton density was statistically significant during periods of low productivity (r = 0.89) and during times of high productivity (r = 0.94) as well. Similarly, chlorophyll *a* concentrations were positively correlated with primary productivity during low (r = 0.95) and high (r = 0.87) periods of productivity. Chlorophyll levels also were positively correlated with phytoplankton counts; coefficients of 0.93 during both periods were detected.

Delinck and Lamble concluded from these observations that the low carbon-fixation values cannot be explained entirely on the basis of variations in chlorophyll concentrations or phytoplankton abundance. Because the slopes of the regression lines differ during periods of high and low productivity, it appears that phytoplankton communities during the two periods were physiologically dissimilar, and their growth was limited by different factors.

The studies of the effects of temperature on phytoplankton photosynthesis indicated that phytoplankton responded differently to experimental temperature regimes. During November and December, temperature elevations resulted in a decrease in productivity. During all other months, however, the phytoplankton responded to temperatures of 5-15°C over ambient by increases in photosynthetic rate. The authors concluded that since the experimental temperature regimes used in the study were twice as high as expected temperature increases at the proposed Zion plant, heated effluents in all probability will not result in large increases in phytoplankton photosynthesis.

Grand Traverse Bay

Saunders *et al.* (1962) measured primary productivity at a fixed station (44°47.3', 85°37.5') in Grand Traverse Bay. The authors attempted to evaluate and compare various calculations and theoretical methods with actual measurements of *in situ* primary productivity (Table 16). Quadruplicate samples of water from six depths (0, 5, 10, 15, 20, and 25 m) were injected with ^{14}C-labeled Na_2CO_3 and incubated for 24 hr on 11 dates during July-August 1959. Production rates ranged from a low of 295 to a high of 536 mg $C/m^2/day$ on 3 July and 20 August, respectively. Volumetric estimates of photosynthetic rate varied with depth and time. Maximum rates normally occurred at depths of 5-10 m rather than at the surface. Some of the calculative and theoretical methods used to estimate integral production were in reasonably good agreement with the *in situ* measurements (Table 16).

REGIONAL VARIATIONS IN PRIMARY PRODUCTIVITY

Several studies have been undertaken specifically to detect regional differences in primary productivity in the Lake. The design and salient observations of each study are summarized in the following text.

North-to-South Transects

An investigation by Parkos *et al.* (1969) provides the only data on spatial variations in primary productivity along north-to-south transects in the Lake. The primary objectives of the study were to determine regional differences in photosynthetic rates, to evaluate seasonal variations in primary productivity, and to compare primary productivity in four of the Great Lakes.

The authors conducted two sampling cruises, each consisting of a north-bound and a south-bound transect, during July and October 1967, from the SS Cason J. Calloway. Samples of surface water were collected by a weighted plastic jug, poured into BOD bottles, and injected with ^{14}C-labeled $NaHCO_3$. Light and dark bottles were incubated aboard in chambers at 1000 footcandles and at a temperature of 15.5°C. After a 4-hr incubation, samples were filtered through 0.45-μm Millipore filters and washed with 250 ml of distilled water. Filters were dried in a desiccator, stored, and assayed by using a liquid scintillation spectrometer. Temperature, pH, bicarbonate alkalinity, and total solids were measured, and free CO_2 and total available CO_2 were computed (APHA, 1960).

The results, expressed as 4-hr rates, are shown for selected dates in Figures 51 and 52. The sampling run of 1-3 July consisted of a south-bound cruise bisecting the Lake and a north-bound cruise following the eastern shoreline. The range in primary productivity for 21 determinations was large, varying between 0.73 (Station 2) and 4.33 mg $C/m^3/hr$ (Station 18). The mean for all determinations was 2.03 mg $C/m^3/hr$. Stations 1, 2, 20, and 21 in the northern region of the Lake and Stations 9, 13, and 14 in the south-central region were below the mean. The highest levels in the southern basin were detected inshore near Chicago (Stations 11 and 12). The south- and north-bound cruises yielded nearly identical average values, 2.04 and 2.01 mg $C/m^3/hr$, respectively. On the average, primary productivity was low in the south-central region and relatively higher in the northern and north-central part of the Lake.

The results of the 17-19 July cruise (not shown on Figs.) were similar to those of the previous cruise. Estimates of primary productivity beyond Station 7 on the south-bound trip were discarded because of experimental error. Primary productivity ranged from 0.70 (Station 9) to 4.38 mg $C/m^3/hr$ (Station 1), with a mean of 2.03 mg $C/m^3/hr$ for 17 determinations. The highest values occurred in the northern portion of the Lake, except for Station 2. The production rates were noticeably lower in the southern basin. The high rates observed in inshore water during early July were not in evidence, although Station 8 was located farther offshore than Stations 11 and 12 of the early July cruise.

The third sampling cruise, conducted on 6-8 October (Fig. 52), consisted of 24 stations spaced within 40 km of one another. Levels of primary productivity were much higher than in July, ranging from 2.35 (Station 1) to 9.28 mg $C/m^3/hr$ (Station 13). A mean of 4.13 mg $C/m^3/hr$ was twice the average

value detected for the July cruises. Estimates (range 2.35-5.53, mean 3.20 mg $C/m^3/hr$) made along the mid-section of the south-bound cruise were lower than on the north-bound cruise nearer the eastern shore (range 3.48-9.28, mean 5.05 mg $C/m^3/hr$). Extremely high photosynthetic rates were observed at Stations 12 (5.53 mg $C/m^3/hr$) and 13 (9.28 mg $C/m^3/hr$) near Chicago, and at Stations 17-22 ($\sim$5.0 mg $C/m^3/hr$) along the eastern shore.

The fourth sampling cruise, conducted on 23-26 October (not shown on Figs.), included a south-bound cruise through mid-lake and a north-bound cruise following the western shore. Productivity values were high, similar to levels observed in early October. Rates for the 21 stations ranged from 1.03 (Station 20) to 8.30 (Station 12) mg $C/m^3/hr$, with a mean of 4.38 mg $C/m^3/hr$. Lowest values were detected at Stations 18-21 along the north-central shore (<2.5 mg $C/m^3/hr$); highest values were detected at Stations 6-17 (excluding Station 10) in the central and southern region of the Lake. Station 12, situated off Chicago, exhibited the highest level of primary productivity. In general, levels of primary productivity were higher on the south-bound ($\bar{x}$ = 5.05 mg $C/m^3/hr$) than on the north-bound ($\bar{x}$ = 3.50 mg $C/m^3/hr$) cruise, and values generally were higher in the southern half of the Lake.

Northern versus Southern Basin and Green Bay

Schelske and Callender (1970) carried out a comparative study on primary production rates of surface water in northern and southern Lake Michigan and in Green Bay as part of a general study on the eutrophication of Lake Michigan. The authors also measured concentrations of nitrate-nitrogen and ammonia, silica, orthophosphate, and Secchi-disc transparency in the three regions in summer 1969. Sixteen sites in southern Lake Michigan were visited during 22-24 July and 30 stations in the northern basin, including Green Bay, were sampled during 15-23 August. Water for chemical analyses was taken at 2 m and at 1 m above the bottom. Primary productivity was measured with radiocarbon (Strickland and Parsons, 1968). Lake water from 2 m and 5 (or 10) m was placed in 265-ml Pyrex glass-stoppered reagent bottles and incubated in a Plexiglass incubator. Water from 3.5 m was pumped continuously through the incubator to maintain ambient lake temperature. Light bottles were enclosed in two or three layers of plastic window screen to reduce light intensity by 53 and 68% respectively, and thereby simulate different depths in the euphotic zone. Incubation periods ranged from 4 to 6 hr; samples were filtered through 0.45-μm Millipore filters and counted later with a Nuclear Chicago Planchet Counting System (Model 4338).

The results of the survey are given in Tables 17 and 18. In the northern basin, productivity measurements ranged from 1.77 to 5.85 mg $C/m^3/hr$ (Table 17), with a mean of 3.06 ± 1.29 mg $C/m^3/hr$; estimates made in the southern basin ranged from 1.04 to 6.47 mg $C/m^3/hr$ (Table 18), with a mean of 3.55 ± 2.32. Primary production rates at inshore stations in the extreme southern part of the Lake are well above the mean. In Green Bay, photosynthetic rates were much higher in the southern than in the northern region; the three estimates from the southern part of the bay are an order of magnitude higher than those in the northern region and in the entire Lake.

Variations in the concentrations of dissolved silica and nitrate-nitrogen, along with data on primary productivity, are of particular interest because they exhibit patterns that can be interpreted in terms of lake eutrophication.

Table 17. Carbon Fixation and Other Selected Parameters at Northern Lake Michigan Stations*

Station	Depth, m	Secchi Disc, m	Carbon Fixation, mg C/m^3/hr	SiO_2, mg/l S	SiO_2, mg/l B	NO_3-N, µg/l S	NO_3-N, µg/l B	NH_3-N, µg/l S	NH_3-N, µg/l B	Ortho PO_4-P, µg/l S	Ortho PO_4-P, µg/l B
Northern Lake Michigan											
3		10.0	1.79	0.39		126		16.9		0.0	
5A	40	9.5	-	0.38	1.47		119	6.4	13.4	0.0	<0.5
7		8.0	2.33	0.25		126		12.4		0.7	
10		7.7	3.85	0.24		123		1.0		<0.5	
13	82	8.8	-	0.22	1.03	113	199	13.2	20.8	<0.5	0.8
16		6.5	2.46	0.21		119		13.2		<0.5	
19		7.5	1.77	0.24		108		31.6		<0.5	
20	46	9.0	3.31	0.22	1.37	112	193	22.7	12.6	0.7	0.8
21		9.0	1.89	0.26		111		33.6		0.6	
22		7.0	2.28								
23	50	7.5	2.31	0.23	1.46	116	207	19.7	28.4	0.8	1.1
24	81	8.5	2.69	0.22	1.19	119	216	7.9	21.3	<0.5	1.0
26	136	7.5	2.27	0.23	1.14	126	232	12.2	16.4	<0.5	1.5
Northern Green Bay											
27		8.0	-	0.28		126		15.0		0.0	
29	16	4.5	5.49	0.53	1.04	82	163	21.3	18.0	0.0	0.7
31		4.0	4.18		0.74		134	24.7		0.7	
32	16	5.2	4.17	0.68	0.36		171	18.3	38.0	0.8	0.5
35	29	5.0	4.78	0.52		92	210	13.7	16.1	0.0	0.0
37	31	4.5	4.48	0.34	1.20	74	201	17.8	15.1	<0.5	0.0
39	38	5.2	3.34	0.44	1.04	89	196	22.2	17.9	0.0	<0.5
41	38	5.0	-	0.42	1.08	86	199	11.3	20.8	<0.5	<0.5
Southern Green Bay											
2	16	2.5	18.2	0.78	3.24	53	221	12.2	35.5	0.5	2.5
5	15	1.8	45.9	0.25	1.84	36	137	15.1	25.8	1.2	1.3
42	27	2.5	20.2	0.74	2.05	28	213	11.1	14.4	1.9	1.8
43	15	2.2	-		3.77				15.6		4.2
Northern Lake Michigan											
46	43	4.8	3.77	0.40	1.17	102	221	19.6	14.3	0.5	<0.5
47	213	8.5	2.25	0.28	1.19	120	239	10.0	10.6	0.5	1.8
48	252	9.5	3.06	0.30	1.18	115	240	13.8	11.7	<0.5	2.5
49	164	7.0	5.84	0.29	1.13	111	237	33.1	17.7	0.7	1.7
51	37	6.5	5.85	0.15	1.29	113	249	16.2	18.4	0.9	<0.5
53	72	8.0	-	0.24	1.55	120	243	17.5	5.9	0.9	2.2

Data from Schelske and Callender (1970).

Symbols: S and B denote surface and bottom samples.

Dissolved silica concentrations were higher in the surface water of the northern basin (0.26 ± 0.07 mg/l) than in the southern basin (0.15 ± 0.07 mg/l). Although the ranges of values for bottom water in the two regions overlap, silica levels in the southern basin are noticeably lower than in the northern region. In most analyses, concentrations of dissolved silica also are lower in surface than in bottom water. The only exceptions to this general observation are stations in shallow water off Chicago and near Benton Harbor.

Silica concentrations in surface water of Green Bay were higher in the southern (0.59 ± 0.30 mg/l) than in the northern part of the bay (0.46 ± 0.13 mg/l), and the bottom water in the southern region had higher concentrations (2.73 ± 0.92 mg/l) than bottom water in the northern part of the bay and in the Lake. The greatest differential between silica concentrations in surface and bottom water occurred in the southern part of the bay.

Concentrations of nitrate-nitrogen in the surface water of the Lake averaged about one-half that of the bottom water. Average concentrations of

Table 18. Carbon Fixation and Other Selected Parameters at Southern Lake Michigan Stations*

Station	Depth, m	Secchi Disc, m	Carbon Fixation, mg C/m^3/hr	SiO_2, mg/l		NO_3-N, µg/l		NH_3-N, µg/l		Ortho PO_4-P, µg/l	
				S	B	S	B	S	B	S	B
3	79	8.5	2.05	0.11	1.13	102	184	2.7	11.3	3.1	1.9
4	70	5.5	4.41	0.12	2.50	67	235	7.9	5.0	1.0	4.8
5	17	4.1	6.47	0.11	1.21	92	193	21.0	20.7	<0.5	<0.5
6	76	7.7	3.82	0.16	1.83	113	202	13.0	5.8	<0.5	1.6
7	57	-	-	0.14	2.01	-	210	-	12.0	<0.5	<0.5
8	18	3.8	4.82	0.12	1.26	105	175	16.3	38.0	<0.5	<0.5
9	63	7.5	2.01	0.14	1.65	108	227	12.6	24.7	<0.5	<0.5
10	19	3.5	9.79	0.22	0.13	111	-	7.8	-	<0.5	<0.5
11	66	8.0	2.07	0.15	1.94	105	250	13.6	16.9	<0.5	<0.5
12	72	7.9	3.93[a]	0.09	2.23	106	273	10.3	20.6	<0.5	<0.5
13	43	10.0	2.18	0.05	1.66	100	212	18.8	36.9	<0.5	<0.5
14	19	-	-	0.12	0.05	101	137	10.7	43.9	<0.5	<0.5
15	19	5.8	2.34	0.13	0.09	84	113	6.9	39.8	2.5	2.2
16	21	4.8	3.05	0.15	0.22	69	104	5.8	50.1	1.9	5.3
17	101	9.8	1.71	0.16	0.96	111	212	4.2	17.5	<0.5	3.4
18	160	10.0	1.04	0.39	1.14	144	243	1.5	15.7	<0.5	7.1

*Data from Schelske and Callender (1970).

[a]Samples were incubated only 20 minutes.

Symbols: S and B denote surface and bottom samples.

nitrate-nitrogen at the surface were lower in the southern (101 ± 18 µg/l) than in the northern basin (116 ± 7 µg/l); however, levels of nitrate-nitrogen in the bottom water of both basins were fairly similar. Nitrate-nitrogen concentrations in the surface water of Green Bay were markedly lower in the southern region (39 ± 13 µg/l) than in the northern region (92 ± 18 µg/l). The bottom water in both regions, however, appeared to have similar concentrations.

Schelske and Callender concluded from these observations that levels of primary productivity are highest in southern Green Bay, and higher at nearshore stations in the southern basin of the Lake than in the open water. This pattern is directly related to the observed concentration differences in dissolved silica and nitrate-nitrogen. Low concentrations of nutrients in surface water are due to high rates of biological utilization and are associated with regions of high primary productivity, such as southern Green Bay and inshore water in the southern basin. These data partially support a hypothesis concerning the artificial eutrophication of Lake Michigan and are discussed further in the section on Phosphorus, Silica, and Eutrophication (p. 114).

A recent, comparative study by Schelske and Roth (1973) resulted in 13 estimates of primary productivity from the surface water of six stations in the northeastern portion of the Lake. Rates of productivity in July 1970 ranged from 0.86 to 3.09 and averaged 2.40 mg C/m^3/hr; in most cases, primary productivity ranged from 2.0 to 3.0 mg C/m^3/hr. These estimates are comparable to measurements made earlier in the northern basin by Schelske and Callender (1970).

Grand Traverse Bay

As part of an investigation on the effects of nutrient enrichment of Grand Traverse Bay, Stoermer *et al.* (1972) estimated primary productivity at 12 stations during May and June 1970 (Fig. 20). The sites were spaced to

determine differences between the arms of the bay and to compare these regions with the open water in the central and northern regions of the bay. Portions of these data are presented in Tables 8 and 14.

Estimates of primary productivity, along with measurements on phytoplankton standing crop, Secchi-disc transparency, particulate phosphorus, nitrate-nitrogen, and dissolved silica, are summarized in Table 9. In May, estimates ranged from a low of 4.05 mg $C/m^3/hr$ (Station 1) to a high of 8.63 mg $C/m^3/hr$ (Station 9), with a mean of 5.51 mg $C/m^3/hr$. A general pattern emerges from these measurements: estimates at the four stations in the western arm were above the mean, those in the eastern arm were below the mean, and stations in the open water (except number 5) also were below the mean.

Photosynthetic rates in June were more variable, ranging from 2.74 (Station 6) to 13.44 mg $C/m^3/hr$ (Station 10), with a mean of 5.88 mg $C/m^3/hr$. The regional pattern of primary productivity is similar to that observed in May: the four stations in the west arm exhibited values above the mean and those in the eastern arm were lower than the mean. Except for the relatively high rates observed at Station 12, all stations in the upper part of the bay exhibited relatively low values and were comparable to those in the east arm.

These differences in primary productivity are correlated with several parameters that usually vary either directly or indirectly with production rates. The standing crop of phytoplankton was higher in the west arm than in the east arm, and concentrations of dissolved silica were lower in the west than in the east arm. Since the phytoplankton was composed largely of diatoms, it is reasonable to assume that differences between silica levels were due to higher rates of biological utilization in the west arm. The concentrations of silica and nitrate-nitrogen at stations in the west arm decrease as the distance from the mouth of the Boardman River increases. This trend also is in phase with proportional increases in standing crop, productivity, and particulate phosphorus. The results, coupled with the observations presented in the sections on Primary Productivity (p. 98), and Floral Composition and Community Structure (p. 23), indicate that higher levels of primary productivity and phytoplankton abundance are directly associated with nutrient loadings from the Boardman River.

Milwaukee-to-Ludington Transects

Fee (1973a) used his model to estimate integral primary productivity at five stations along a transect from Milwaukee, Wisconsin, to Ludington, Michigan. The results of his studies are of paramount importance because they represent some of the most extensive data on primary productivity for the Great Lakes, and because they provide the first estimates of annual primary production in the offshore water of Lake Michigan.

Samples were taken aboard the SS Badger at intervals of 8-16 days from May 1970 through February 1971. The two inshore stations (Stations 1 and 5) were located 4.8 km from the breakwalls of the harbors at Milwaukee and Ludington, respectively. The two *quarter* stations were 29 km from the Wisconsin shore (Station 2) and the Michigan shore (Station 4). The mid-lake site (Station 3) was 48 km from the Wisconsin shore and 54 km from the eastern shore.

Estimates of primary productivity during the period June 1970-February 1971 are shown for each station in Figure 54. These data show that the seasonal pattern of integral primary productivity is bimodal at all stations. Minimal production rates were detected in winter and mid-summer; maximum rates occurred during spring and fall. Average rates for the study period and estimated annual values of primary productivity for the stations are shown in Table 19. These data clearly demonstrate that primary productivity is considerably higher inshore, especially near Milwaukee, and that offshore locations have similar average and annual primary production rates.

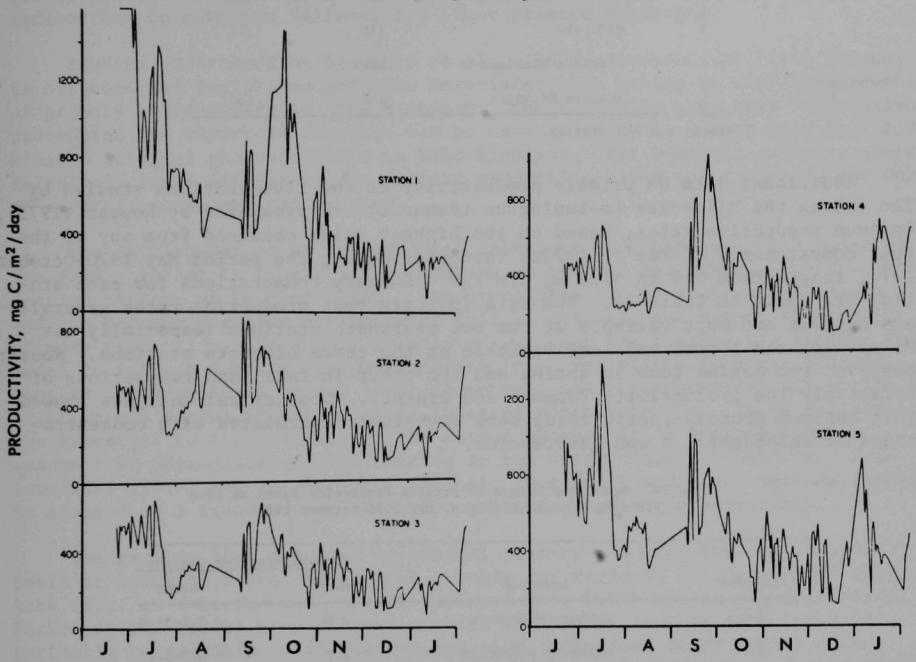

Fig. 54. Computed Daily Integral Primary Productivity at Five Stations in Lake Michigan, June 1970-February 1971. Modified from Fee (1973a) (with permission, see credits).

Fee's studies have shown the utility of the model for estimating integral productivity and for assessing the importance of environmental factors influencing production rates. Decreases in integral primary productivity during mid-summer suggest that production rates are limited by biological factors which may be related to nutrient availability. In winter, there is low input of solar energy and high efficiencies of carbon fixation, and physical factors are undoubtedly of greatest importance in regulating productivity. Fee stated that perhaps the most striking observation of the study was that variations in the daily distribution and intensity of solar radiation at the water's surface can produce extremely large variations in productivity. This observation suggests that *in situ* primary productivity measurements made at weekly intervals are inadequate for describing seasonal trends in photosynthesis and for estimating annual production rates in Lake Michigan.

Table 19. Average and Estimated Annual Primary Production Rates at Five Stations in Lake Michigan, June 1970-February 1971

Stations	Location	Productivity	
		Average, mg $C/m^2/day$	Annual, mg $C/m^2/yr$
1	Inshore Wisconsin	670	247
2	Offshore Wisconsin	380	139
3	Mid-Lake	331	121
4	Offshore Michigan	381	139
5	Inshore Michigan	512	187

*Data from Fee (1973a).

Additional data on primary productivity at the five stations studied by Fee (along the Milwaukee-to-Ludington transect) are presented by Rousar (1973). Optimum production rates, based on the highest value obtained from any of the four compartments of Fee's (1973a) incubator during the period May 1970-October 1971, ranged from 0.6 to 31.0 mg $C/m^3/hr$. Summary computations for each station are shown in Table 20. The data indicate that production rates generally are highest and most variable at the two nearshore stations (especially near Milwaukee) and lowest and less variable at the three offshore stations. Rousar observed two maxima (one in spring and the other in fall) and two periods of relatively low productivity (summer and winter). Statistical analyses showed that optimum photosynthetic rates were positively correlated with concentrations of chlorophyll *a* and carotenoids.

Table 20. Means and Ranges of Primary Production Rates at Five Stations in Lake Michigan, May 1970-October 1971*

Stations	Location	Productivity, mg $C/m^3/hr$	
		Mean	Range
1	Inshore Wisconsin	8.6	3.1-31.0
2	Offshore Wisconsin	2.7	0.9-5.2
3	Mid-Lake	2.3	0.6-5.2
4	Offshore Michigan	2.5	0.8-5.3
5	Inshore Michigan	3.4	1.0-10.6

*Data from Rousar (1973).

Note: Station numbers and locations are identical to those of Fee (1973a) in Table 19.

CONCLUSIONS AND DISCUSSION

The data presented in the previous sections reveal that relatively few estimates of primary productivity are available for Lake Michigan. The paucity of information can be attributed largely to the expense of making measurements and to logistical problems. The existing data, however, allow a number of generalizations to be made.

Previous studies in fresh water and with laboratory cultures of algae demonstrate that analytical errors and biases can occur with the use of the radiocarbon technique. Long-term incubations (*e.g.* eight hours or more) can increase the fraction of photosynthetically fixed carbon that is excreted or respired. Short-term incubations (*e.g.* four hours or less) are preferred, but it is necessary to *degas* filters when $CaCO_3$ is present, and to extrapolate counts to *infinite* thinness in order to reduce self-absorption errors in planchet counting. Recent studies by Nalewajko and Lean (1972) and Berman (1973) discuss some of the potential errors associated with retention of radiocarbon on membrane filters, and other related phenomena.

Studies undertaken by Saunders *et al.* (1962) represent the first attempt to overcome the logistical problems associated with making *in situ* measurements of primary productivity in Lake Michigan. Their results show that calculative procedures and empirical formulae can be used to estimate rather than directly measure integral photosynthesis in Lake Michigan. For synoptic surveys, where relatively large differences in primary production rates are expected, any one of several procedures can be used.

The development of an experimental technique and computer-based model by Fee (1969, 1973a) is timely and represents an immense contribution to the production biology of Lake Michigan. The procedures are economically feasible, and can provide accurate estimates of daily, seasonal, and annual integral primary production. It should be pointed out that Fee (1973b) has refined the model to include vertical inhomogeneities (*e.g.* variations in algal biomass, complex photosynthesis versus light responses, and nonexponential extinction of light versus depth) in estimates of integral photosynthesis. These refinements are essential to the validity of the method because it is not necessary to assume that phytoplankton distribution in the water column is uniform. Vollenweider (1970) has recommended, in fact, that Fee's model and methods should be adopted as a standard procedure for measuring primary productivity.

The factors that regulate or control primary productivity on a seasonal basis at specific locations or that account for regional differences in the Lake (*e.g.* as detected in synoptic surveys) have not been clearly elucidated. Parkos *et al.* (1969) have discussed seven individual factors that could be partially responsible: (*i*) the existence of individual water masses with different standing crops of phytoplankton, (*ii*) local differences in nutrient concentrations, (*iii*) variations in light intensity and quality, (*iv*) temperature differences, (*v*) local regions of upwelling of nutrient-rich bottom water, (*vi*) differences in zooplankton grazing, and (*vii*) the presence of toxic substances that kill or reduce photosynthetic rates of certain phytoplankton populations.

Several studies demonstrate the effects of selected physical and chemical parameters on primary productivity. Fee's investigations show clearly that daily variations in integral photosynthesis at five stations can be attributed in part to short-term fluctuations in solar insolation. Investigations by Schelske and Stoermer (1971, 1972) demonstrate that phosphorus and silica are principal nutrients limiting the growth of phytoplankton (*cf.* see section on Phosphorus, Silica, and Eutrophication; subsection Offshore Station, p. 132). In eastern Lake Michigan, Schelske *et al.* (1971) demonstrated that upwelling of bottom water apparently resulted in higher levels of primary productivity. The importance of water temperature and seasonal variations in solar radiation are clearly shown by Fee's (1973a) studies.

Only two of the seven variables discussed by Parkos *et al.* (1969) have been entirely neglected in studies on Lake Michigan. The effects of toxic substances or external metabolites on photosynthetic rates are unknown, although Stoermer *et al.* (1971) provided circumstantial evidence that secretions by blue-green algae reduced photosynthetic rates. Selective grazing by herbivorous zooplankton populations probably regulates primary productivity; however, no data on the effects of grazing on primary productivity appear to be available for Lake Michigan.

Although relatively few studies have been conducted on primary productivity in Lake Michigan, sufficient data are available to document the fact that production rates generally are higher inshore in the southern basin than offshore in the northern basin of the Lake (Table 16). Moreover, primary productivity is significantly higher offshore in the southern basin than in the northern region of the Lake. In Green Bay, production rates are markedly higher in the southern region, especially near the Fox River, than in the northern extremity. Similarly, photosynthetic rates are higher near the mouth of the Boardman River than in the west arm or in the open water of Grand Traverse Bay. These patterns of carbon fixation in the Lake and in the two bays are generally related to nutrient loadings. Certain areas of the Lake, especially nearshore, that receive relatively large quantities of nutrients from tributaries generally exhibit higher levels of primary productivity than regions removed from the direct influence of nutrient-rich tributaries.

PHOSPHORUS, SILICA, AND EUTROPHICATION

The observation that inshore water in some regions of Lake Michigan exhibits conditions of moderate or advanced degrees of eutrophication has prompted two questions: (*i*) Has the offshore water of the Lake been affected adversely by inputs of nutrients? (*ii*) What nutrient or nutrients have the potential to cause or accelerate eutrophication of the offshore environment?

Evidence from Schleske and Stoermer (1971, 1972) shows that significant alterations in the phytoplankton community have occurred recently in the Lake, and that this can be attributed directly to changes in the chemical environment. The data and arguments of these authors suggest that disturbances, equivalent at least to incipient cultural eutrophication, have occurred in offshore water, especially in the southern basin. The authors forecast that even more pronounced degrees of cultural eutrophication will occur in the near future. The relationships between phosphorus, silica, and eutrophication are treated here, and the trophic state of the Lake is discussed and compared with the other Great Lakes.

THE PHOSPHORUS, SILICA, AND EUTROPHICATION HYPOTHESIS

Schelske and Stoermer contended that phosphorus is the element controlling the rate of eutrophication of Lake Michigan. They argued that continued inputs at current loading rates have resulted in substantial increases in diatom abundance, the principal component of the phytoplankton. Because silica is a major nutrient required for diatom growth, supplies of silica in the euphotic zone are being severely depleted. Continued inputs of phosphorus, therefore, will result in larger standing crops of diatoms, until ambient silica concentrations are reduced to levels limiting the growth of diatoms. Schelske and Stoermer

predicted that when the size of the diatom community is reduced due to silica limitation and high levels of phosphorus and other nutrients are present, green and blue-green algae will become the dominant components of the phytoplankton.

These authors assembled data from their own observations and experiments, and drew upon information generated in other investigations. There are four lines of evidence indicating that Lake Michigan is undergoing cultural eutrophication:

1. Changes have occurred recently in phytoplankton abundance and composition.

2. Concentrations of dissolved silica are decreasing on a lake-wide basis.

3. Diatoms utilize silica in the euphotic zone and reduce concentrations in some regions to limiting levels.

4. Nutrient-enrichment experiments indicate that phosphorus is the principal limiting nutrient, but that silica stimulates diatom growth when ambient concentrations are at limiting levels. The contention that phosphorus is the key element in the eutrophication process also is supported by observations of the correlation between particulate phosphorus of seston and primary productivity, and by ratios of silica to phosphorus in tributaries.

Each of these contentions is examined in detail in the following text.

Changes in the Phytoplankton

Schelske and Stoermer argued that the phytoplankton of Lake Michigan has changed substantially in recent years and supported this contention with evidence from several sources. An investigation by Ahlstrom (1936) indicates that the diatom flora during 1930-1931 was characterized by diatoms occurring principally in oligotrophic environments. By the early 1960's, however, the composition of the flora shifted to one containing numerous species characteristic of eutrophic water, including *Stephanodiscus binderanus*, *Stephanodiscus tenuis*, *Diatoma tenue* v. *elongatum*, *Asterionella bleakleyi*, *Stephanodiscus subtilis*, *Nitzschia dissipata*, *Thalassiosira* spp., and *Coscinodiscus* spp. (Stoermer, 1967). Stoermer also detected 35 eutrophic, euplanktonic taxa, over 70% of which were not observed by Ahlstrom. In addition, Stoermer and Yang (1970) observed that many species characteristic of oligotrophic water have decreased in relative abundance, in nearshore and offshore areas, especially in southern Lake Michigan.

An analysis of samples from southern Lake Michigan in 1962-1963 indicated, however, that the phytoplankton was still dominated numerically by diatoms (Stoermer and Kopczynska, 1967). These investigators recorded diatom cell counts that were greater than 70% of the total assemblage. By 1969, however, Schelske and Stoermer (1972) noted significant shifts in phytoplankton composition; twenty-two samples taken from the Lake in fall 1969 were dominated by algae other than diatoms. Green, blue-green, and golden-brown algae were the major phytoplankton components.

Additional evidence supporting the contention that a shift in composition has occurred is provided by Stoermer (1974) and Schelske *et al.* (1971) in Tables 3-6. These observations indicated that in August and September phytoplankton composition at an offshore station near Grand Haven, Michigan, was dominated by blue-green and green algae, not by diatoms. On a cell basis, these groups constituted 56 to 85% of the phytoplankton during August and September and 30 to 45% during late September.

These observations prompted Stoermer (1974) to undertake a detailed study of phytoplankton in southern Lake Michigan. Forty-one stations were established along one north-to-south transect and two east-to-west transects. The stations are geometrically spaced with respect to distance from shore, being closely spaced nearshore and widely spaced offshore. Surface-water samples from each of the stations were analyzed, and total cell counts and the percentage of blue-green algae were computed. The results for the period April-October 1971 are shown in Figures 55-62.

The analyses reveal dramatic shifts in community composition during the growing season. In April and May, the phytoplankton is dominated by diatoms and golden-brown algae. The highest phytoplankton abundance levels occur in the southeastern quadrat, and all inshore localities support larger populations than open-water stations. The initiation of thermal stratification occurs in June when the phytoplankton is composed primarily of diatoms, but offshore populations, relative to inshore populations, are larger in June than earlier in the season. During July, the highest standing crops are observed in inshore regions. In midsummer, populations of blue-green algae begin to

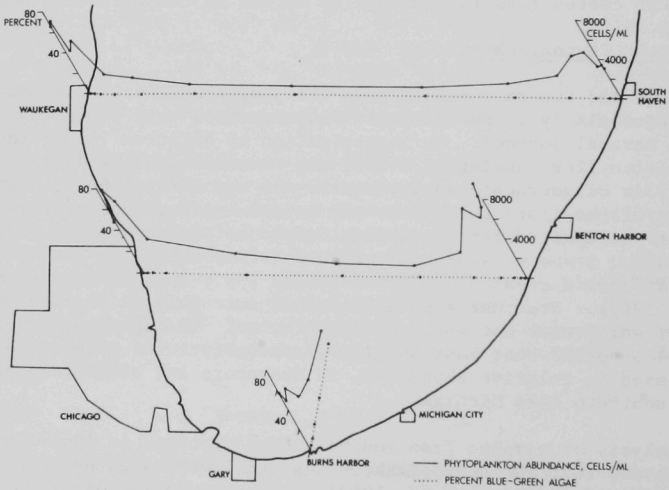

Fig. 55. Phytoplankton Abundance and Percentage Composition of Blue-Green Algae in Lake Michigan Surface Water during Early April 1971. Redrawn and modified from Stoermer (1974) to show general distributional patterns.

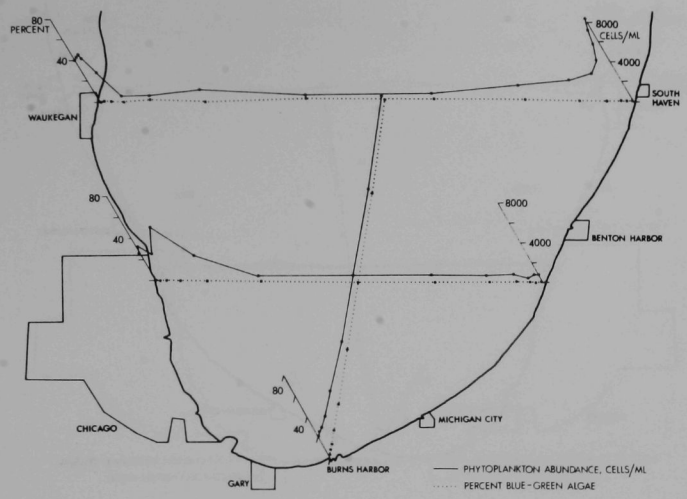

Fig. 56. Phytoplankton Abundance and Percentage Composition of Blue-Green Algae in Lake Michigan Surface Water during Mid-May 1971. Redrawn and modified from Stoermer (1974) to show general distributional patterns.

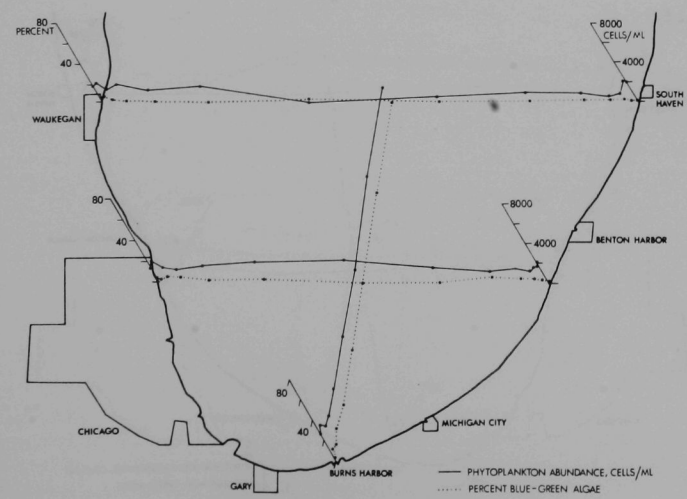

Fig. 57. Phytoplankton Abundance and Percentage Composition of Blue-Green Algae in Lake Michigan Surface Water during Late June 1971. Redrawn and modified from Stoermer (1974) to show general distributional patterns.

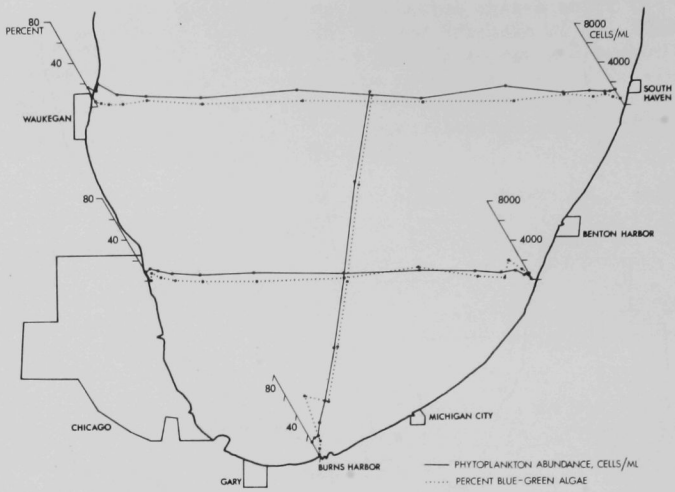

Fig. 58. Phytoplankton Abundance and Percentage Composition of Blue-Green Algae in Lake Michigan Surface Water during Mid-July 1971. Redrawn and modified from Stoermer (1974) to show general distributional patterns.

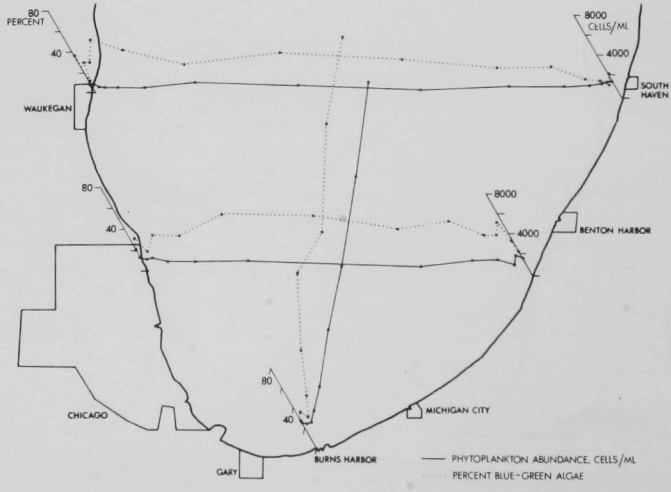

Fig. 59. Phytoplankton Abundance and Percentage Composition of Blue-Green Algae in Lake Michigan Surface Water during Late August 1971. Redrawn and modified from Stoermer (1974) to show general distributional patterns.

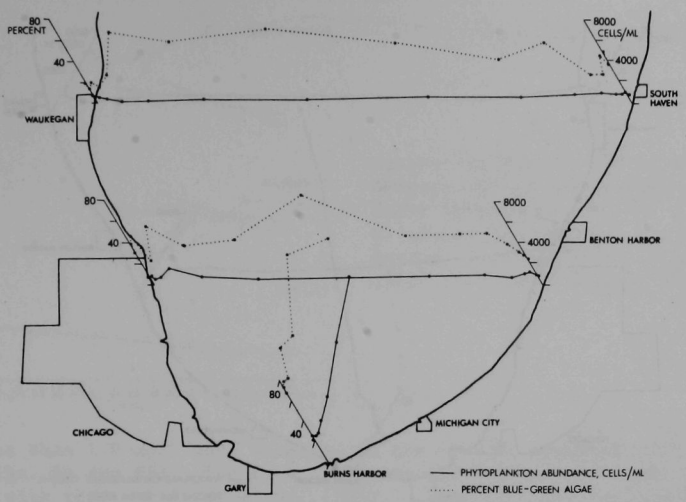

Fig. 60. Phytoplankton Abundance and Percentage Composition of Blue-Green Algae in Lake Michigan Surface Water during Mid-September 1971. Redrawn and modified from Stoermer (1974) to show general distributional patterns.

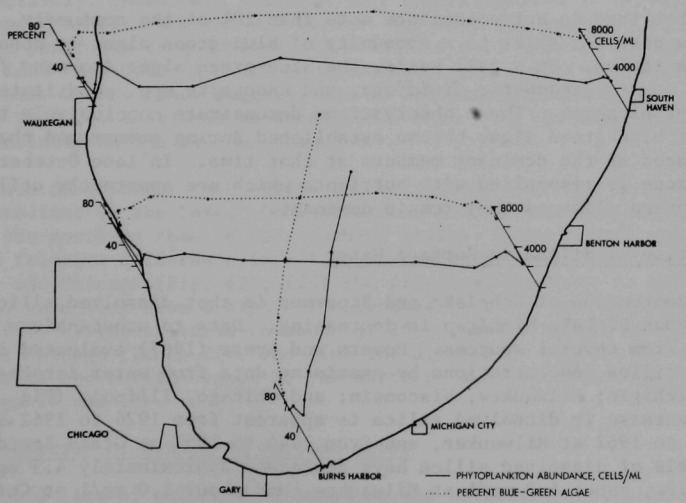

Fig. 61. Phytoplankton Abundance and Percentage Composition of Blue-Green Algae in Lake Michigan Surface Water during Early October 1971. Redrawn and modified from Stoermer (1974) to show general distributional patterns.

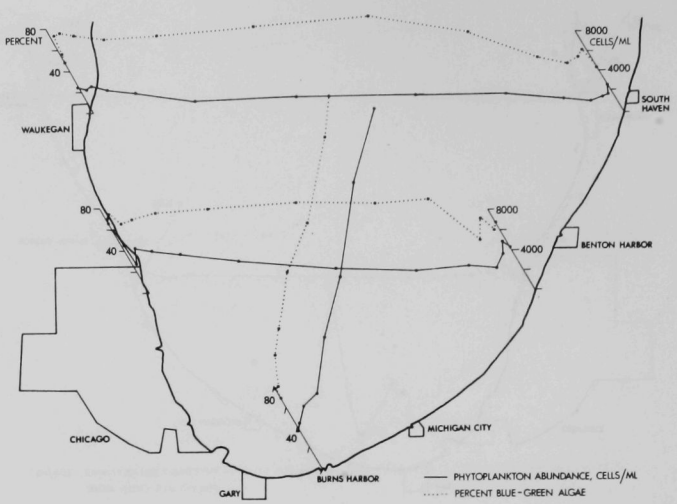

Fig. 62. Phytoplankton Abundance and Percentage Composition of Blue-Green Algae in Lake Michigan Surface Water during Late October 1971. Redrawn and modified from Stoermer (1974) to show general distributional patterns.

develop, but they do not constitute more than 10% of the community. By August, however, a distinct shift to a community of blue-green algae is observed over the entire region. On a cell basis, the blue-green algae *Anabaena flos-aquae, Anacystis cyanea, Anacystis dimidiata*, and *Anacystis* spp. constitute up to 80% of the phytoplankton. These observations demonstrate conclusively that populations of blue-green algae become established during summer and that diatoms are displaced as the dominant members at that time. In late October, the euphotic zone is resupplied with nutrients which are apparently utilized by the blue-green algae as they remain dominant.

Concentration of Silica in Surface Water

One contention of Schelske and Stoermer is that dissolved silica in the euphotic zone of Lake Michigan is decreasing. Data to substantiate this are available from several sources. Powers and Ayers (1967) evaluated long-term trends in silica concentrations by examining data from water intakes at Grand Rapids, Michigan; Milwaukee, Wisconsin; and Chicago, Illinois (Fig. 63). The gradual decrease in dissolved silica is apparent from 1926 to 1962 at Chicago, from 1948 to 1962 at Milwaukee, and from 1944 to 1962 at Grand Rapids. Since 1948, levels of dissolved silica have decreased approximately 4.5 mg/l at Grand Rapids, about 5.0 mg/l at Milwaukee, and about 1.0 mg/l at Chicago.

Recent investigations demonstrated that decreases in dissolved silica have not been limited to inshore regions but apparently have occurred in open water. During two synoptic cruises covering the entire Lake in 1955 (Ayers *et al.*, 1958), silica concentrations generally were less than 2.5 mg/l, and

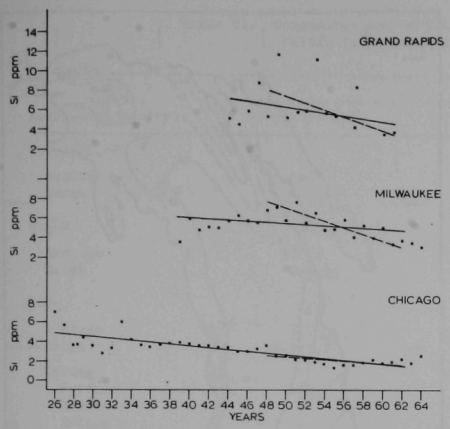

Fig. 63.

Concentrations of Silica in Water Samples Collected from Municipal Water Intakes at Chicago, Illinois; Milwaukee, Wisconsin; and Grand Rapids, Michigan (Powers and Ayers, 1967) (with permission, see credits).

levels less than 1.0 mg/l were detected in the extreme southern basin during August (Figs. 64 and 65). The data of Risley and Fuller (1965) are in general agreement with those of Ayers *et al.* (1958). They detected concentrations of 0.6 mg/l in surface water of the southern basin (Table 21). Furthermore, Schelske and Callender (1970) reported mean concentrations of dissolved silica in the surface water at 16 stations in the southern basin and 18 stations in the northern region during summer; these concentrations were 0.15 ± 0.07 mg/l and 0.26 ± 0.07 mg/l, respectively (Tables 17 and 18).

Collectively, these data indicate that concentrations of dissolved silica have decreased in offshore surface water. In 1926, for example, silica concentrations generally ranged between 5.0 and 6.0 mg/l near Chicago; present levels of less than 0.20 mg/l can be detected in the southern basin during summer. These observations suggest, but do not conclusively prove, that silica has been decreasing at an accelerated rate over the last 10 to 15 years, especially in the southern basin.

The data demonstrate that silica concentrations decrease along a north-to-south gradient in the Lake. Concentrations during summer appear to be higher in the northern than in the southern basin. These trends are evidenced by (*i*) the relative difference in silica concentrations at Grand Rapids, Milwaukee, and Chicago (Fig. 63), (*ii*) the principal gradient in silica concentrations extending from a high off Milwaukee to a low off Chicago (Figs. 64 and 65), (*iii*) a similar north-to-south gradient, where silica reaches low levels near Chicago (Table 21), and (*iv*) the difference between average concentrations in the surface water of the northern and southern regions of the Lake (Tables 17 and 18).

Seasonal Depletion of Silica in Surface Water

The third line of evidence is based on the utilization of silica by diatoms during the growing season. Since increased rates of phosphorus supply have resulted in large standing crops of diatoms, silica is being depleted early in the growing season, *e.g.* by early or mid-summer. In July and August, silica concentrations are reduced to levels that will not sustain diatom

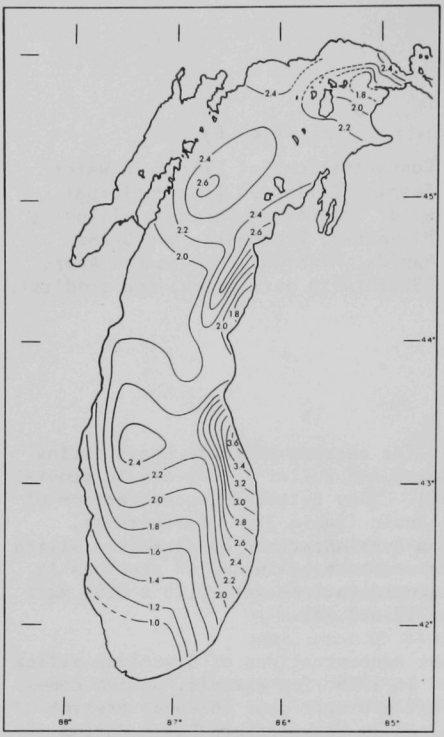

Fig. 64. Concentrations of Silica (mg/l) in Lake Michigan Surface Water, 9 August 1955. Modified from Ayers *et al.* (1958) (with permission, see credits).

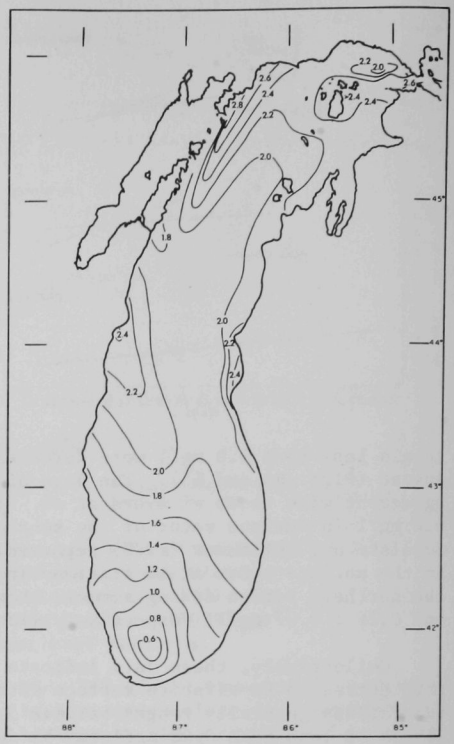

Fig. 65. Concentrations of Silica (mg/l) in Lake Michigan Surface Water, 10 August 1955. Modified from Ayers *et al.* (1958) (with permission, see credits).

growth. Without the competitive effects of diatoms for nutrients other than silica, the euphotic environment can be colonized successfully by other algae, specifically green and blue-green algal populations.

Data documenting this phenomenon are provided by at least four recent investigations. Synoptic surveys conducted by Ayers *et al.* (1958) include the depth distribution of dissolved silica along six transects on 9 August 1955 (Synoptic VI) and seven transects on 10 August 1955 (Synoptic VII). With minor exceptions, silica concentrations in surface water are markedly lower than in the hypolimnion (Figs. 66 and 67). The difference between epilimnetic and hypolimnetic silica concentrations is especially pronounced in the southern basin along the Waukegan-to-Michigan City transect. Measurements provided by Risley and Fuller (1965) also document silica depletion in the euphotic zone that is especially evident during summer (Table 21). Data further substantiating silica reductions in surface water are given by Schelske and

Table 21. Concentrations of Total Phosphate, Nitrate-Nitrogen, and Silica in Southern Lake Michigan, 1962-1963*

*Nutrients, mg/l***	*Latitude*			
	41°30'-41°45'	*41°45'-42°00'*	*42°00'-42°15'*	*43°30'-43°45'*
Total PO_4-P				
Average	0.06	0.04	0.02	0.02
Range	0-0.57	0-0.29	0-0.16	0-0.08
NO_3-N				
Average	0.12	0.09	0.10	0.19
Range	0-0.84	0.01-0.38	0.01-0.29	0.02-0.27
SiO_2				
Average	1.7	1.6	1.9	2.9
Range	0.4-3.7	0.5-3.0	0.7-4.2	1.8-5.1
Spring				
Surface	1.3	1.9	2.8	2.6
Middle	-	2.7	2.4	2.7
Bottom	-	2.8	3.5	2.7
Summer				
Surface	1.5	1.2	1.4	2.1
Middle	1.4	2.1	1.2	3.5
Bottom	2.7	2.6	2.4	3.8
Fall				
Surface	1.4	1.5	1.7	-
Middle	1.4	1.6	1.9	-
Bottom	2.0	1.6	1.9	-

Data from Risley and Fuller (1965).

***Values are averages and ranges of all data collected; silica concentrations are also given by season and depth.*

Callender (1970). As pointed out above, silica concentrations average 0.15 and 0.26 mg/l in the surface water of the southern and northern basins, respectively. Dissolved silica in bottom water averaged 1.26 ± 0.16 mg/l for 16 southern locations and 1.63 ± 0.49 mg/l for 18 northern stations.

Additional evidence is available to substantiate the phenomenon of silica depletion due to diatom growth (Stoermer, 1974). These studies in southern Lake Michigan were carried out in conjunction with observations of phytoplankton abundance and the percentage composition estimates of blue-green algae (Figs. 55-62). Seasonal variations in chlorophyll *a* and dissolved silica concentrations over the southern region of the Lake for the period April-October 1971 are shown in Figures 68-75.

These observations reveal that chlorophyll *a* levels and dissolved silica concentrations are inversely related. In early April, relatively high levels of chlorophyll and dissolved silica were noted at the inshore station. By May, chlorophyll concentrations at inshore stations increased and dissolved silica levels decreased. In late June, silica and chlorophyll concentrations were reduced in the southern part of the Lake, especially nearshore. These trends continued through August, except for a single station near the east shore where higher silica levels resulted from upwelling of bottom water rich in silica. In September, there was a slight increase in phytoplankton abundance and relatively low silica levels over most of the region. In late August and September, silica concentrations generally were less than 0.2 mg/l. By late October, there was a downward mixing of the thermocline coupled with increases in both chlorophyll and silica concentrations over the whole region.

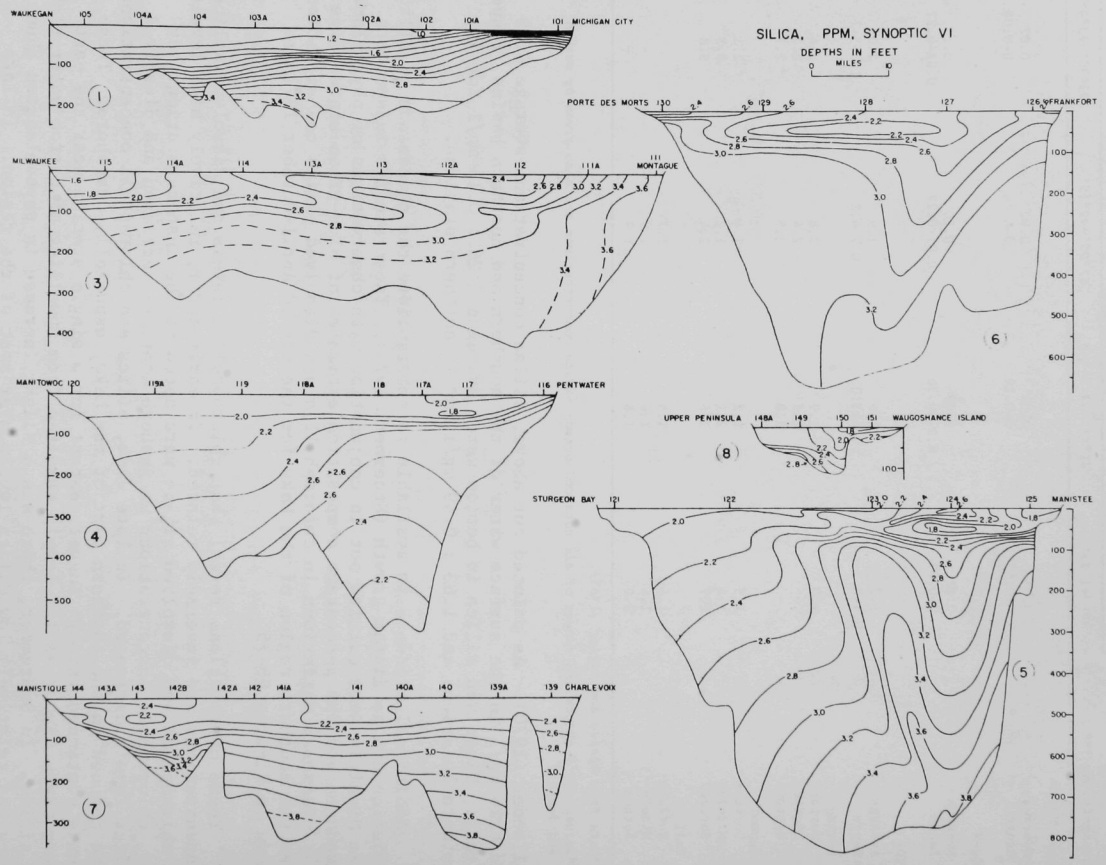

Fig. 66. Subsurface Concentrations of Dissolved Silica (mg/l) along Seven Transects in Lake Michigan (Ayers *et al.*, 1958) (with permission, see credits).

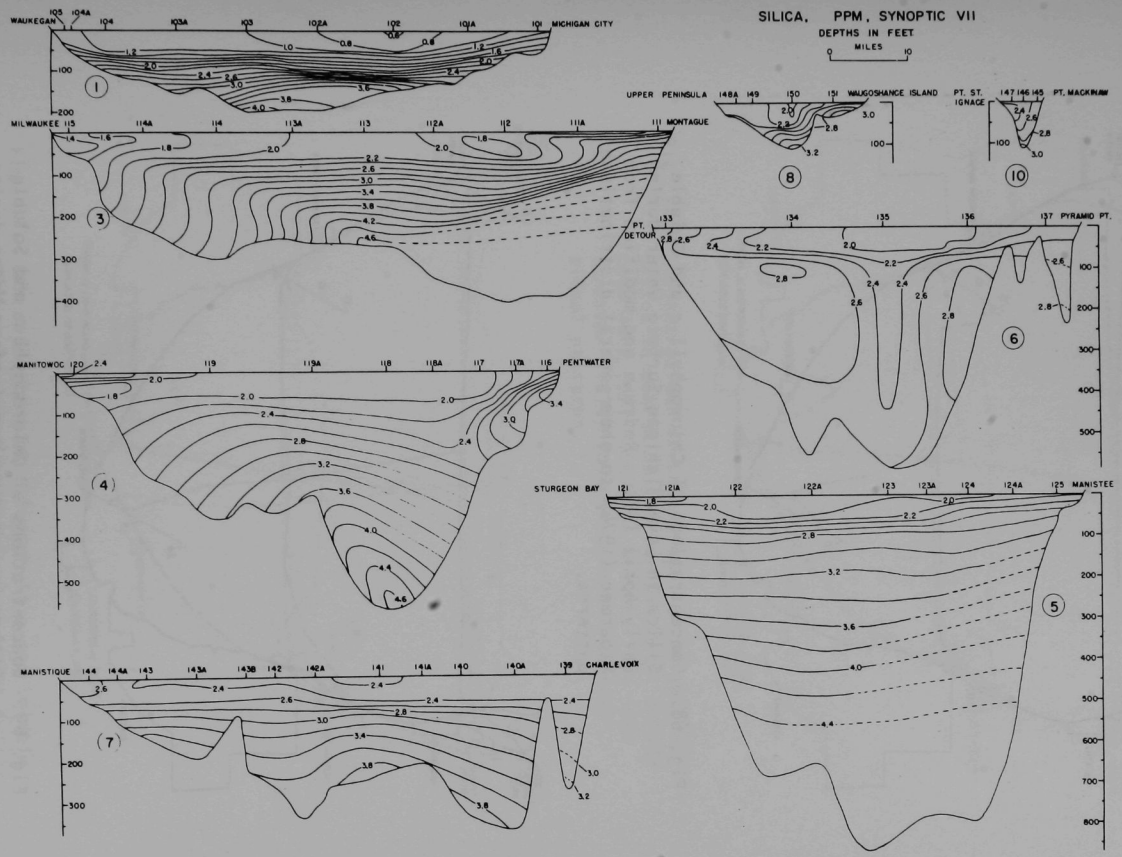

Fig. 67. Subsurface Concentrations of Dissolved Silica (mg/l) along Eight Transects in Lake Michigan (Ayers *et al.*, 1958) (with permission, see credits).

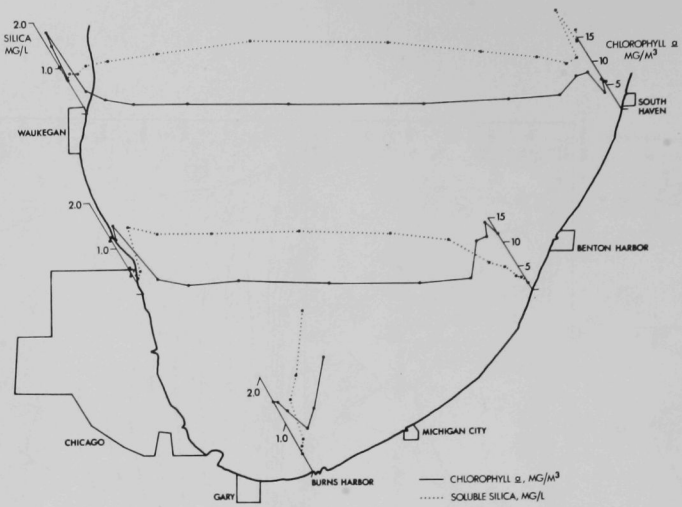

Fig. 68. Concentrations of Chlorophyll *a* and Soluble Silica in Lake Michigan Surface Water during Early April 1971. Redrawn and modified from Stoermer (1974) to show general distributional patterns.

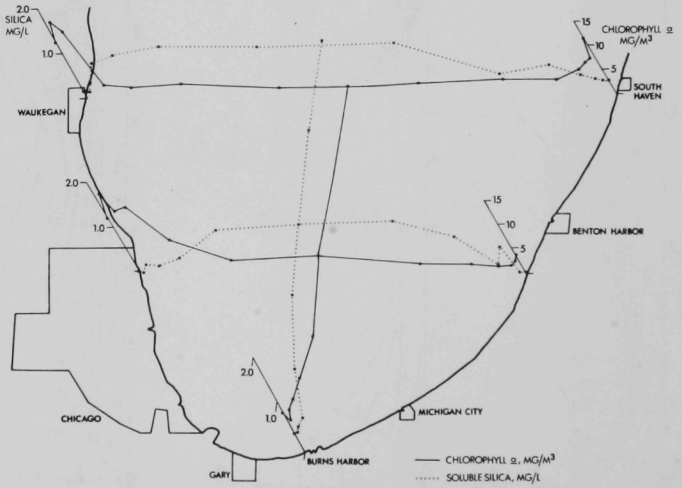

Fig. 69. Concentrations of Chlorophyll *a* and Soluble Silica in Lake Michigan Surface Water during Mid-May 1971. Redrawn and modified from Stoermer (1974) to show general distributional patterns.

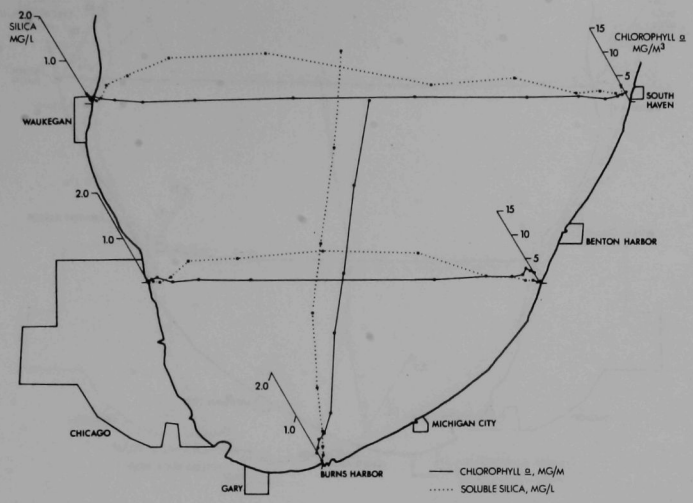

Fig. 70. Concentrations of Chlorophyll *a* and Soluble Silica in Lake Michigan Surface Water during Late June 1971. Redrawn and modified from Stoermer (1974) to show general distributional patterns.

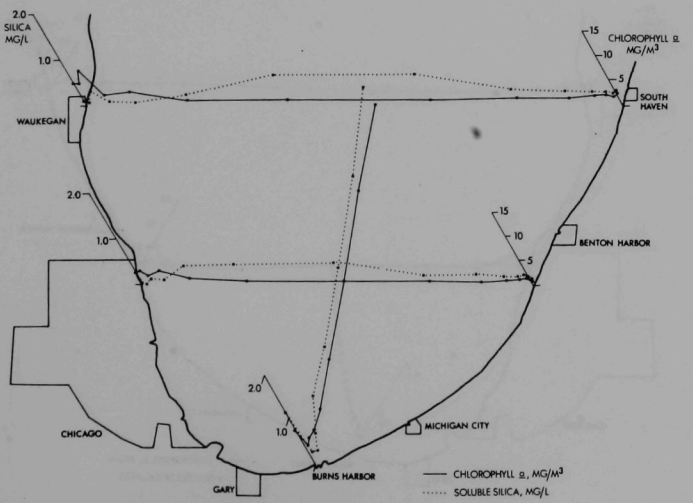

Fig. 71. Concentrations of Chlorophyll *a* and Soluble Silica in Lake Michigan Surface Water during Mid-July 1971. Redrawn and modified from Stoermer (1974) to show general distributional patterns.

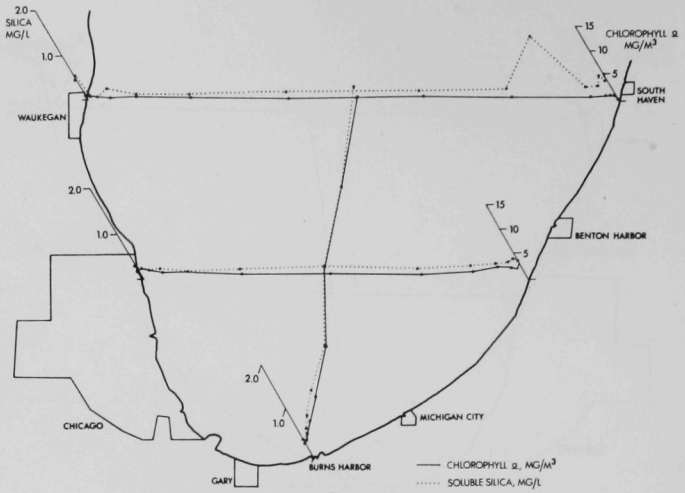

Fig. 72. Concentrations of Chlorophyll *a* and Soluble Silica in Lake Michigan Surface Water during Late August 1971. Redrawn and modified from Stoermer (1974) to show general distributional patterns.

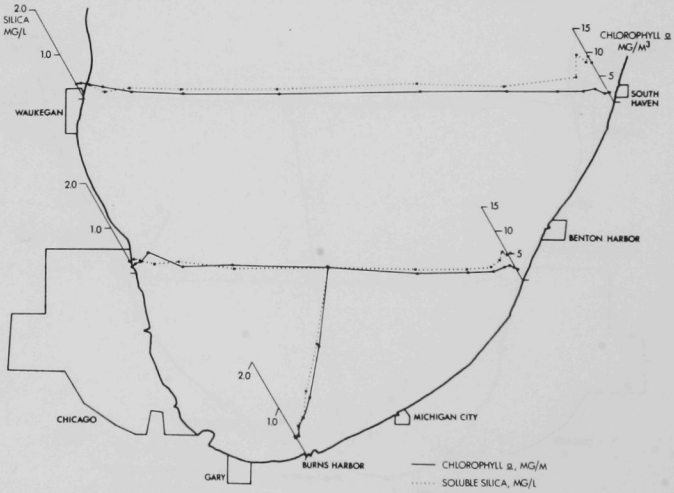

Fig. 73. Concentrations of Chlorophyll *a* and Soluble Silica in Lake Michigan Surface Water during Mid-September 1971. Redrawn and modified from Stoermer (1974) to show general distributional patterns.

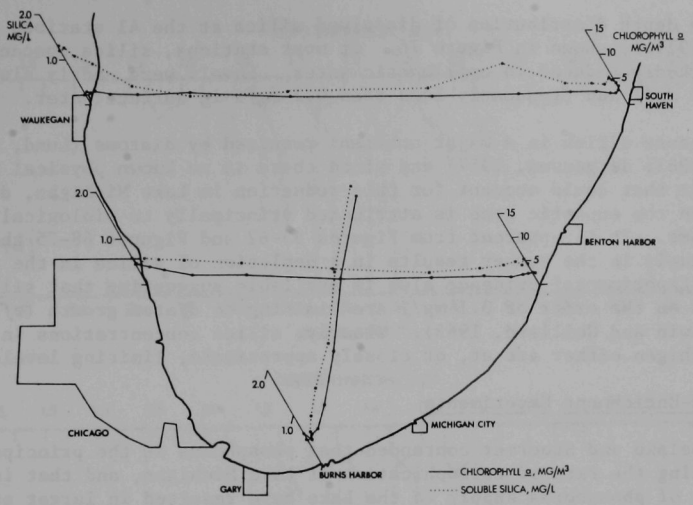

Fig. 74. Concentrations of Chlorophyll a and Soluble Silica in Lake Michigan Surface Water during Early October 1971. Redrawn and modified from Stoermer (1974) to show general distributional patterns.

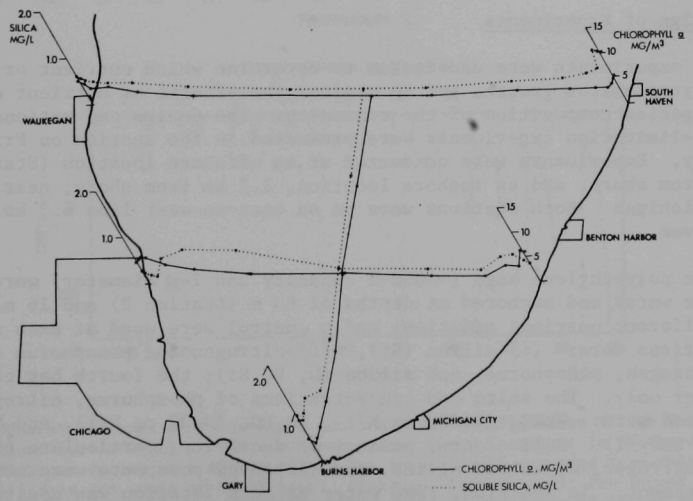

Fig. 75. Concentrations of Chlorophyll a and Soluble Silica in Lake Michigan Surface Water during Late October 1971. Redrawn and modified from Stoermer (1974) to show general distributional patterns.

The depth distribution of dissolved silica at the 41 stations during August 1971 is shown in Figure 76. At most stations, silica concentrations were markedly reduced in epilimnetic water. Levels were nearly always less than 0.5 mg/l and frequently less than 0.2 mg/l in surface water.

Because silica is a major nutrient required by diatoms (Lund, 1965; Lewin, 1961; Jørgensen, 1957) and since there is no known physical or chemical mechanism that could account for this reduction in Lake Michigan, depletion of silica in the euphotic zone is attributed principally to biological utilization by diatoms. It is apparent from Figures 55-62 and Figures 68-75 that diatom growth early in the summer results in a depletion of silica in the surface water. Experimental evidence also is available suggesting that silica concentrations on the order of 0.1 mg/l are limiting to diatom growth (*cf.* Jørgenson, 1957; Lewin and Guillard, 1963). Clearly, silica concentrations in southern Lake Michigan either are at, or closely approximate, limiting levels.

Nutrient-Enrichment Experiments

Schelske and Stoermer contended that phosphorus is the principal element controlling the rate of eutrophication of Lake Michigan, and that increases in the rate of phosphorus supply to the Lake have resulted in larger standing crops of diatoms. The biomass of diatoms during summer has increased to a point that silica is depleted to limiting or near-limiting concentrations in the euphotic zone. Direct experimental evidence supporting these contentions has been presented in two publications (Schelske and Stoermer, 1971, 1972). Since these results constitute an integral part of the phosphorus-silica-eutrophication hypothesis, the data are presented in detail.

Design of Experiments

The experiments were undertaken to determine which nutrient or nutrients limit phytoplankton growth, and to monitor the effects of nutrient enrichment on the species composition of the community. The design and rationale of nutrient-limitation experiments were presented in the section on Primary Productivity. Experiments were conducted at an offshore location (Station 2), 6.7 km from shore, and an inshore location, 1.2 km from shore, near Grand Haven, Michigan. Both stations were on an east-to-west line 6.3 km south of Grand Haven.

Four polyethylene bags (∿4000-l capacity and 2-m diameter) were filled with lake water and anchored at depths of 60 m (Station 2) and 16 m (Station 1). Three different nutrient additions and a control were used at each station. The additions were: (*i*) silica (Si), (*ii*) nitrogen and phosphorus (N, P), and (*iii*) nitrogen, phosphorus, and silica (N, P, Si); the fourth bag contained lake water only. The salts and concentrations of phosphorus, nitrogen, and silica used were: $NaNO_3$ (0.200 mg N/l), Na_3PO_4 (0.02 mg P/l), and $Na_2SiO_3 \cdot 9H_2O$ (0.70 mg SiO_2/l). Cell counts, primary productivity, particulate phosphorus, nitrate-nitrogen, dissolved silica, and dissolved phosphate were monitored in each treatment. In addition, lake water at each location was monitored (see Schelske *et al.*, 1971) for Secchi-disc transparency, water temperature, dissolved silica, nitrate-nitrogen, pH, primary productivity, and phytoplankton abundance and composition (see section on Floral Composition and Community Structure, Fig. 18 and Tables 3-6).

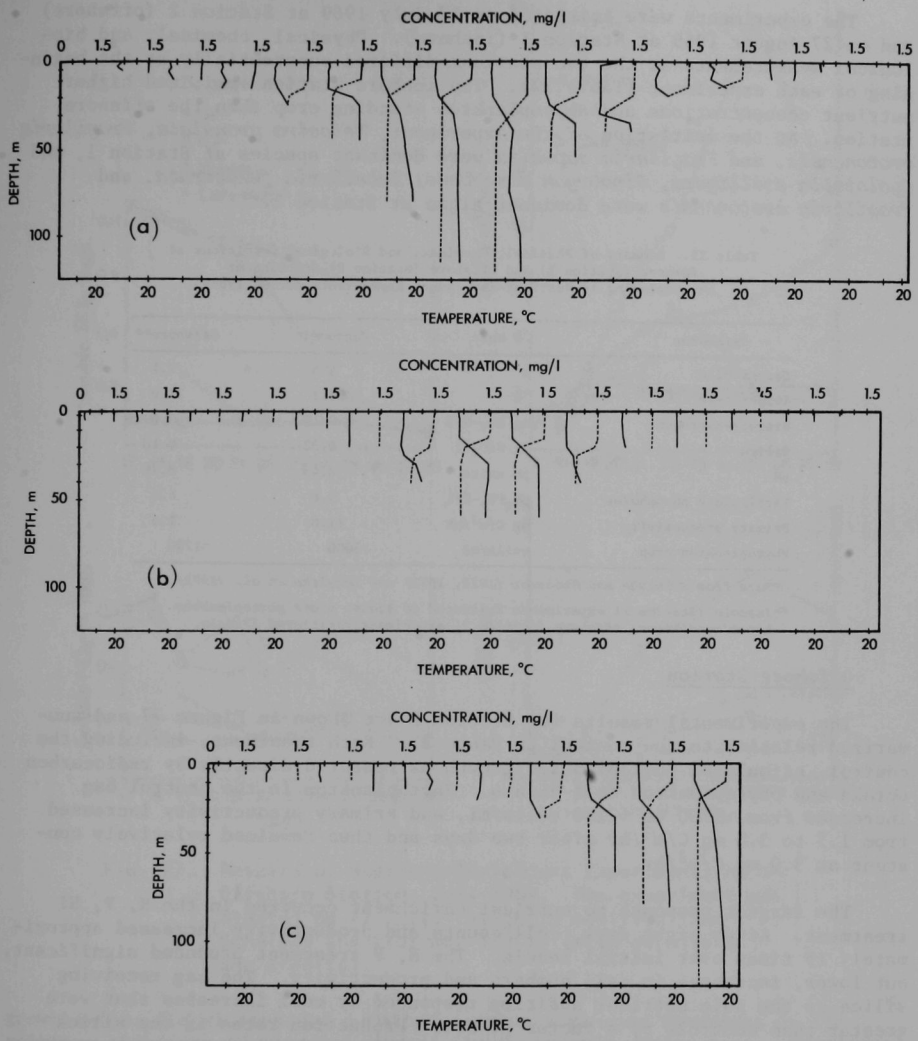

Fig. 76. General Patterns of Temperature (dotted line) and Dissolved Silica Concentrations (solid line) at Various Depths along Three Transects in Southern Lake Michigan during Late August 1971. One transect (a) extended from Waukegan, Illinois, to south of South Haven, Michigan (16 stations); the second (b) extended from Montrose Harbor, Illinois, to an area south of Benton Harbor, Michigan (15 stations); and the third (c) extended from the vicinity of Burns Harbor, Indiana, up into the axis of the Lake (10 stations). Redrawn and modified from Stoermer (1974).

The experiments were initiated on 17 July 1969 at Station 2 (offshore) and on 27 August 1969 at Station 1 (inshore). Physical, chemical, and biological measurements at the two stations differed substantially at the beginning of each experiment (Table 22). The inshore station exhibited higher nutrient concentrations and phytoplankton standing crop than the offshore station. At the initiation of the experiment, *Melosira granulata, Fragilaria crotonensis*, and *Fragilaria capucina* were dominant species at Station 1, and *Cyclotella stelligera, Dinobryon divergens, Tabellaria fenestrata*, and *Fragilaria crotonensis* were dominant algae at Station 2.

Table 22. Summary of Physical, Chemical, and Biological Conditions at Inshore (Station 1) and Offshore (Station 2) Stations at the Beginning of Nutrient-Enrichment Experiments during 1969*

Parameter	*Unit*	*Inshore***	*Offshore***
Secchi-disc	m	4.5	7.5
Temperature	°C	22.1	21.0
Nitrate-nitrogen	mg NO_3-N/l	0.19	0.09
Silica	mg SiO_2/l	0.32	0.10
pH	pH units	8.45	8.78
Particulate phosphorus	mg PO_4-P/l	5.6	4.6
Primary productivity	mg C/m^3/hr	11.0	1.5
Phytoplankton crop	cells/ml	>3000	∿1700

**Data from Schelske and Stoermer (1971, 1972) and Schelske et al. (1971).*

***Inshore (Station 1) experiments initiated 26 August under phytoplankton bloom conditions; offshore (Station 2) experiments initiated 17 July.*

Offshore Station

The experimental results for Station 2 are shown in Figure 77 and summarized relative to the control in Table 23. Each treatment, including the control, stimulated phytoplankton growth as measured directly by radiocarbon uptake and phytoplankton cell counts. Phytoplankton in the control bag increased from ∿1700 to ∿2200 cells/ml, and primary productivity increased from 1.5 to 3.5 mg C/m^3/hr after two days and then remained relatively constant at 3.0 mg C/m^3/hr.

The largest response to nutrient enrichment occurred in the N, P, Si treatment. After eight days, cell counts and productivity increased approximately 15 times over initial levels. The N, P treatment produced significant, but lower, increases in cell numbers and productivity. The bag receiving silica as the sole nutrient addition responded by cell increases that were greater than controls by a factor of 2.3. Production rates in the silica treatment, however, apparently were not significantly different than in the control. Minimum responses were detected by additions of silica (productivity) and nitrogen and phosphorus (cell counts).

The response of phytoplankton composition to the treatments is summarized in Table 24. Although more than 50 species were detected during analyses, the abundance of eight species constituted more than 80% of the community. The relative abundance of each species, except the chrysophyte *Dinobryon divergens*, increased in the N, P, Si treatment. The N, P treatment resulted in larger increases in relative abundance of species that do not require silica for

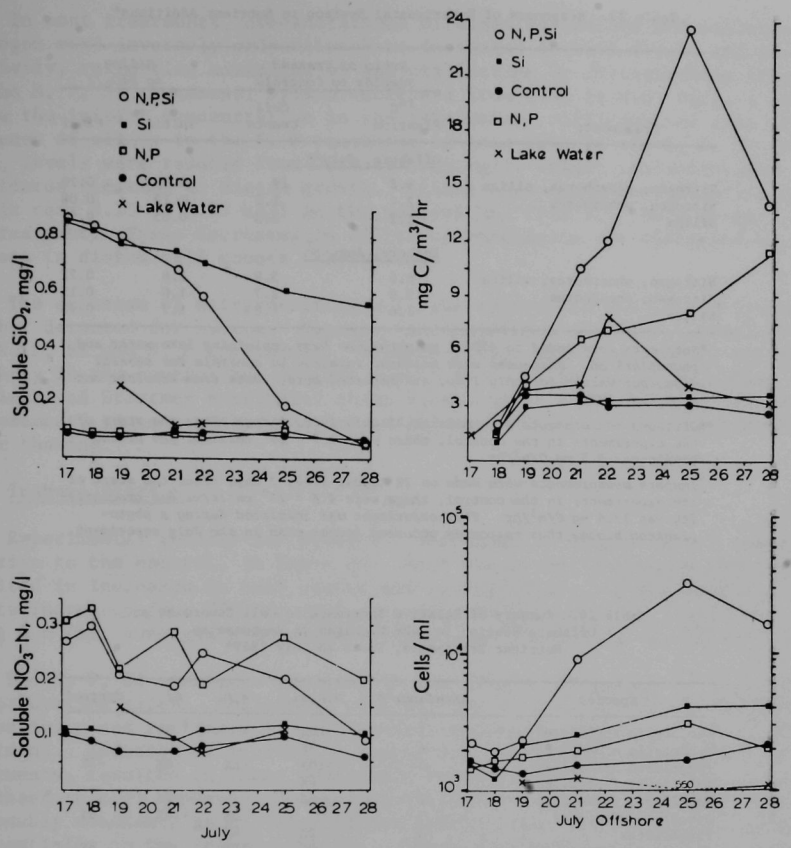

Fig. 77. Results of Nutrient-Enrichment Experiments at an Offshore Station, July 1969. The experiment was started on 17 July. Slightly modified from Schelske and Stoermer (1972) (with permission, see credits).

growth--*i.e.* flagellates and a colonial green alga--and decreases in the relative abundance of diatoms, especially *Fragilaria crotonensis*. Treatment with silica alone caused moderately large increases in the relative abundance of the diatoms *Cyclotella stelligera*, *F. crotonensis*, and *Tabellaria flocculosa*. The conditions in the control bag were conducive to increases in the relative abundance of *D. divergens* and colonial green algae, but did not stimulate diatom growth; in fact, the relative abundance of *F. crotonensis* decreased substantially in the control bag.

Phytoplankton growth in the experimental treatments was reflected by increases in the concentrations of particulate phosphorus and by changes in concentrations of soluble silica and nitrate-nitrogen. Particulate phosphorus

Table 23. Responses of Experimental Systems to Nutrient Additions*

Treatments	Ratio of Treated Samples to Controls: ^{14}C Fixation	Ratio of Treated Samples to Controls: Cell Counts	Silica, mg SiO_2/l: Initial	Silica, mg SiO_2/l: Final
	Offshore, July**			
Nitrogen, phosphorus, silica	6.8	19	0.85	0.20
Nitrogen, phosphorus	2.4	1.8	0.10	0.08
Silica	1.1	2.3	0.85	0.57
	Inshore, August†			
Nitrogen, phosphorus, silica	6.6	3.9	1.6	0.22
Nitrogen, phosphorus	2.9	2.7	1.0	0.15
Silica	1.6	1.8	1.7	0.98

*Nutrients were added to 4000-l polyethylene bags containing lake water and phytoplankton. Responses were measured relative to controls for several days, but values for only 1 day are reported here. Data from Schelske and Stoermer (1971).

**Offshore measurements were made on 25 July 1969, 8 days after the start of the experiment; in the control, there were 1.7×10^3 cells/ml and productivity was 3.5 mg $C/m^3/hr$.

†Inshore measurements were made on 29 August 1969, 3 days after the start of the experiment; in the control, there were 4.8×10^3 cells/ml and productivity was 13.6 mg $C/m^3/hr$. This experiment was initiated during a phytoplankton bloom; thus responses occurred sooner than in the July experiment.

Table 24. Summary of Relative Increases in Cell Counts at an Offshore Station in Lake Michigan in Response to Nutrient Treatments, 18 to 28 July 1969*

Species	Abundance**	N,P,Si	N,P	Si	Control
Cyclotella stelligera	1	>10X		3X	
Cyclotella michiganiana	6	3X			
Fragilaria crotonensis	4	>10X	<2X	6X	<2X
Tabellaria flocculosa		4X			
Tabellaria fenestrata	2	3X		2X	
Dinobryon divergens	3		3X	>10X	6X
Flagellates	5	2X	4X		
Unidentified green colony		8X	>10X	5X	6X

*Experiment started July 17. Data from Schelske and Stoermer (1972).

**Abundance indicates rank of cell counts from highest to lowest in control treatment.

Symbols: 3X = 3-fold increase from 18 to 28 July, etc.

was 4.6 mg/l at the offshore station (Table 22) and averaged 4.2 mg/l phosphorus in the four treatments at the beginning of the experiment (see Table 25). Incorporation of phosphorus into the particulate fraction (phytoplankton and other seston components) is enhanced by the N, P, Si and N, P treatments. Particulate-phosphorus levels were reasonably constant in the control and Si treatments but appear to have decreased with time. Increases in particulate phosphorus were well correlated with increases in cell counts and productivity in the N, P, Si treatment, and apparently reflect increases in these parameters in the N, P treatment. The slight increases in cell counts in the Si treatment and the control, however, were not reflected by increases in particulate phosphorus. This point will be discussed in a following subsection (Interpretation of Results, p. 137).

In most treatments, concentrations of dissolved silica and nitrate-nitrogen were inversely proportional to increases in cell counts and productivity, reflecting assimilation and utilization by phytoplankton (Fig. 77). In the N, P, Si treatment, silica decreased from 0.86 to 0.05 mg/l, a level below the initial concentration in the lake water. Although the rate of decrease of silica in the N, P treatment is less than in the N, P, Si treatment, levels were reduced from 0.10 to 0.05 mg/l. These concentrations are considered limiting to diatom growth. Silica also decreased gradually from levels near 0.10 to 0.05 mg/l in the control and from 0.86 to 0.56 mg/l in the Si treatment. These decreases in silica concentration are reflected by increases in diatom cell counts (Table 24).

The decrease of nitrate-nitrogen in the treatments was not as pronounced as that detected for silica. Nitrate concentrations decreased erratically in the N, P, Si and N, P treatments. Nitrate levels also appeared to decrease slightly in the control but did not appear to do so in the Si treatment. Schelske and Stoermer attributed these anomalies to analytical errors in measurement, since samples were frozen and not always analyzed immediately after thawing.

Inshore Station

Experimental results for Station 1 are shown in Figure 78 and summarized, relative to the control, in Table 25. Each treatment, including the control, resulted in increases in cell counts and productivity. In the control, cell counts increased from 2000 to 4800 cells/ml and productivity, initially 11 mg $C/m^3/hr$, averaged approximately 10 mg $C/m^3/hr$ during incubation.

The N, P, Si treatment resulted in the largest increases in cell numbers and production rates. Enrichment with N, P produced significant increases in productivity and increases in cell numbers nearly equivalent to the N, P, Si treatment. Addition of silica, in comparison with the N, P, Si and N, P treatments, resulted in lower production rates; however, there were equivalent increases in cell numbers. Primary productivity in the control bag remained reasonably constant, as at the offshore station, but cell counts increased substantially in the inshore control. These observations are discussed later (Interpretation of Results, p. 137).

Phytoplankton growth responses in the treatments also were reflected by increases in particulate phosphorus and by decreases in nitrate-nitrogen and dissolved silica concentrations. Added phosphorus was assimilated rapidly into the particulate fraction (Table 25). Levels of particulate phosphorus were highest in the N, P, Si and N, P treatments. Since the amount of phosphorus added to these two treatments was 0.020 mg/l and the initial concentration was 0.005 mg/l, it is apparent that nearly all of the added phosphorus was incorporated into the particulate fraction. Increases in particulate phosphorus, however, were not reflected by increases in cell numbers observed in the Si treatment and in the control. Concentrations of particulate phosphorus in the two treatments were nearly constant.

Dissolved silica and nitrate-nitrogen concentrations decreased during the experiment (Fig. 78). In the N, P, Si and N, P treatments, silica was depleted rapidly to a concentration of approximately 0.05 mg/l. Silica was reduced from a concentration of 0.95 to 0.48 mg/l in the control, and from 1.75 to $\sim$0.45 mg/l

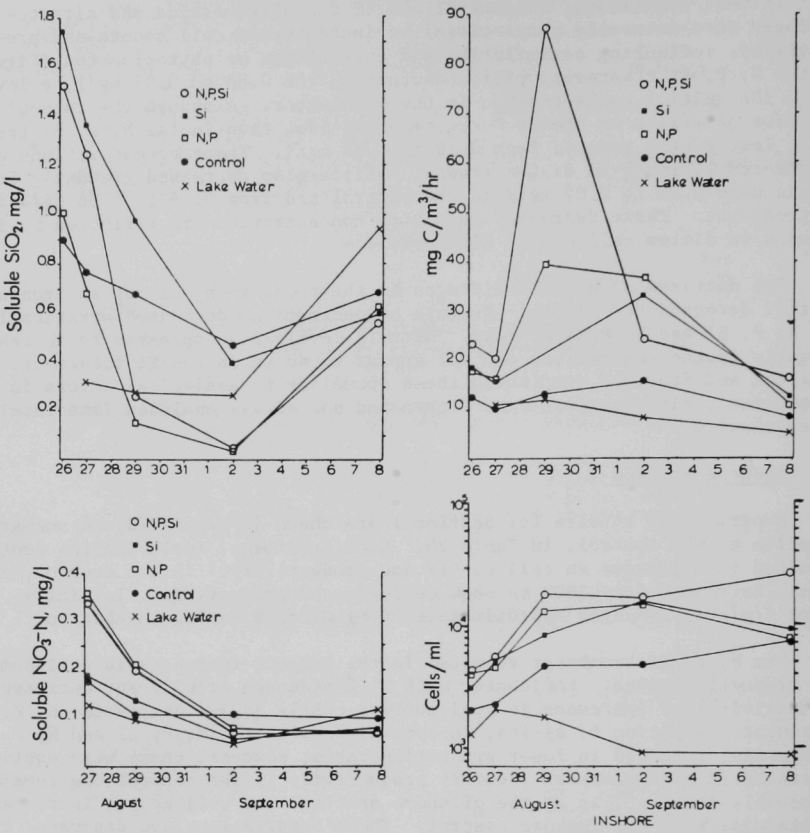

Fig. 78. Results of Nutrient-Enrichment Experiments at an Inshore Station, August and September 1969. The experiment was started on 29 August. Slightly modified from Schelske and Stoermer (1972) (with permission, see credits).

in the silica treatment. Nitrate-nitrogen was depleted rapidly in the N, P, Si and N, P treatments, *i.e.* from 0.35 to 0.08 mg/l. Nitrate decreased initially in the control and then remained constant at about 0.1 mg/l. Treatment with silica also caused a rapid decrease in nitrate-nitrogen to a level of 0.06 mg/l. If all nitrate supplies were utilized by phytoplankton, then 0.270 mg/l were assimilated in the N, P, Si treatments, 0.120 mg/l in the silica treatment, and 0.080 mg/l in the control. These results suggest that even in the control bag, sufficient quantities of phosphorus and silica were available to sustain phytoplankton growth.

Table 25. Concentration of Particulate Phosphorus ($mg\ PO_4$-P/m^3) in Nutrient-Enrichment Experiments, July-September 1969*

Dates	Treatments			
	N,P,SiO₂	*N,P*	*SiO₂*	*Control*
	Offshore, July			
17	4.0	3.9	4.4	4.6
18	6.3	6.6	3.5	3.6
19	7.7	8.6	3.3	3.9
21	9.6	7.8	2.9	3.6
22	11.0	9.2	3.0	4.2
25	14.8	7.7	3.8	4.2
28	20.4	-	-	-
	Inshore, August and September			
26	10.8	9.6	7.2	5.6
27	27.6	21.5	8.2	6.6
29	21.3	20.7	6.8	11.3
2	25.6	14.7	5.3	-

Data from Schelske and Stoermer (1972).

Experiments with Phosphorus and Nitrogen

The experiments demonstrated that phytoplankton respond to silica enrichment when additions are made simultaneously with phosphorus and nitrogen. These experiments do not show that nitrogen is a limiting nutrient. Schelske and Stoermer (1972) contended that since nitrate-nitrogen concentrations were never less than 0.05 mg/l and could be reduced below pretreatment levels during experiments, it apparently does not limit phytoplankton growth.

Nutrient-enrichment experiments at Little Traverse Bay, Petoskey, Michigan, were undertaken to test the effects of phosphorus and nitrate-nitrogen on phytoplankton growth. The experimental design was similar to experiments conducted near Grand Haven, except that smaller bags were used (∿1000-l capacity) and phosphorus was added in different concentrations. Phytoplankton response was evaluated by measuring primary production rates.

The experimental results are summarized in Table 26. The response of phytoplankton was similar in all treatments. Productivity in the controls remained relatively constant over the experiment, and production rates in each treatment were greater than in controls. Enrichment with 20 mg/m^3 phosphorus resulted in production rates equivalent to all other treatments, including combined additions of nitrogen and phosphorus. The authors concluded that phosphorus, not nitrogen, limits phytoplankton production. The observation that larger additions of phosphorus failed to produce higher production rates suggests that other nutrients may become limiting when phosphorus is added in relatively large amounts.

Interpretation of Results

Although initial conditions in the experiments near Grand Haven were dissimilar, the response of phytoplankton to nutrient enrichment at the two stations was essentially the same; phytoplankton growth was stimulated by each nutrient addition. On the basis of productivity, the relative effects of the treatments were N, P, Si > N, P > Si (Table 23). When phytoplankton response

Table 26. Effects of Phosphorus and Nitrogen on ^{14}C-Carbon Fixation in Nutrient-Enrichment Experiments in Little Traverse Bay near Petoskey, June 1970*

*Treatments,** mg/m³*	*June 1970*								
	8	*9*	*10*	*11*	*12*	*13*	*14*	*15*	*17*
20 P	3.0	1.9	7.5	9.1	10.4	10.8	11.9	19.2	25.4
20 P	2.6	2.2	7.2	8.4	9.9	12.7	9.9	17.5	20.7
40 P	2.5	4.9	6.2	9.8	9.9	9.9	6.6	14.4	24.2
40 P	2.4	5.7	6.6	10.0	9.3	10.0	9.1	20.4	25.1
80 P	1.9	1.3	4.8	8.3	8.0	10.8	10.5	14.9	20.7
80 P	1.5	1.6	5.1	6.1	6.9	9.5	8.1	14.6	19.8
400 N, 80 P	2.1	1.9	5.7	7.9	9.3	12.4	11.4	17.8	34.9
400 N, 80 P	2.0	2.4	5.3	7.6	8.9	11.8	9.6	18.9	25.5
Control	3.0	3.9	4.3	5.3	4.0	3.9	3.6	3.8	4.1
Control	3.1	4.7	4.5	3.9	4.3	3.8	3.0	4.5	4.4

**Data from Schelske and Stoermer (1972).*

***Phosphorus was added in three concentrations, and nitrogen and phosphorus were added in one concentration. Each treatment, including the control, was replicated.*

was measured by increases in cell numbers, the N, P, Si treatment resulted in the largest response, but the addition of silica alone yielded larger increases in cell numbers than the N, P treatment. The authors concluded that both silica and phosphorus were elements limiting phytoplankton growth. This contention does not violate nutrient-limitation theory, *i.e.* only one nutrient at a time can limit growth (*cf.* discussions by Droop, 1973, and O'Brien, 1972). At the initiation of the experiments, both silica and phosphorus were at limiting or near-limiting concentrations, such that the addition of one element caused the other to become limiting. In these experiments, silica depletion is attributed directly to utilization by diatoms. The contention that silica acts as a limiting nutrient was demonstrated by increases in cell numbers when silica alone was added (Figs. 77 and 78); however, treatment with phosphorus (in the N, P, Si bag) permitted diatoms to reduce silica concentrations to below pretreatment levels, *i.e.* less than 0.05 mg/l. This effect was especially dramatic inshore, where both treatments involving phosphorus resulted in a rapid depletion of dissolved silica.

The above results were duplicated by the authors during summer 1969 at four other locations in the Lake. All of these results suggest that limitation by phosphorus and silica is not restricted to one region or to particular circumstances in the Lake. The authors have cautioned, however, that phytoplankton can respond to nutrients other than phosphorus and silica. Stoermer *et al.* (1971) and Schelske *et al.* (1971) also speculated that a response to nutrient enrichment may not occur where the water is already rich in nutrients, such as in regions of upwelling, or where algal populations are senescent or are affected by toxins secreted by certain species of blue-green algae. These conditions and their effects on enrichment experiments were discussed in the section on Primary Productivity.

There are several anomalies in the experiments described above. Although they do not alter the basic conclusions of Schelske and Stoermer (1971, 1972), they merit discussion. Specifically, the response of phytoplankton to nutrient enrichment is not necessarily reflected by simultaneous increases in both cell numbers and productivity, and increases in cell numbers in some treatments are not reflected by increases in particulate-phosphorus concentrations.

As pointed out above, increases in cell numbers are not proportional to increases in primary productivity (Figs. 77 and 78). This phenomenon was pronounced in the N, P, and Si treatments, and occurred in the control bags. In the silica treatment, for example, the size of the offshore phytoplankton community increased substantially; however, productivity remained relatively constant. There are plausible explanations for this phenomenon. First, it is possible that cell size or cell carbon content diminished during growth. The *biomass* of the population, therefore, could have remained constant while the population increased *numerically*. Evidence supporting this line of reasoning can be obtained by examining variations in particulate-phosphorus concentrations (Table 25). Particulate-phosphorus levels offshore remained relatively constant in the Si treatment and in the control. The same phenomenon was observed inshore, except that the control bag exhibited increases in particulate-phosphorus concentrations.

Second, other investigators have observed similar or related phenomena. Goldman and Armstrong (1969) detected increases in phytoplankton abundance in Castle Lake after phosphorus addition; however, primary productivity decreased relative to controls. Similarly, Schindler *et al.* (1971) observed that after fertilization of a Canadian Shield lake with repeated applications of nitrogen and phosphorus, phytoplankton standing crop increased but the rate of primary production did not increase substantially. These authors suggest that nutrient enrichment may alter respiration or sedimentation rates, or both. Although increased sedimentation may not be applicable to the above experiments (unless algae settled to the bottom of the bags), increased respiration rates could result in higher losses of photosynthetically fixed carbon.

A third explanation for this discrepancy could involve a rapid and relatively large release of photosynthetically fixed carbon by external metabolite secretion. Fogg (1964), for example, demonstrated that 80-90% of the carbon fixed photosynthetically in the euphotic zone of Lake Windermere, England, was excreted into the water, particularly under conditions of light inhibition. Similarly, Watt (1966) detected excretion rates in the Tring Reservoir, England, amounting to 30% or more of photosynthetically fixed carbon.

Correlation of Particulate Phosphorus with Primary Productivity

The relationship between particulate-phosphorus concentration and productivity (Table 26) prompted Schelske and Stoermer (1972) to examine the correlation between the parameters. They utilized their data from a cruise in southern Lake Michigan (Schelske and Callender, 1970), from nutrient-enrichment experiments, and from measurements at 14 stations in southern Lake Michigan (Fig. 79). The correlation coefficients for the 14 stations were 0.80 and 0.68 for 20 paired data points and are highly significant. Five data points in Figure 79 were not included because they were from upwelled water and from phytoplankton blooms. The observation that inshore measurements are not correlated suggests that the parameters may not be related where nutrient supplies are highly variable due to upwelling or *slugs* of nutrients entering the Lake from tributaries.

Ratios of Silica to Phosphorus in Diatoms and the Loading Rates of Silica and Phosphorus

Phytoplankton growth in Lake Michigan, as in other lakes, is dependent partly upon the absolute nutritional requirements of the algae and partly upon

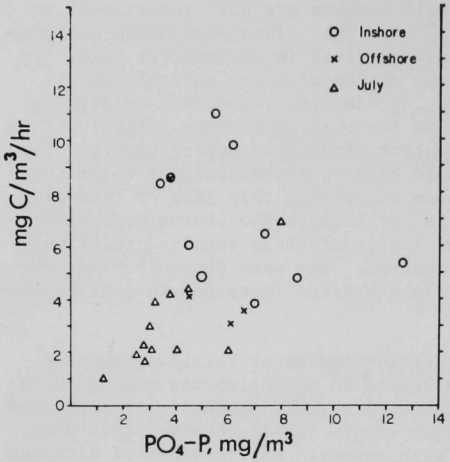

Fig. 79.

Plot of Productivity versus Concentration of Particulate Phosphorus in Samples Collected in 1969. Slightly modified from Schelske and Stoermer (1972) (with permission, see credits).

the quantity and rate at which nutrients are added to the water. If nutrients are not supplied in proportions required for optimum growth, one or more elements will limit phytoplankton growth. The authors contend that phosphorus is being supplied in quantities in excess of those required by diatoms for silica utilization. The net effects of this imbalance are silica depletion, replacement of diatoms by non-silica-requiring algae (such as green and blue-green algae), and acceleration of the eutrophication process.

Several lines of evidence substantiate this contention: (*i*) mass ratios of silica to phosphorus in diatoms, (*ii*) rates of phosphorus and silica supply from tributaries, and (*iii*) ratios of silica to phosphorus uptake measured directly in nutrient-enrichment experiments.

Diatoms normally contain relatively large amounts of silica. Lund (1965) estimated the silica content of 10 species to be between 26 and 63% of total dry weight. On this basis, Schelske (1975) computed mass ratios of SiO_2:P for *Asterionella* (cited in Hutchinson, 1967) ranging between 170:1 and 500:1. Variations in the ratio are due to the fact that different species have dissimilar absolute requirements for these elements and that the physiological state of a species varies depending on nutrient supply and other factors. Diatoms, for example, may contain 10 to 100 times the amount of phosphorus needed for optimum growth because of luxury consumption and storage. In such cases, mass ratios of SiO_2:P will be lower.

Recently, Ayers (1970) summarized data on inputs of phosphorus and silica from 19 tributaries (Fig. 80). Data on total soluble phosphorus and dissolved silica were used to compute loading rates for each element and mass ratios of silica to phosphorus (Table 27). Six rivers (Fox, Grand, St. Joseph, Menominee, Burns Ditch, and Kalamazoo) contribute about 80% of the total phosphorus loading from the tributaries. Ratios of silica to phosphorus in the tributaries are variable, ranging from 14:1 (Milwaukee River) to 796:1 (Pere Marquette).

If diatoms are to maintain dominance in the phytoplankton, they require supplies of silica proportional to supplies of phosphorus. Low SiO_2:P ratios

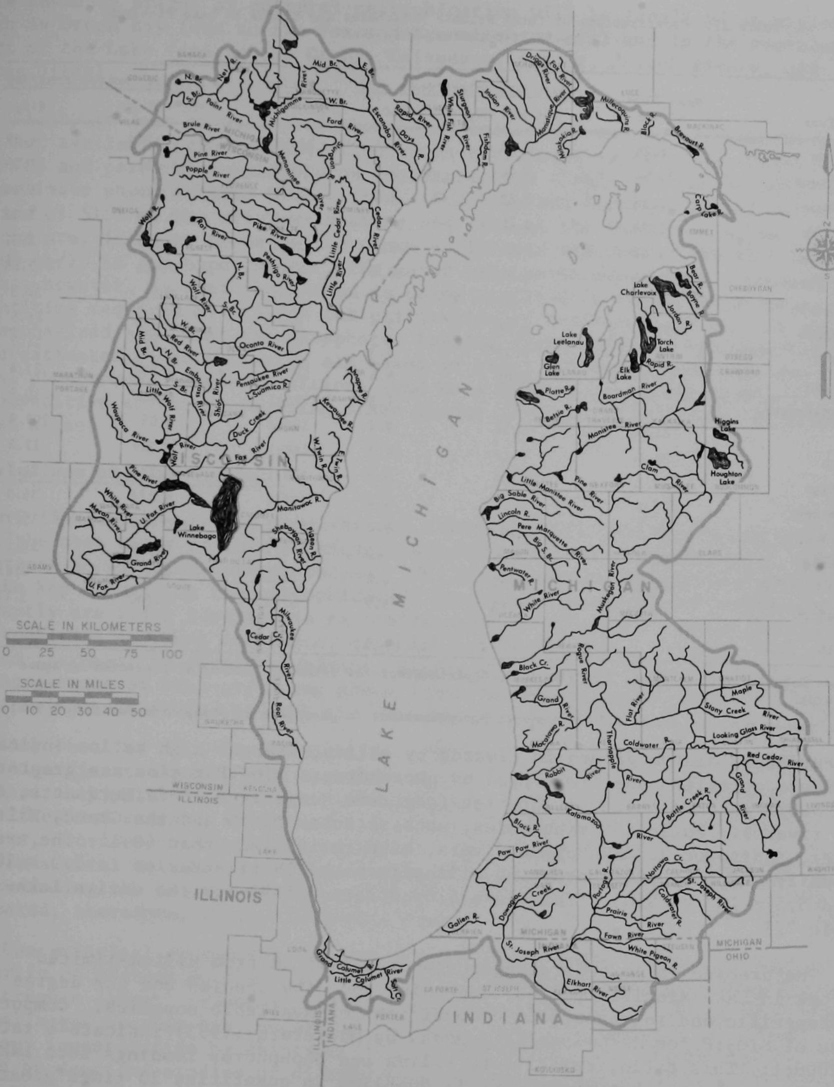

Fig. 80. Map of Lake Michigan Drainage Basin Showing Major Tributaries (White, 1976--unpublished).

Table 27. Contributions of Total Soluble Phosphorus and Silica to Lake Michigan by 19 Tributaries, 1963-1964*

River	Mean Flow, m^3/sec	Mean Concentrations, mg/l		Ratios	Loading, metric tons/day	
		Tot Sol PO_4	SiO_2	SiO_2:P**	Tot Sol PO_4	SiO_2
Boardman	5.26	0.20	7.5	114:1	0.125	4.69
Manistique	23.9	0.04	5.8	574:1	0.082	12.00
Manitowoc	2.35	0.62	5.7	28:1	0.125	1.16
Sheboygan	3.73	0.40	3.9	30:1	0.129	1.26
Milwaukee	5.41	0.61	2.8	14:1	0.285	1.31
Burns Ditch	4.24	1.8	10.	17:1	0.661	3.68
St. Joseph	58.4	0.24	6.4	82:1	1.21	32.3
Kalamazoo	32.3	0.21	5.9	86:1	0.586	16.5
Grand	53.8	0.52	5.3	31:1	2.42	24.7
Muskegon	49.0	0.06	5.6	285:1	0.254	23.8
Pere Marquette	16.1	0.03	7.8	796:1	0.041	10.9
Fox	125.0	0.28	9.4	103:1	3.03	101.8
Oconto	22.4	0.17	9.2	166:1	0.329	17.8
Peshtigo	25.2	0.08	9.8	375:1	0.174	21.4
Menominee	92.1	0.11	4.4	122:1	0.877	35.0
Ford	9.54	0.04	7.0	536:1	0.033	5.77
Escanaba	28.8	0.06	7.0	357:1	0.149	17.5
Rapid	2.27	1.59	3.1	58:1	0.311	0.61
Whitefish	6.43	0.18	5.7	97:1	0.100	3.17
Totals					10.9	335.

*From Schelske (1975). Data from the U. S. Department of the Interior (1968b) as presented by Ayers (1970).

**PO_4 values were divided by 3.06 to convert concentrations to phosphate as phosphorus for SiO_2:P ratios.

indicate that diatom growth is limited by silica, whereas high ratios indicate an excess of silica and limitation by phosphorus. SiO_2:P ratios are greater than 500:1 in unpolluted tributaries (*e.g.* the Manistique, Pere Marquette, and Ford rivers). Polluted tributaries, such as Burns Ditch and the Grand, Milwaukee, Manitowoc and Sheboygan rivers, have ratios less than 40:1. The average daily input of phosphorus and silica from the 19 tributaries is 5.9×10^3 kg P and 5.5×10^5 kg SiO_2. This is a SiO_2:P ratio of 93 for the entire Lake (Table 27).

The precise ratio separating phosphorus-limited from silica-limited diatoms in Lake Michigan varies, depending upon the species and the degree of interspecific and intraspecific competition for available supplies. Computations of SiO_2:P for *Asterionella formosa* by Mackereth (1953) indicate a ratio of 2000:1. This ratio, relative to silica and phosphorus loadings into Lake Michigan, suggests that phosphorus is supplied in quantities 20 times greater than that needed by diatoms. Mackereth's ratio, however, may be inaccurate due to an analytical error in measurement. Schelske's (1975) calculations for *A. formosa* are lower and fall in the range of 170:1 to 500:1. If the SiO_2:P ratio for Lake Michigan diatoms is set arbitrarily at an average value of 200:1, the current rate of phosphorus supply is roughly twice as great as the silica supply (Schelske, 1975). These computations demonstrate that phosphorus is being supplied in quantities in excess of those required by diatoms for the total utilization of available silica. These data also suggest that

more advanced stages of cultural eutrophication will be localized in regions such as Green Bay (due to the Fox and Menominee rivers) and in the southeastern part of the Lake (due to the Grand, Kalamazoo, and St. Joseph rivers, and Burns Ditch).

Although data on silica-to-phosphorus ratios for diatoms in Lake Michigan are not available, the results of nutrient-enrichment experiments (Figs. 77 and 78) and particulate-phosphorus concentrations (Table 25) can be used to approximate phytoplankton Si:P ratios. Schelske and Stoermer (1972) calculated ratios of 51:1 at the offshore station and 84:1 at the inshore station. These values are, in fact, conservative since silica was reduced to limiting levels (0.05 mg/l) in the experiments. The major conclusion drawn from these computations, however, is that phosphorus is being supplied in excess relative to the quantities required by diatoms for utilization of available silica. It should be emphasized also that the phosphorus loading (Table 27) may be significantly underestimated since estimates are based on total soluble phosphorus, not total phosphorus. These conditions lead to a decline of diatom abundance and a competitive advantage favoring other groups of algae, *i.e.* green and blue-green algae.

Conclusions and Discussion

Evidence presented by Schelske and Stoermer (1971, 1972) substantiates that the open water of Lake Michigan, especially in the southern basin, has undergone accelerated eutrophication. The basic premise is that *phosphorus* is the key element in the eutrophication process. Quantities of phosphorus currently are being supplied in excessive amounts relative to other nutrients. The resulting nutrient imbalance, especially with respect to silica, has *caused* increases in diatom abundance, shifts in diatom species composition, the appearance of blue-green and green algae in summer, and a severe reduction of dissolved silica in the euphotic zone during summer.

Any one line of evidence might be challenged as insufficient to prove that significant changes have occurred in the Lake, or that phosphorus *is* the critical nutrient. Each line of evidence, coupled with measurements on the quantities and rates of supply of silica and phosphorus from tributaries, however, provides corroborating evidence. The data presented in this section are fundamental to understanding phytoplankton dynamics in Lake Michigan, and to predicting the consequence of continued enrichment of the Lake. They are evaluated, therefore, in the following text.

One principal contention is that phytoplankton composition, consisting primarily of diatoms in the past, has shifted recently to species characteristic of eutrophic lakes. Stoermer's (1967) observations on net phytoplankton could be challenged because his comparison was made with the results of a single previous investigation by Ahlstrom (1936). The contention, however, is supported by detailed studies of diatoms by Stoermer and Yang (1969, 1970). They noted that the relative abundance of eutrophic diatoms has increased during the last several decades. In addition, observations on spatial and temporal diatom distribution in Lake Michigan by Holland (1969) and Holland and Beeton (1972) reveal that eutrophic species occur offshore.

Precise comparisons among the results of Holland, Stoermer, and other investigators are difficult to make because sampling techniques and quantitative counting methods differ and because different locations were sampled in

Lake Michigan. One approach to this problem is to analyze diatom assemblages in open-water sediments of the southern basin. Since diatoms are relatively well preserved in most lake sediments, the structure and composition of assemblages could be reconstructed historically (*cf.* Stockner and Benson, 1967; Stockner, 1971, 1972). If such studies are carried out in conjunction with studies on historical variations in primary production (*cf.* Wetzel, 1970), recent changes in the flora could be detected and related to past changes in the chemical environment. No such investigations have been undertaken in a systematic way as yet in Lake Michigan.

The mechanisms accounting for displacement of oligotrophic by eutrophic diatoms are not well understood. Generally these shifts in composition are attributed to a species' ability to tolerate or adapt to changing nutrient levels in the environment (*cf.* Hutchinson, 1967). Kilham (1971) suggested that dissolved-silica concentrations may be a principal factor determining the displacement of oligotrophic by eutrophic species. A discussion of this mechanism was presented in the section on Floral Composition and Community Structure (p. 23). Presently, there is no observational or experimental evidence verifying the operation of this mechanism in the Lake. Experimental studies and an evaluation of existing data, however, may reveal that competition for silica is an important factor in seasonal succession and in the ability of species to adapt to eutrophic conditions.

The prediction of Schelske and Stoermer (1971, 1972) that blue-green and green algae will become dominant components of offshore phytoplankton has already occurred (Figs. 55-62). Phytoplankton in southern Lake Michigan is dominated numerically by diatoms and golden-brown algae during spring and early summer. As dissolved-silica concentrations reach limiting levels, however, populations of blue-green and green algae replace diatoms and are dominant until thermal stratification is disrupted in late fall.

It should be pointed out that other data verify the presence of blue-green algae in Lake Michigan. Parkos *et al.* (1969) have shown that in October, blue-green algae are dominant organisms in open water of the northern, central, and southern regions of the Lake (Table 13). The co-occurrence of species such as *Microcystis incerta*, *Coelosphaerium* sp., *Lyngbya contorta*, *Chroococcus* sp., and *Merisomopedia glauca* may be regarded as an association characteristic of moderately-enriched water. Their data, however, may be criticized because samples were taken only at the surface where blue-green algae may be disproportionately represented. Settling in Imhoff cones, preservation in formalin, and counting by the Sedgewick-Rafter technique also undoubtedly exaggerates the importance of large algal forms. Nevertheless, these data indicate the presence of eutrophic species in the open water of the Lake.

Studies by Nalco Chemical Company provide important information on the presence of blue-green algae in southwestern Lake Michigan. Piala and Lamble (1971) demonstrated that blue-green algae (*Anabaena* sp., *Oscillatoria tenuis*, *Spirulina major*, *Coelosphaerium naegelianum*, and *Chroococcus turgidus*) occur in moderate numbers inshore and offshore (Figs. 47 and 48). Similarly, Gulo and Lamble (1971) have shown that blue-green algae comprise between 0.8 and 14% of the nearshore community (Figs. 49 and 50). The data of Huh *et al.* (1972) include a listing of 49 species of blue-green algae. Although the mean value of blue-green algae at stations near Waukegan was less than 8.0% during most months, *Coelosphaerium naegelianum* reached near-bloom proportions from September

to December. This species, normally regarded as a eutrophic form, was generally more abundant in nearshore water, and its abundance ranged between 10 and 67% during fall and winter. Similar data showing the abundance of blue-green algae during certain months are included in Delinck and Lamble (1971).

It is virtually impossible to identify the point in time when blue-green algae first occurred in significant abundance in the Lake. Eddy's (1927, 1934) investigations indicate that numerous species of blue-green algae were present in the Lake in the 1930's. Similarly, Griffith's (1955) results are of importance because they show that the blue-green alga *Anacystis* sp. was the dominant species in the phytoplankton in the early 1950's (Fig. 37). It is not possible to infer, however, that her results are different than those of Daily (1938) and Damann (1941). The quantitative techniques used by Griffith were substantially different than those used by the two previous investigators, and her quantitative data are expressed in arbitrary units rather than as individuals or biomass. In addition, it is unlikely that *Anacystis* was dominant on the basis of biomass since its cells are very small relative to most other algae.

The factors that cause or lead to dominance by blue-green algae in north-temperate lakes are imperfectly understood. Observational and experimental evidence suggests that blooms develop in warm water that receives large supplies of phosphorus and sodium (as has occurred in Lake Michigan) when ammonia and nitrate-nitrogen concentrations are low (*cf.* Vollenweider, 1971; Hammer, 1964; Holm-Hansen, 1967). The development of blue-green algae in southern Lake Michigan is not a simple case of reduction in size of diatom populations (due to silica depletion) and a competitive *takeover* by blue-green algae. Recent studies indicate that the availability of dissolved carbon dioxide may be one of several factors conducive to dominance by blue-green algae.

King (1971) contended that high pH and total alkalinity levels are correlated with phytoplankton composition. He postulated that blue-green algae can utilize low levels of carbon dioxide more efficiently than other algae. This contention of a competitive advantage favoring blue-green algae has been verified partially by Shapiro (1973). He observed that aeration of lake water with gaseous CO_2 resulted in a shift from a community dominated by blue-green algae to one dominated by green algae. If the observations of King and Shapiro are generally applicable to moderately buffered lakes, then alkalinity and pH levels in southern Lake Michigan currently are at levels conducive to development of blue-green algae. Data compiled by the U. S. Department of the Interior (1968b) and from other sources (*e.g.* Rousar, 1973) indicate that alkalinity levels at inshore and offshore stations are over 100 mg/l $CaCO_3$ in the southern basin. Inshore and offshore water also exhibit pH values ranging from 8.5 to 9.3. These data on southern Lake Michigan show that the water is receiving relatively large inputs of phosphorus (see Lee, 1974, and Table 27). The water also has increased in sodium content (Beeton, 1969) and is moderately low in CO_2 concentrations in the upper region of the euphotic zone during mid- and late summer.

Another possible mechanism leading to development of and dominance by blue-green algae is related to selective grazing by zooplankton. Although it appears that no investigations have been undertaken to evaluate selective grazing of Lake Michigan phytoplankton, sufficient data from other studies are available to show that blue-green algae may not be grazed extensively because

they are too large, unpalatable, or toxic to zooplankton (*cf.* Burns, 1968, 1969a, 1969b; McQueen, 1970; Frost, 1972; Porter, 1973; Berman and Richman, 1974). It is possible, therefore, that some blue-green algae become dominant in Lake Michigan because other algal populations are removed by zooplankton grazing. Experimental investigations are required before one can evaluate the impact of zooplankton grazing on seasonal succession and blue-green algal populations in Lake Michigan.

It is apparent that blue-green algae have become established in southern Lake Michigan, at least during late summer and early fall, and there is every reason to suspect that continued inputs of phosphorus, at rates recently reported, will lead to larger populations of blue-green algae and more pronounced symptoms of cultural eutrophication.

The phenomenon of silica depletion in Lake Michigan might be questioned on several grounds: (*i*) long-term trends at water intakes (Fig. 63) may not represent conditions in open water, (*ii*) estimates of dissolved silica concentrations may be inaccurate due to analytical errors [*e.g.* the effects of freezing samples before analyses (*cf.* Armstrong and Schlindler, 1971)], and (*iii*) it is not clear if determinations are on filtered or unfiltered samples. The data, however, indicate that silica decreases along a north-to-south transect in open water (Figs. 64 and 65), and depletion is greater in the southern basin than in the northern basin during summer (Figs. 66 and 67, Tables 20 and 21). On a seasonal basis the depletion of silica is especially pronounced in the euphotic zone in the southern basin, and these decreases are correlated with diatom growth (Figs. 55-62 and 68-75). These observations are supported by data collected by the U. S. Department of the Interior (1968b) and by recent investigations on dissolved-silica concentrations in the Lake (Howmiller and Beeton, 1973; Rousar and Beeton, 1973; Rousar, 1973). In addition, studies by Huh *et al.* (1972) in southwestern Lake Michigan demonstrate that silica is reduced to limiting levels at inshore and offshore stations during summer.

Schelske and Stoermer contend that silica will not be entirely depleted in the offshore euphotic zone, because winter overturn will replenish silica supplies in the epilimnion. Silica, however, will be used by diatoms in the spring and will be reduced to limiting concentrations by early or mid-summer. This phenomenon has been demonstrated by Lund (1969) for Belham Tarn, England, and by numerous investigators for other north-temperate lakes subjected to increased phosphorus loadings.

Recently, Lee (1974) examined unpublished data on silica provided by the City of Chicago, Department of Water and Sewers. Over the period 1926 to 1970, dissolved silica levels decreased but leveled off at approximately 1.0 mg/l in 1950. Since 1950, silica concentrations have remained relatively constant. If the plot of dissolved silica versus time for the Chicago intake (Fig. 63) is extrapolated to zero, silica would reach undetectable levels by 1976. Lee also maintained that silica supplies will not be totally exhausted in Lake Michigan in the future. He suggested that if present practices of nutrient discharge into the Lake are maintained, dissolved silica will still be present in quantitites of approximately 1.0 mg/l. He attributed this to factors affecting the dissolution rate of silica in natural waters, *i.e.* the rate of weathering of silicate minerals in the basin is often dependent on silica concentrations in the water.

In the interpretation of nutrient-enrichment experiments (Figs. 77 and 78), it should be emphasized that the element controlling the rate of eutrophication may not be the one limiting phytoplankton growth. Schindler (1971) and Schindler *et al.* (1971) have cautioned against extrapolating short-term experimental results to long-term, whole-lake responses. The experimental results, however, are consistent with the hypothesis presented by Schelske and Stoermer. Additions of silica, especially in combination with phosphorus and nitrogen, stimulated the growth of phytoplankton assemblages dominated by diatoms. This response was not unexpected; it has been detected by Hamilton (1969) in Lake Cayuga, New York, and by investigators in other north-temperate lakes. The stimulatory effect of silica can be interpreted as a *side effect* of the cultural eutrophication of Lake Michigan, *i.e.* phosphorus additions cause increases in diatom abundance which in turn create an increased demand for silica.

Schelske and Stoermer also contended that nitrate-nitrogen generally is present in sufficient quantities in the Lake and in most instances is probably not a limiting nutrient. Schelske *et al.* (1974) recently investigated the effects of phosphorus and nitrogen on phytoplankton growth in Grand Traverse Bay. These experiments, based on a factorial statistical design, use chlorophyll as the growth response. Phosphorus and nitrogen concentrations were added at 5, 15, 25, 40, and 60 μg/l and at 0.23, 0.84, and 1.12 mg/l, respectively. The results indicate that phytoplankton growth is controlled by phosphorus and not by nitrogen (Schelske and Stoermer, 1972; Schelske, 1974, 1975). The authors suggested that these findings further confirm their earlier contentions--phosphorus is the critical nutrient which limits phytoplankton growth in Lake Michigan.

Although the experiments of Schelske and Stoermer (1971, 1972) and Schleske *et al.* (1974) provide important information on nutrient limitation, they are costly, and enormous logistical problems must be overcome to conduct them. Other techniques that detect phosphorus and nitrogen limitation in phytoplankton are available and have potential application to Lake Michigan studies. Fitzgerald (1968) developed a method to determine nitrogen limitation in phytoplankton, and Fitzgerald and Nelson (1966) developed several techniques to detect phosphorus limitation in algae. Recently, Lin and Blum (1973) modified one of the bioassay techniques of Fitzgerald and Nelson (1966) and carried out a study near Milwaukee, Wisconsin, on phosphorus limitation in nearshore algal populations.

The absolute quantities and relative rates of supply of phosphorus and silica to Lake Michigan provide direct evidence of a nutrient imbalance. Two points should be clarified regarding nutrient supplies (*cf.* Schindler *et al.*, 1971): (*i*) phytoplankton biomass generally will be proportional to the nutrient that is most limiting; in most instances this is not directly related to ionic ratios *per se*, and (*ii*) factors other than nutrients can limit phytoplankton productivity. Dense algal populations in the euphotic zone can become light-limited, and toxic waste products or external metabolites can reduce or inhibit growth. In areas adjacent to polluted tributaries (see Tables 27 and 31), silica undoubtedly will be a limiting nutrient. In regions near unpolluted tributaries, phosphorus will limit the growth of diatom assemblages. Although precise Si:P ratios are not available for diatoms in Lake Michigan, nutrient-enrichment experiments suggest that Si:P ratios are <100:1 in open water near Grand Haven. All available evidence suggests that ratios on the order of at

least 200:1 should characterize proportions of these elements needed for optimum growth of planktonic diatoms.

It should be pointed out also that computed silica-to-phosphorus ratios in tributaries may actually underestimate the availability of phosphorus and overestimate the availability of silica for algal growth. A portion of the organic phosphorus pool is undoubtedly converted rapidly to dissolved inorganic phosphorus by bacterial decomposition processes, and it is well known that the turnover rate of dissolved inorganic phosphorus in lake water is high (*cf.* Redfield *et al.*, 1963; Rigler, 1964). Conversely, the dissolution of silica from diatom cell walls is a relatively slow process (*cf.* Lewin, 1961).

LOADING RATES OF PHOSPHORUS AND NITROGEN AND THE TROPHIC STATE OF LAKE MICHIGAN

Numerous physical, chemical, and biological parameters have been used to assess the trophic state of Lake Michigan (*cf.* Beeton, 1965, 1966, 1969; Beeton and Edmondson, 1972). Estimates of total phosphorus concentrations in lake water (Table 28) and phosphorus loading also provide a means of evaluating the degree of lake eutrophication. Vollenweider (1968, 1971) predicted that the degree of eutrophication is directly related to phosphorus and nitrogen loadings. The scale established by Vollenweider is based on annual loading

Table 28. Critical Total Phosphate-Phosphorus Concentrations in Lakes of Dissimilar Trophic State*

Lake Type	*Total Phosphate-Phosphorus, mg/m*^{3}
Ultraoligotrophic	<5.0
Oligo-mesotrophic	5-10
Mesotrophic-eutrophic	10-30
Highly eutrophic	30-100

**Data from Vollenweider (1971).*

rates and the logarithm of mean lake depth ($\bar{z}$). Deeper lakes generally have the capacity to tolerate higher nutrient inputs per unit area but lower inputs per unit volume than shallower lakes. The *permissible* and *dangerous* loading levels used by Vollenweider are given in Table 29. These loading limits can be ascertained from Vollenweider's (1968, 1971) graph or approximated from the following equations (Schindler *et al.*, 1971):

$$\log_{10} P_a = 0.60 \log_{10} \bar{z} + 1.40, \quad (6)$$

$$\log_{10} P_d = 0.60 \log_{10} \bar{z} + 1.70, \quad (7)$$

$$\log_{10} N_a = 0.60 \log_{10} \bar{z} + 2.57, \text{ and} \quad (8)$$

$$\log_{10} N_d = 0.60 \log_{10} \bar{z} + 2.87, \quad (9)$$

where P_a and P_d are *permissible* and *dangerous* rates of phosphorus supply, and N_a and N_d are *permissible* and *dangerous* rates of nitrogen supply (all equations are in mg/m^2/yr).

Table 29. *Permissible* and *Dangerous* Loading Levels for Nitrogen and Phosphorus in Lakes*

Mean Depth, up to	Loading Levels, g/m^2-yr: Permissible, up to — Total N	Permissible, up to — Total P**	Dangerous, in excess of — Total N	Dangerous, in excess of — Total P**
5 m	1.0	0.07	2.0	0.13
10 m	1.5	0.10	3.0	0.20
50 m	4.0	0.25	8.0	0.50
100 m	6.0	0.40	12.0	0.80
150 m	7.5	0.50	15.0	1.00
200 m	9.0	0.60	18.0	1.20

*Data from Vollenweider (1971).

**Biochemically active.

Recently, Vollenweider (1975) modified his phosphorus loading model by including a term for the mean residence time (τ_w) of water in a lake. By plotting specific surface loading against $\bar{z}/\tau_w$ (mean depth/water residence time = areal water loading), a more realistic prediction of a lake's ability to tolerate phosphorus loadings is obtained. To date, most authors have used Vollenweider's (1968) first model to predict the tolerance of Lake Michigan to phosphorus loadings. Their calculations and conclusions are presented in this section.

Schelske (1974, 1975) computed phosphorus loading from tributaries using Ayers' data (1970) (Table 30). The loading is 0.037 g $P/m^2/yr$.* Since the

Table 30. Estimated Long-Term Inputs and Outputs of Some Nutrients for Lake Michigan*

Nutrient	metric tons/day — Input	Output
NH_3-N	55.9	4.54
NO_3-N	44.1	2.27
Organic N	39.5	ND
Total Sol PO_4-P	5.91	1.06
SiO_2	550	199
Cl	1430	926

*From Schelske (1975). Results summarized by Ayers (1970) from data collected by the U. S. Department of the Interior (1968b) between April 1962 and July 1964. This includes Ayers' corrections for ungauged streams.

Symbols: ND = no data.

average depth of the Lake is 84 m, a loading of 0.037 g $P/m^2/yr$ is well within the *permissible* range. According to Vollenweider's model, the *dangerous* loading level for the average depth of Lake Michigan is 0.71 $g/m^2/yr$ (see Table 35).

*This value was incorrectly reported as 0.3 g $P/m^2/yr$ in an earlier version of Schelske's (1975) manuscript (Schelske, 1976--personal communication).

Although Schelske's value is an order of magnitude below the *danger* limit, two points should be emphasized: (*i*) estimates are based on total soluble phosphorus, not total phosphorus, and quantities of phosphorus entering the Lake from groundwater, surface runoff, and wet or dry fallout are not included, and (*ii*) the value of 0.037 g $P/m^2/yr$ is based on the mean depth of the entire Lake. Approximately 25% of the phosphorus entering the Lake can be traced to two rivers, the Fox and the Menominee, which flow into Green Bay (Fig. 80, Table 27). This loading rate puts Green Bay at or above the *dangerous* level. Similarly, shallow water in the southeastern region is fed by the Grand, Kalamazoo, and St. Joseph rivers and Burns Ditch. Collectively, these tributaries supply about 30% of the phosphorus entering the Lake. This region of the Lake is near or surpasses the *dangerous* level on Vollenweider's scale. In contrast, the open-water mass receives loadings that certainly are less than 0.037 g $P/m^2/yr$. A more accurate estimate is not possible since the mass transport of phosphorus from inshore to offshore water is unknown.

Schelske (1974) pointed out that the utility of Vollenweider's loading scale can depend on factors other than mean depth. Any process causing phosphorus to be retained in a lake will tend to decrease *permissible* loadings--*e.g.* depth of the euphotic zone, volume of the epilimnion relative to volume of the hypolimnion, residence time of water, and rates of mixing in relation to lake surface area. The *permissible* loadings for Lake Michigan, in fact, may be lower than Vollenweider's value. Ayers' (1970) estimates of long-term inputs and outputs of total soluble phosphorus are 5.91 and 1.06 metric tons/day (Table 30), respectively, indicating that significant amounts of phosphorus are retained in the basin. If substantial amounts of phosphorus are released or returned to the euphotic zone from the sediments by some internal loading mechanism, the quantities available for algal growth are certainly much higher than would be expected strictly on the basis of external loading rates alone.

In 1968, the U. S. Department of the Interior (1968c) and the states bordering Lake Michigan adopted recommendations requiring a minimum 80% reduction in total phosphorus discharged directly into the Lake or into one of its tributaries from waste-treatment plants. These recommendations were to have gone into effect in December 1972.* Lee (1974) discussed three pertinent issues regarding reduced phosphorus-loading rates and the trophic state of Lake Michigan:

1. Will an 80% reduction in phosphorus loading produce a measurable increase in the water quality of the Lake?
2. How rapidly will Lake Michigan recover when phosphorus discharges are reduced under the regulation?
3. To what extent will phosphorus loading increase as a result of future urbanization?

Lee computed a phosphorus loading of 17.1 million lb/yr or, including atmospheric sources, approximately 18.0 million lb/yr (8136×10^3 kg/yr). These computations are based on an initial summary report prepared by Zar

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**The progress in reducing phosphorus loading has not been as rapid as originally hoped. For a statement of current loading rates, the reader is referred to the report of the Great Lakes Water Quality Board (1976c).*

(1974) (Table 31). The amounts of phosphorus derived from specific sources according to Lee (1974) are shown in Table 32.

Table 31. Total Phosphorus Loading to Lake Michigan from Tributaries*

Tributary	*Total Drainage Area, mi^2*	*Average Discharge, cfs*	*Phosphorus Loading to Lake, 1000 lb/yr*
Root	196	184	191
Milwaukee	845	470	379
Sheboygan	440	232	168
Manitowoc	442	195	142
West Twin	166	85	36
East Twin	140	71	30
Kewaunee	146	80	40
Fox	6,443	6,130	2,654
Pensaukee	160	144	25
Oconto	933	825	162
Peshtigo	1,155	1,010	99
Menominee	4,150	3,427	809
Big Cedar	387	309	30
Ford	468	435	25
Escanaba	920	1,104	108
Whitefish	315	386	30
Manistique	1,450	2,327	274
Boardman	347	331	123
Pine (Charlevoix)	370	396	31
Manistee	2,010	2,418	238
Pere Marquette	772	846	166
Pentwater	172	182	21
White	480	496	48
Muskegon	2,780	2,990	529
Grand	5,534	4,431	2,180
Black (Holland)	176	133	44
Kalamazoo	2,069	2,535	648
Black (S. Haven)	83	359	84
St. Joseph	4,311	5,635	2,107
Burns Ditch	330	327	199
Indiana Harbor		2,700	850[a]
Totals	38,190	41,193	12,470

**Data from Zar (1974).*

[a]May include phosphorus originally taken from the Lake by industrial cooling-water use.

Note: Unmonitored tributary non-point source contribution is considered as 725,000 lb/yr (100 lb phosphorus/mi^2); total contribution from tributaries, thus, is estimated at 13.2 million lb.

These computations reveal that nearly 4 million lb/yr of phosphorus enter the Lake directly from point waste-water sources, whereas more than 9 million lb/yr of phosphorus enter the Lake from non-point waste-water sources. On the basis of an 80 or 90% projected reduction in phosphorus supplied by waste water in 1971, Lee computed loading values for 1973 (Table 33). His calculations indicate that the Lake's total phosphorus loading can be reduced by at least one-half provided bordering states adopt an effluent standard of 1.0 mg total P/l. This practice should result in marked improvements in nearshore water quality; eventually offshore conditions also should improve.

Lee (1974) used a residence-time model based on chemical reactivity, rather than the commonly used hydraulic residence-time model, to estimate the recovery rate of Lake Michigan. Phosphorus residence time is computed on the basis of total phosphorus content of the Lake and the average rate of phosphorus

Table 32. Sources and Computed Annual Loadings of Phosphorus in Lake Michigan*

Source	*Loading, million lb/yr*
Direct waste water	3.9
Indirect waste water	9.3
Total waste water	13.2
Erosion and other diffuse sources	1 to 7
Generalized total load, excluding precipitation and dustfall	14 to 20
1969 total load (estimated and measured), excluding precipitation and dustfall	17.1
Combined sewer overflow	0.8
Precipitation and dustfall on surface of Lake Michigan	1.1

**Data from Lee (1974).*

Table 33. Loading Values of Phosphorus Assuming an 80 or 90% Reduction in Waste Water Entering Lake Michigan

	Loading, million lb/yr		
Source	*1971*	*1973 80%*	*1973 90%*
Waste water	13.2	2.6	1.3
Diffuse sources	3.0	3.0	3.0
Combined sewer overflow	0.8	0.8	0.8
Precipitation and dustfall	1.1	1.1	1.1
Total	18.1	7.5	6.2
Percent reduction from 1971 loadings		58	66

loading. The model accounts for a variety of chemical reactions transporting phosphorus into and out of lake sediments. On this basis, Lee indicated that phosphorus residence time in the Lake is on the order of six years. About 15 to 20 years will be required, therefore, to achieve a 95% recovery and a new steady state phosphorus value.

Lee also attempted to evaluate the effects of further urbanization of the Lake's watershed and the future water quality of Lake Michigan. Although it is difficult to make precise demographic projections, Lee estimated that the total population will increase by approximately 6.0 million persons in 50 years, and the number of persons utilizing sewage facilities will increase by 6.5 million persons in 50 years (these estimates exclude population increases in Illinois). Based on these statistics, he predicted that phosphorus loading into Lake Michigan will increase by approximately 2.1 million lb/yr by 2020. This loading rate would be about one-half that which entered the Lake in 1971. Lee stated, however, that technology for phosphorus control is likely to improve during this period, and that the total phosphorus load to the Lake may not increase by more than 1.0 to 2.0 million lb/yr during the next 50 years.

Data on nitrogen loading rates and the concentrations of nitrate-nitrogen in open water of Lake Michigan suggest that this nutrient is not a key element in eutrophication. Ayers (1970) calculated the nitrogen loading rate to be on the order of 140×10^3 kg/day, whereas phosphorus is supplied at a rate of 5.91×10^3 kg P/day (Table 30). The N:P ratio based on loading data is approximately 24:1. Since N:P ratios of healthy phytoplankton generally are close to 10:1, but may range to 20:1, it appears that nitrogen is being supplied in quantities in excess of those required by phytoplankton. It should be pointed out, however, that the ratio of 24:1 may be an overestimate because the phosphorus loading rate is based on total soluble phosphorus, not total phosphorus.

Concentrations of nitrate-nitrogen in the surface water of the northern and southern basins apparently are high enough to sustain phytoplankton growth (Schelske and Callender, 1970). Data presented by these authors indicate that nitrate-nitrogen is rarely, if ever, reduced to levels limiting phytoplankton growth. Some experimental evidence substantiating these observations is available. Schelske and Stoermer (1971, 1972) and Schelske *et al.* (1974) did not detect a stimulatory effect of nitrogen on phytoplankton growth in nutrient-enrichment experiments (Table 26). In experiments involving treatment with N, P, Si, a N:P ratio of 10:1 was calculated, suggesting that concentrations of nitrate-nitrogen relative to those of phosphorus and silica are sufficient to sustain algal growth.

Nitrogen, however, may limit phytoplankton growth in localized regions receiving large quantities of phosphorus. In Green Bay, for example, surface-water concentrations of nitrate-nitrogen ranged between 0.02 and 0.04 mg/l during summer (Schelske and Callender 1970), whereas concentrations of nitrate-nitrogen in the hypolimnion indicate storage of this nutrient (*cf.* Table 17). This severe reduction in surface-water concentration during summer is related directly to dense concentrations of phytoplankton that utilize available nitrogen supplies. The consequences of excessive phosphorus input and nitrate-nitrogen depletion in Green Bay will be discussed further in the section on Phytoplankton Ecology in Green Bay. An analogous situation occurs in inshore water near the Grand River. Stephenson and Waybrant (1971) reported that the river discharges 1.03×10^6 kg total PO_4-P and 4.00×10^6 kg NO_3-N each year. The N:P ratio is 4:1, indicating insufficient supplies of nitrate-nitrogen relative to phosphorus.

Relative Trophic Status of Lake Michigan and Selected Great Lakes

The trophic state of a lake is difficult to quantify or express in absolute terms. The ranking of a lake is largely dependent on the criteria and the classification scheme used to assess trophy. Data on phosphorus loading rates and mean concentrations of phosphorus, along with selected physical, chemical, and biological measurements, however, allow the trophic state of Lake Michigan to be assessed and compared with other Laurentian Great Lakes.

Vollenweider's (1968, 1971) nutrient-loading model for phosphorus and nitrogen has been applied to only a few lakes in North America, largely because it is difficult to obtain accurate loading estimates. Sufficient data for the Great Lakes are available, however, to allow first-order comparisons with Lake Michigan (Int. Joint Comm., 1969; Great Lakes Water Quality Board, 1973; Vollenweider, 1971; Vollenweider *et al.*, 1974). Summary computations on phosphorus loading, along with morphometric and hydrologic data for the five lakes, are presented in Table 34. Annual phosphorus loading estimates for Lakes Superior and Huron are available from Great Lakes Water Quality Board (1973)

Table 34. Estimates of Phosphorus Loadings, Morphometric Characteristics, and Hydrologic Data for the Great Lakes*

Lake	Area, 10^3 km^2	Volume, 10^3 km^3	Mean Depth, m	Water Renewal, yr	Phosphorus Loading, g/m^2/yr	Reference
Erie	25.7	0.46	17	3	1.06	Int. Joint Comm., 1969; Vollenweider, 1968
Erie					0.98[a]	Patalas, 1972 (calc.)
Ontario	19.7	1.64	86	8	0.65	Int. Joint Comm., 1969; Vollenweider, 1968
Ontario					0.86[a]	Patalas, 1972 (calc.)
Huron	59.6	3.53	53	22	0.15[a]	Patalas, 1972 (calc.)
Superior	82.4	12.2	148	190	0.03[a]	Patalas, 1972 (calc.)
Michigan	58.0	4.87	84	100	0.04[b]	Schelske, 1974, 1975
Michigan					0.13[c]	Zar, 1974
Michigan					0.14[d]	Lee, 1974
Michigan					0.29[a]	Patalas, 1972 (calc.)

*Morphometric and hydrologic data from Schelske (1974).

[a]The calculated loading rates presented by Patalas (1972) are based on the criteria proposed by Vollenweider (1971). The estimation is based on the following equation:

$$L_p = \frac{E_s A_d}{A_o} + \frac{E_c C}{A_o} + 0.15\, L_{pa} \frac{A_{o(a)}}{A_o},$$

where E_s = export of P from soil as g total P per m^2 of land drainage per yr, A_d = area of land drainage in m^2, A_o = area of lake surface in m^2, E_c = per capita discharge of phosphorus entering the lake in g total P/person/yr, C = population in basin, L_{pa} = total P input from the upstream lake in g/m^2/yr, and $[A_{o(a)}]/A_o$ = ratio of the area of the upstream lake to the area of the lake in question. Patalas assumed that total P export from oligotrophic, mesotrophic, and eutrophic soils is <0.02, between 0.02 and 0.05, and >0.05 g/m^2/yr, respectively; that a density of 150 persons/km^2 in the drainage basin contributes 0.25 g/m^2/yr; and that 85% of the P loading was retained in the lake.

[b]The loading rate computations presented by Schelske (1974, 1975) are based on Ayers' (1970) corrections of data gathered for the year 1963-1964 by the U. S. Department of the Interior (1968b) (see Tables 27 and 30). Estimates of phosphorus concentration and loading rates are based on total soluble phosphate-phosphorus.

[c]The loading rate computed by Zar (1974) is based on estimated and measured quantities of P that entered the Lake in 1969. Estimated quantities are based on the following assumptions: (*i*) 10 mg/l total P is the average concentration in waste water, (*ii*) 3.65 lb total P/person/yr is an average per capita estimate, and (*iii*) 120 gpd is the average per capita use of water. During 1969, approximately 13.2 million lb of total P entered the Lake from 31 tributaries.

[d]The loading rate (18,000,000 lb/yr) computed by Lee (1974) for 1969 is based on Zar's (1974) estimate of 13.2 million lb of total P from direct and indirect waste-water sources, 1 to 7 million lb/yr P derived from erosion and other diffuse sources, and approximately 1.0 million lb/yr of P derived from precipitation and dustfall on the surface of the Lake.

and Patalas (1972), and calculations of Lake Michigan loading rates are given by Schelske (1974, 1975), Lee (1974), and Zar (1974). Lakes Erie and Ontario are subject to the highest loadings relative to surface area, whereas Lake Superior receives the lowest phosphorus input. Lakes Michigan and Huron are intermediate between these extremes and receive approximately equivalent specific-surface loadings. The relative degrees of lake eutrophication are compared in Table 35, using the loading rate expressed as the ratio between actual or calculated load and Vollenweider's limits for *dangerous* and *permissible* supply (*cf.* Table 29). Computations are based on the data given in Table 34, and *permissible* and *dangerous* loading values are computed using the equations (see p. 148) given by Schindler *et al.* (1971).

Table 35. A Summary of Phosphorus Loadings into the Great Lakes, Relative to Vollenweider's (1971) Critical Limits for *Permissible* and *Dangerous* Supply Levels*

Lake	$Log_{10}\ \bar{z}$	$Log_{10}\ P_a$	$Log_{10}\ P_d$	P_a, mg/m^2	P_d, mg/m^2	P_l, mg/m^2	P_l/P_a	P_l/P_d	*Reference*
Erie	1.23	2.14	2.44	138	275	1060	7.68	3.85	Int. Joint Comm., 1969; Vollenweider, 1968
Erie	1.23	2.14	2.44	138	275	980	7.10	3.56	Patalas, 1972 (calc.)
Ontario	1.93	2.56	2.86	363	724	650	1.79	.90	Int. Joint Comm., 1969; Vollenweider, 1968
Ontario	1.93	2.56	2.86	363	724	860	2.37	1.19	Patalas, 1972 (calc.)
Huron	1.72	2.43	2.73	269	537	150	.56	.28	Patalas, 1972 (calc.)
Superior	2.17	2.70	3.00	501	1000	30	.06	.03	Patalas, 1972 (calc.)
Michigan	1.92	2.55	2.85	354	707	40	.11	.06	Schelske, 1974, 1975 (based on Ayers, 1970)
Michigan	1.92	2.55	2.85	354	707	130	.37	.18	Zar, 1974
Michigan	1.92	2.55	2.85	354	707	140	.39	.20	Lee, 1974
Michigan	1.92	2.55	2.85	354	707	290	.82	.41	Patalas, 1972 (calc.)

**See Table 34 for related data.*

Symbols: $\bar{z}$ = mean depth, m; P_a = permissible phosphorus loading, $mg/m^2/yr$; P_d = dangerous phosphorus loading, $mg/m^2/yr$; P_l = phosphorus loading for the lake, $mg/m^2/yr$.

These data indicate that Lakes Ontario and Erie are significantly above *permissible* loading levels, and that the three other lakes are below this limit. Lake Ontario is either approaching or is at the *dangerous* loading level. Lake Erie, especially the western basin, is far above the *danger* limit. Lake Michigan and Lake Huron are subject to comparable specific surface loadings, and can tolerate present-day phosphorus inputs according to Vollenweider's (1968) first model. In contrast, Lake Superior is two orders of magnitude below *dangerous* loadings.

Vollenweider *et al.* (1974) evaluated the relationship between annual phosphorus loading and annual primary production in the five lakes (Fig. 81). They observed that annual primary production of the Great Lakes system is directly related to annual phosphorus loadings. This plot indicates that the correlation between the two parameters is highly significant and nonlinear, and it provides a useful first-order model for predicting the effects of phosphorus loadings on primary production in the Great Lakes.

The mean concentration of total phosphorus in the epilimnion of lakes has been proposed by Vollenweider and others as a trophic-state parameter (Table 28). Beeton and Chandler (1963) have computed the average total phosphorus content of the five Great Lakes: Superior (5 mg/m^3), Michigan (13 mg/m^3), Huron (10 mg/m^3), Erie (61 mg/m^3), and Ontario (75 mg/m^3). Even though these estimates are approximations (Vollenweider, 1971), they appear to rank the lakes in the same order as areal phosphorus loading rates, except that Ontario appears to be more eutrophic than Erie. Lake Superior would be judged oligotrophic, Lakes Michigan and Huron mesotrophic, and Lakes Erie and Ontario highly eutrophic. The only significant departure from these trophic-state rankings is Lake Ontario; based on mean phosphorus concentrations, it would be considered more eutrophic than Lake Erie. The areal loading rate of phosphorus into Ontario, however, suggests that it is near or at the *dangerous* level, whereas those for Lake Erie indicate the lake to be grossly polluted. This

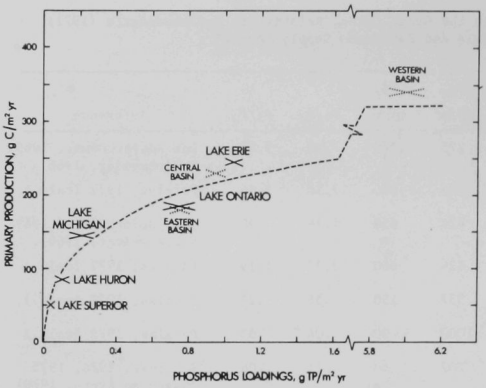

Fig. 81.

Relationship between Annual Primary Production and Annual Phosphorus Loading. Modified from Vollenweider *et al.* (1974) (with permission, see credits).

ranking is similar to that reported by Schelske (1975) for four of the lakes and is discussed in the following text.

Other physical, chemical, and biological parameters can be used to assess the relative trophic state of Lake Michigan. Although phytoplankton abundance has been used frequently, quantitative information on standing crop levels in Lake Michigan cannot be used because most estimates are based on units other than biomass (see Sampling Problems and Quantitative Phytoplankton Methods, p. 169). Vollenweider *et al.* (1974) recently summarized and compared phytoplankton biomass in the Great Lakes, but Lake Michigan was excluded for lack of information.

Recently, Schelske (1974, 1975) summarized existing information on primary productivity, chlorophyll *a* and total phosphorus concentrations, and Secchi-disc transparency for Lakes Michigan, Huron, Superior, and Erie. Each parameter has fundamental significance as an indicator of trophic state (*cf.* Vallentyne, 1969; Vollenweider, 1971; Brezonik, 1969; Shannon and Brezonik, 1972). Primary productivity and chlorophyll *a* are related to phytoplankton standing crop and generally are correlated. A rationale for the use of total phosphorus has been presented above. Secchi-disc transparency tends to be inversely proportional to the above parameters, being high in oligotrophic water and low in eutrophic, turbid lakes. Primary productivity, chlorophyll *a*, and total phosphorus generally increase in value from oligotrophy through mesotrophy to eutrophy.

The data are tabulated in Table 36 and summarized graphically in Figure 82. Levels of three parameters (primary productivity, chlorophyll *a*, and total phosphorus) are lowest in Lake Superior and highest in Lake Erie. Water transparency is inversely proportional to this trend. Based on these data, Lake Superior can be judged as the most oligotrophic of the Great Lakes and Lake Erie as the most eutrophic. Saginaw Bay and the western basin of Lake Erie are the most eutrophic regions in the Great Lakes. Lakes Michigan and Huron are intermediate between these extremes and can be judged as mesotrophic bodies of water.

Dobson *et al.* (1974) summarized recent data obtained by the Canada Centre for Inland Waters for comparison of water quality in the Great Lakes (Lake

Table 36. Average and Standard Deviations of Chlorophyll *a*, Primary Productivity, Secchi-Disc Transparency, and Total Phosphorus in the Great Lakes*

Location	*Chlorophyll a, mg/m³*	*Primary Productivity, mg C/m³/hr*	*Secchi-Disc Transparency, m*	*Total P, mg/m³*
Superior				
Near shore	1.5 ± 0.14 (5)	0.73 ± 0.20 (4)	6.6 ± 1.1 (5)	
Open lake	0.66 ± 0.42 (27)	0.37 ± 0.17 (18)	12.6 ± 3.4 (30)	2.5 ± 1.5 (14)[a]
All stations	0.78 ± 0.49 (32)	0.44 ± 0.22 (22)	11.8 ± 3.8 (35)	
Huron				
Open lake	0.79 ± 0.47 (18)	1.1 ± 0.45 (13)	8.0 ± 2.4 (18)	4.6 ± 2.7 (11)[a]
Saginaw Bay	6.5 ± 3.5 (7)	30 ± 19 (5)	2.5 ± 1.8 (7)	
Michigan				
Northern	1.3 ± 0.62 (7)	2.2 ± 0.9 (4)	4.8 ± 0.6 (6)	6–7[b]
Southern		3.6 ± 2.3 (14)[c]		7–13[d]
Erie				
Western basin (north)	3.7 ± 1.3 (5)	10 ± 3.1 (3)	2.0 ± 0.4 (5)	
Western basin (south)	12.1 ± 3.8 (7)	59 ± 19 (5)	2.0 ± 0.53 (7)	55 ± 46 (15)[e]
Central basin	7.3 ± 6.7 (8)	24 ± 15 (5)	4.4 ± 1.2 (8)	28 ± 25 (15)[e]
All stations	8.1 ± 5.7 (20)	34 ± 25 (13)	3.0 ± 1.5 (20)	

**From Schelske (1975). Data, except as noted, from Schelske and Roth (1973).*

[a] *Canada Centre for Inland Waters (1968): Limnological Data Report No. 1, Lake Huron Cruise 68-201 (5-13 August); Lake Superior Cruise 68-301 (18-28 August).*

[b] *Holland (1969). No standard deviations for averages.*

[c] *Schelske and Callender (1970).*

[d] *Risley and Fuller (1965). No standard deviations for averages. Data omitted for southernmost stations.*

[e] *Canada Centre for Inland Waters (1968): Limnological Data Report No. 1, Lake Erie Cruise 68-102 (17-24 May); 68-104 (15-19 June); and 68-108 (29 July-3 August). Limnological Data Report No. 2, Lake Erie Cruise 68-109 (31 August-3 September); 68-111 (28 September-4 October); and 68-112 (4-10 November).*

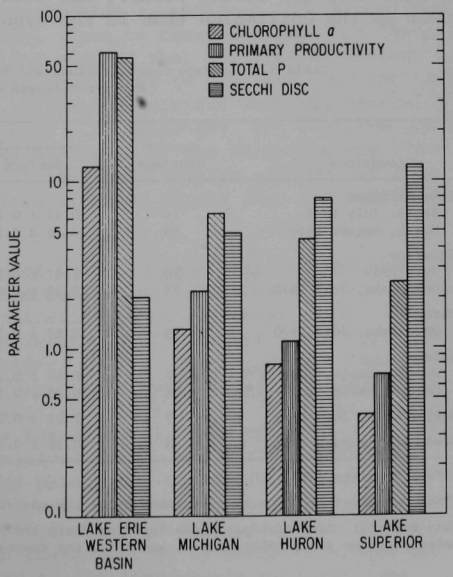

Fig. 82.

Chlorophyll *a* (mg/m³), Primary Productivity (mg C/m³/hr), Total Phosphorus (mg PO_4-P/m³), and Secchi-Disc Transparency (m) in the Great Lakes. Modified from Schelske (1974) (with permission, see credits).

Michigan was excluded). An indexing system was developed on the basis of the following parameters: concentrations of nitrate-nitrogen, ammonia, silica, phosphorus, and chlorophyll; and water transparency, turbidity, and hypolimnetic oxygen saturation. Lakes Superior and Huron were judged as oligotrophic (although primary productivity data suggest that Lake Huron has mesotrophic characteristics). Lake Ontario and the eastern and central basins of Lake Erie exhibit eutrophic symptoms, and the western basin of Lake Erie is highly eutrophic. On a relative basis, the ranking of lakes by Dobson *et al.* (1974) and Schelske (1974, 1975) are reasonably similar, although Dobson's scheme suggests that Lake Huron is more oligotrophic than Schelske's ranking.

Since phosphorus inputs generally result in increases in phytoplankton standing crop, concentrations of dissolved silica and nitrate-nitrogen are reduced during the growing season (*cf.* discussion by Vollenweider *et al.*, 1974). Silica depletion in the euphotic zone is attributed to diatom growth and nitrate utilization is attributed to the growth of diatoms and other phytoplankton components. An empirical model based on this phenomenon is presented by Schelske (1975) to assess trophic state in the Great Lakes. The model is formulated on the degree of silica and nitrate-nitrogen utilization during summer. Net utilization is defined as the difference between the concentration of the elements in surface and bottom water. Details will not be presented here, but the model allows Lake Michigan to be compared with Lakes Huron, Erie, and Superior (Table 37, Fig. 83). The difference between concentrations of soluble silica and nitrate-nitrogen in surface and bottom water is least for Lake Superior, greatest for Lake Michigan, and intermediate between these extremes for Lake Huron. This ranking is in general agreement with that based on four trophic-state parameters (Fig. 82). There are highly significant amounts (>50%) of nitrate-nitrogen utilized in the euphotic zone of Lake Michigan during summer, and dissolved silica concentrations are grossly lower in the epilimnion than in the hypolimnion.

Table 37. Average Concentrations and Standard Deviations of Soluble Silica and Nitrate-Nitrogen in the Great Lakes

Locations	*No. of Stations*	*SiO_2, mg/l*		*NO_3-N, µg/l*	
		Surface	*Bottom***	*Surface*	*Bottom***
Lake Michigan					
South, July 1969	16	0.15 ± 0.07	1.63 ± 0.49	101 ± 18	218 ± 29
North, August 1969	16	0.26 ± 0.07	1.26 ± 0.16	116 ± 7	216 ± 36
Superior					
July 1969	20	1.87 ± 0.11	2.01 ± 0.14	269 ± 21	276 ± 16
Open lake, July 1970	25	2.28 ± 0.07	2.28 ± 0.20	254 ± 14	264 ± 7
Huron					
Open lake, July 1970	19	0.87 ± 0.22	1.79 ± 0.16	139 ± 29	175 ± 46
Erie					
Western basin, July 1970	7	0.66 ± 0.26	0.85 ± 0.20	86 ± 33	125 ± 51
Central basin, July 1970	8	0.25 ± 0.10	1.36 ± 0.76	34 ± 24	103 ± 57
Saginaw Bay, July 1970	7	1.03 ± 0.28	1.06 ± 0.21	36 ± 43	82 ± 52
Green Bay, August 1969	3	0.26 ± 0.07	2.73 ± 0.93	39 ± 13	190 ± 46

**From Schelske (1974).*

***Bottom values are from samples taken below the photic zone.*

Data sources: Lake Michigan, Lake Superior (July 1969), and Green Bay--Schelske and Callender (1970), Lakes Superior (July 1970), Huron, and Erie, and Saginaw Bay--Schelske and Roth (1973).

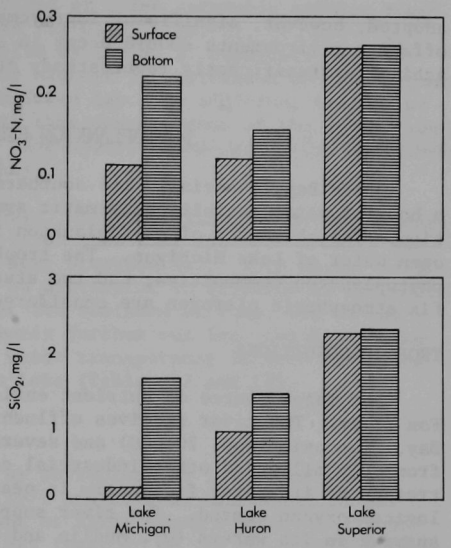

Fig. 83.

Silica and Nitrate-Nitrogen in the Upper Great Lakes. Redrawn from Schelske (1974) (with permission, see credits).

Conclusions and Discussion

The loading rate of phosphorus into Lake Michigan and concentrations of this nutrient indicate that certain regions of the Lake differ in water quality, and also support widely dissimilar phytoplankton assemblages (see Floral Composition and Community Structure, p. 23). Data on concentrations and loading rates of phosphorus, nitrogen, and silica suggest that the present pattern of cultural eutrophication in Lake Michigan is similar to that proposed for large lakes by Beeton and Edmondson (1972). Increased nutrient loadings generally affect the shallow, inshore regions first, *e.g.* Green Bay, the southern basin of the Lake, and inshore water near the discharge of the Milwaukee and Grand rivers. Gradually, offshore water is altered and exhibits symptoms of cultural eutrophication induced by sustained nutrient inputs into the nearshore environment.

Assessments of the trophic status of Lake Michigan suggest that the Lake is a mesotrophic body of water. The contention that phosphorus is the critical element controlling the rate of eutrophication is in agreement with a large body of information on cultural eutrophication of freshwater lakes (*cf.* Schindler, 1971; Schindler *et al.*, 1971; Vollenweider, 1971). It is apparent that phosphorus loadings into Lake Ontario and especially Lake Erie have accelerated the eutrophication process in these lakes (Schelske, 1974, 1975; Int. Joint Comm., 1969; Great Lakes Water Quality Board, 1973). The open water of Lake Michigan now exhibits depletion of dissolved silica and nitrate-nitrogen during summer. It is predicted that as phosphorus is continually added to the Lake, the rate of eutrophication will accelerate, and nitrogen and light will eventually become factors limiting phytoplankton growth. Such conditions presently occur in Green Bay, a region characterized by nuisance blooms of blue-green algae that have the capacity to fix atmospheric nitrogen (see Phytoplankton Ecology in Green Bay, p. 160). If recommendations proposed by the U. S. Department of the Interior and the states bordering the Lake are

adopted, however, significant improvements in the water quality of inshore and offshore environments should occur in several years, and the Lake should achieve a significantly lower steady state phosphorus concentration.

PHYTOPLANKTON ECOLOGY IN GREEN BAY

Green Bay, especially its southernmost extreme, generally is regarded as a body of water exhibiting dramatic symptoms of advanced cultural eutrophication. The character of phytoplankton in the bay is in marked contrast to the open water of Lake Michigan. The trophic characteristics of the bay, its phytoplankton communities, and two studies on the capacity of the plankton to fix atmospheric nitrogen are considered in this section.

TROPHIC CONDITIONS

The major source of nutrient enrichment of the bay can be traced to the Fox River. The river receives effluents from sewage-disposal plants in Green Bay, Wisconsin (Pop. 70,000) and several smaller cities, and assorted wastes from pulp mills and other industrial concerns. The dissolved oxygen concentration of its water frequently is near zero, indicating extremely high biological oxygen demand. The river supports minimal algal growth, and few fish survive in its waters (*cf.* Modlin and Beeton, 1970; Howmiller and Beeton, 1971). Epstein *et al.* (1974) evaluated recent and historical limnological conditions in Green Bay. Their work can be consulted for extensive background data on the bay.

The amount of phosphorus supplied to the bay by the Fox River is extremely large (Fig. 80, Tables 27 and 31). The river contributes about 3.03 metric tons of total soluble phosphorus to the bay each day (or over 7000 lb of total phosphorus each day). Significant amounts of phosphorus also enter the bay from the Menominee and Oconto rivers. These loadings place Green Bay in the *dangerous* category of Vollenweider's trophic scale (Table 29).

The physical and chemical characteristics of the bay and primary productivity levels indicate that conditions in the southern region of the bay are considerably more eutrophic than in the open Lake; however, several harbors receiving high nutrient loadings and industrial pollutants directly from rivers are perhaps more eutrophic than the bay. In southern Green Bay, severe oxygen depletion usually develops in the hypolimnion during summer (Howmiller and Beeton, 1973). Schelske and Callender (1970) showed that Secchi-disc transparency generally is less than 3.0 m, and that dissolved silica, nitrate-nitrogen, and ammonia are severely depleted in the epilimnion during summer. These authors also demonstrated that on a volumetric basis, primary productivity is an order of magnitude higher in the bay's southern extreme than in northern Green Bay and in the open Lake (Tables 17 and 18). They detected rates of 336 mg $C/m^3/12$ hr in southern Green Bay compared with 38 mg $C/m^3/12$ hr in the Lake.

FLORAL COMPOSITION AND COMMUNITY STRUCTURE

The phytoplankton of the bay differs in composition from open-water regions in the Lake. Holland (1968, 1969) showed that the principal diatoms in the bay are *Melosira binderana* and *Melosira granulata*, and Holland and Claflin (1975) detected groups of species normally associated with highly

eutrophic north-temperate lakes. Populations of these eutrophic species reach higher abundance levels in the bay than in the Lake (Figs. 21, 23, and 24; Tables 10 and 15). Similarly, data compiled by the U. S. Department of the Interior (1968a) indicate that some of the highest phytoplankton concentrations detected in Lake Michigan are in southern Green Bay. In addition, studies by Vanderhoef *et al.* (1972, 1974) demonstrate that dense blooms of the blue-green algae *Anabaena flos-aquae, Aphanizomenon flos-aquae, Microcystis, Coelosphaerium*, and *Gloeotrichia* occur in summer in the bay.

The northern part of Green Bay, however, exhibits oligotrophic conditions. Observations by Vanderhoef *et al.* (1972, 1974) show that diatoms normally are dominant components of the phytoplankton near Sturgeon Bay. This change from a eutrophic to an oligotrophic flora can be attributed to dilution of nutrients entering the bay in high concentrations at its southern extreme, and to the incorporation of nutrients into the sediments further out into the bay. Likewise, levels of primary productivity and water transparency in mid- and upper Green Bay are closer to those of the open Lake (Tables 17 and 18).

NITROGEN-FIXATION STUDIES

Investigations of nitrogen fixation by phytoplankton in southern Green Bay were conducted during the summers of 1971 and 1972 by Vanderhoef *et al.* (1972, 1974). The studies were carried out at sites along a transect extending from the extreme southern tip of the bay (near or at the mouth of the Fox River) to a northern site near Sturgeon Bay. The objectives of the first study were to measure nitrogen fixation along the transect, and to relate spatial and temporal variations in nitrogen fixation to variations in phytoplankton abundance and composition and changes in the physical and chemical environment.

The study during the following summer was similar to the initial investigation; however, three of its goals were (*i*) to characterize the shift from a dominant *Microcystis* population to a dominant *Aphanizomenon* population based on fluctuations in the concentrations of soluble phosphorus, nitrate-nitrogen, and ammonia, (*ii*) to investigate the relationship between specific activity and nitrogen-fixation efficiency and concentrations of nitrogen and phosphorus in the water, and (*iii*) to estimate the input of atmospheric nitrogen as part of the nitrogen budget of the bay.

Nitrogen-fixation rates were measured by acetylene reduction. The method is an indirect measure largely because there is no consistent factor allowing acetylene reduction values to be converted directly to nitrogen fixation. Although the technique is imperfect, it is sensitive, simple, and yields data rapidly.

The authors obtained estimates of nitrogen fixation during both summers. Samples were collected from surface water with a Van Dorn bottle or polypropylene pail. Phytoplankton was concentrated by filtration through silk plankton netting (173 mesh) and resuspended in filtered lake water. One-ml aliquots were placed in bottles, and the bottles were injected with acetylene and incubated on deck. Sampling generally was carried out between 0830 and 1300 hr. Assays at each site consisted of four replicates and a control using filtered lake water. Incubations were terminated after 30 min by addition of H_2SO_4 and $CoSeO_3$. Subsamples from the bottles were withdrawn later, and the amount of ethylene produced was determined by flame-ionization gas chromatography. At each site, measurements also were made on temperature, light penetration,

dissolved oxygen, pH, soluble phosphorus, nitrate-nitrogen, nitrite-nitrogen, ammonia, and organic nitrogen (by Kjeldahl digestion). Phytoplankton counts were made to compute algal nitrogen, specific activity, and the efficiency of acetylene reduction (specific activity is defined as acetylene reduction/mg total nitrogen in a sample). Differential species counts were used to compute the fraction of total nitrogen associated with different populations. Efficiency calculations are based on the amount of acetylene reduction/mg total nitrogen for each species population.

Summer 1971

The location of 15 sampling sites in the southern third of the bay is shown in Figure 84. Site 1 was about one mile from the mouth of the Fox River, and Site 15 was located northwest of Sturgeon Bay. Each site was investigated between June and September 1971.

Fig. 84.

Location of Fifteen Sites Visited Weekly during the Summer of 1971 (Vanderhoef *et al.*, 1972) (with permission, see credits).

Phytoplankton composition generally varied spatially on the same day (Fig. 85). The diatom *Asterionella* sp. was dominant at Sites 10-15, and it reached peak abundance of 5500 cells/ml at the northernmost site on 9 June. One week later, blue-green algal populations reached bloom proportions. *Anabaena flos-aquae* dominated at Sites 3-14, and *Aphanizomenon flos-aquae* was the principal species near the mouth of the river on 16 June. *Aphanizomenon* decreased in late June and was replaced by *Microcystis*. The growth of this species was apparent at Sites 1-4 until mid-July, after which time it decreased in abundance. *Aphanizomenon flos-aquae* reappeared in high numbers in mid-July at Sites 1-6.

Acetylene-reduction rates varied spatially on the same day and fluctuated seasonally at the sampling sites (Fig. 86). The mean nitrogen-fixation rate for the sites was greater than 50 μmoles/l/hr. The highest rates occurred in mid- and late June at Sites 3-15 and on 14 July at Sites 1-6. The lowest rates detected during summer were at the northern sites.

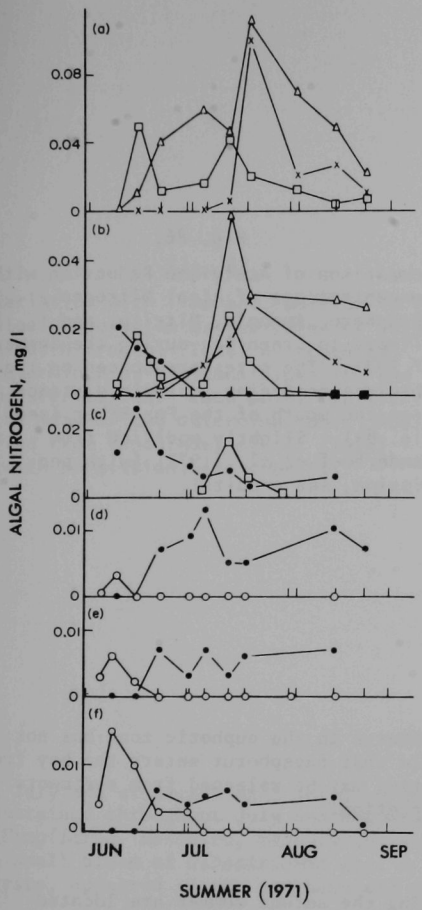

Fig. 85.

Variations in the Algal Population as Indicated by Total Nitrogen at Several Sites during the Summer of 1971. Samples of algae were examined microscopically to estimate roughly the amount of the individual species (as a fraction of the total population). This fraction then was multiplied by the total N/l recorded for that particular site. The algae graphed are: *Oscillatoria* (●) (these included *Lyngbya* spp., *Ulothrix* spp., and *Melosira* spp.); *Aphanizomenon* spp. (□); *Microcystis* spp. (△); *Coelosphaerium* (x); and *Asterionella* spp. (○). Modified from Vanderhoef *et al.* (1972) (with permission, see credits).

Nitrogen-fixation rates did not appear to correlate with temperature, nitrate-nitrogen, nitrite-nitrogen, or ammonia, nor were they related to forms of combined nitrogen (Fig. 86). Variations in dissolved phosphorus, however, were closely correlated with nitrogen-fixation rates. In most instances, relatively high phosphorus concentrations preceded blooms of *Anabaena* and *Aphanizomenon*.

Vanderhoef *et al.* (1972, 1974) concluded that high concentrations of soluble phosphorus are necessary for development of blue-green algal blooms in the bay, and that high rates of acetylene reduction are associated with the presence of rapidly growing populations of *Aphanizomenon flos-aquae* and *Anabaena flos-aquae* (and not with non-heterocyst-forming blue-green algae or other algal populations). The factors causing these blooms, however, are not clearly understood. It appears that warm surface water, calm weather, and high concentrations of dissolved phosphorus act in concert to initiate and

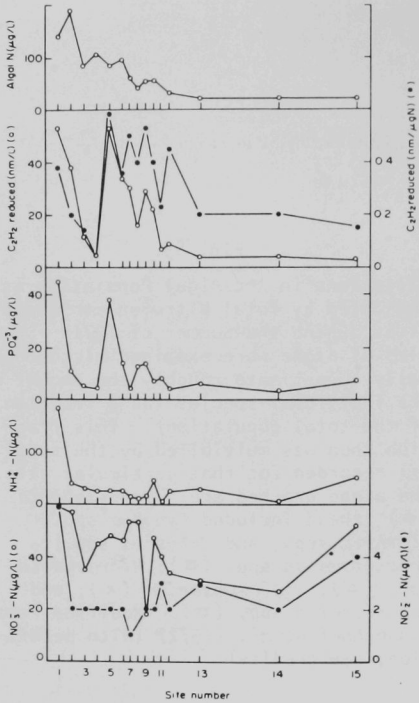

Fig. 86.

Comparison of Acetylene Reduction with Concentrations of Algal Nitrogen, Phosphate, Ammonia, Nitrite, and Nitrate in Green Bay during the Summer of 1971. The sites are spaced on the abscissa according to their distance from the mouth of the Fox River (see Fig. 84). Slightly modified from Vanderhoef *et al.* (1972) (with permission, see credits).

maintain blooms. The source of the phosphorus in the euphotic zone has not been identified, but it is highly probable that phosphorus enters the bay from the Fox River and that a significant portion may be released from sediments during periods of hypolimnetic oxygen depletion.

Summer 1972

The sampling sites investigated during the second summer are located similarly to those shown in Figure 84; however, Site 1 was in the Fox River, Site 2 was directly at the mouth of the Fox River, and Site 14 (the northernmost sampling point in this study) was southwest of Sturgeon Bay.

A succession of phytoplankton species was evidenced during summer; certain species exhibited an apparent preference for distinct regions along the transect. Phytoplankton abundance, expressed as mg N/l, is shown for selected dates in Figure 87. The community at that time was dominated by either *Aphanizomenon* or *Microcystis*. A bloom of *Aphanizomenon* was observed at Sites 3 and 4 on 14 June. This bloom increased in size and dominated the plankton at Sites 5-12 during the remainder of the summer. *Aphanizomenon* reached a peak abundance of 4.07 mg algal N/l at Site 4 on 5 July and a peak of 1.5 mg algal N/l at Sites 5-7 on 13 July. The bloom diminished in size in early August but increased again by mid-August. *Microcystis* reached bloom proportions only at the southernmost stations. Maximum concentrations were observed at Site 3 on

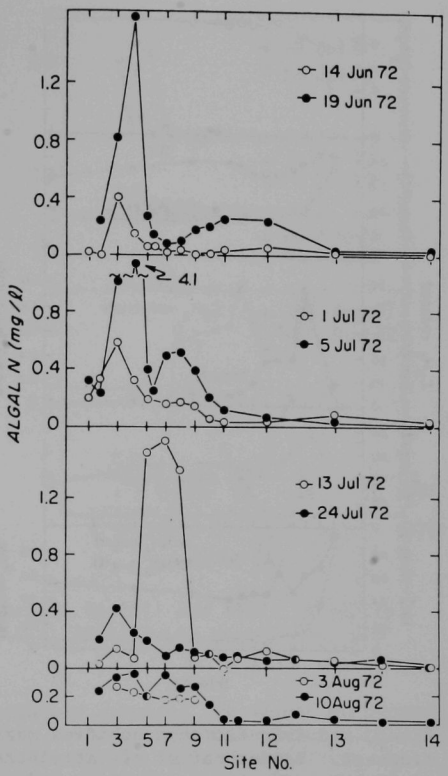

Fig. 87.

Variation with Time and Position in the Algal Population as Indicated by Total Algal Nitrogen. Total nitrogen was determined by Kjeldahl digestion and Nesslerization. Each point represents the mean of two determinations. Modified from Vanderhoef *et al.* (1974) (with permission, see credits).

1 July and at Site 4 on 5 July. Blooms of *Microcystis* at these stations were sustained throughout July and August. At the northernmost sites, diatoms (*Fragilaria*, *Melosira*, *Tabellaria*, and *Asterionella*) generally were dominant. A small bloom of *Gloeotrichia* sp., a filamentous blue-green alga with heterocysts, appeared at the northern end of the transect in mid-August.

Nitrogen-fixation rates varied spatially over the transect and fluctuated seasonally at the sites (Figs. 88 and 89). Fixation rates at all sites were low in early June, high in mid-June at Sites 3-12, and low again in early July, except at Site 3. From mid-July to early August, nitrogen-fixation rates were relatively low, except at Sites 3 and 4. In mid- and late August, acetylene-reduction rates were high at Sites 7-11 and Site 13. The average value for Sites 3-12 during the summer was 65.5 nM/l/hr. The highest rates were associated with populations of *Aphanizomenon*. Nitrogen fixation by this species or associated bacterial populations, however, does not appear to be correlated with air temperature, variations in oxygen content, or specific nutrient concentrations (Fig. 88).

The spatial and temporal distribution patterns of *Microcystis* and *Aphanizomenon* are of particular interest. *Microcystis*, a species incapable of fixing atmospheric nitrogen, reached maximum levels at sites near the Fox

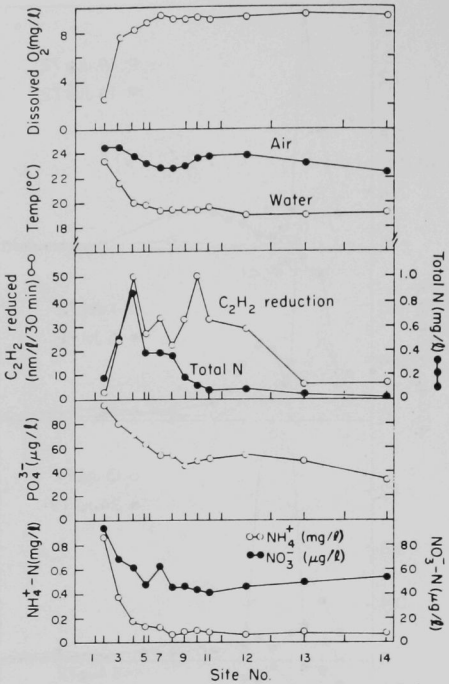

Fig. 88.

Variation in Dissolved Oxygen, Air and Water Temperature, Acetylene Reduction, Total Algal Nitrogen, Phosphate, Ammonia, and Nitrate. Data points represent averages for the entire sampling period. Modified from Vanderhoef *et al.* (1974) (with permission, see credits).

River, and *Aphanizomenon* achieved maximum concentrations in the middle of the transect. Vanderhoef *et al.* attributed the abundance patterns of *Microcystis* to high nutrient concentrations and calm water at the southern stations. This species drastically depleted the ammonia content of the water near the river. The transition to a community dominated by *Aphanizomenon* further out in the bay appeared to be correlated with the ratio of dissolved phosphorus to nitrogen. Concentrations of phosphorus and nitrogen decreased along the transect, but nitrogen decreased more rapidly than phosphorus. Nitrogen-fixation efficiencies associated with *Aphanizomenon* appeared to be inversely related to concentrations of inorganic nitrogen, and directly related to higher levels of dissolved phosphorus at Sites 3-12. The growth of *Aphanizomenon* decreased proportionately with decreases in phosphorus; however, its ability to fix atmospheric nitrogen increased with decreases in soluble inorganic nitrogen. It appears that *Microcystis* loses its competitive advantage when inorganic nitrogen concentrations are low. *Aphanizomenon* apparently has a competitive advantage at higher phosphorus levels and lower inorganic nitrogen levels because of its ability to utilize atmospheric nitrogen.

Vanderhoef *et al.* (1972, 1974) also attempted to determine variations in nitrogen-fixation rates with depth. Water samples were taken at intervals of 1.0 m to a depth of 11 m. They observed that acetylene reduction was highest in the top 10 cm of the water column and decreased with depth; however, fixation was detected at depths of 5 to 6 m.

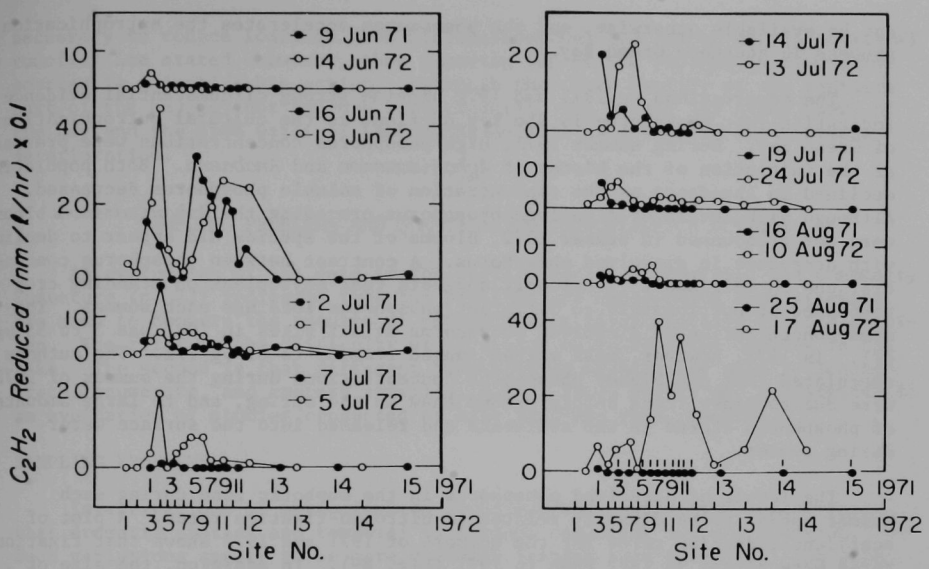

Fig. 89. Comparison of Acetylene Reduction in 1971 and 1972. Slightly modified from Vanderhoef *et al.* (1974) (with permission, see credits).

Based on these estimates, the investigators computed the amount of nitrogen added to the bay by biological fixation, and compared this amount with nitrogen supplies entering the bay from the Fox River. The calculations are based on an area of about 725 km^2 (Sites 3-12), an average fixation rate of 65.5 nM/l/hr, and a 65-day period (14 June-17 August). They assumed the following: 80% of the nitrogen fixed occurs between 0800 and 1200 hr, a surface sample includes the top 10 cm, the production of 1.0 NH_3 from one-half N_2 is equivalent to a reduction of 1.5 C_2H_2, and nitrogen fixation in the euphotic zone is equal to 20 times that occurring within the top decimeter of the water column. The computations indicated that the amount of nitrogen entering the bay by biological fixation was approximately 40% of the amount supplied by the Fox River.

CONCLUSIONS AND DISCUSSION

The conclusions drawn by Vanderhoef *et al.* (1972, 1974) are pertinent to an understanding of phytoplankton dynamics in Green Bay. The authors demonstrated that nitrogen fixation can be attributed to *Aphanizomenon* and *Anabaena* (species of blue-green algae with heterocysts) or to associated bacterial populations. These species have a competitive advantage over other populations of blue-green algae, such as *Microcystis* and *Coelosphaerium*, especially when the concentration of inorganic nitrogen is low or limiting. Furthermore, significant amounts of atmospheric nitrogen can be fixed biologically in the euphotic zone, and these inputs can contribute significantly to the nitrogen economy of the bay. Nitrogen fixation represents a nitrogen source that would

not be available otherwise, and the phenomenon accelerates the eutrophication process in southern Green Bay.

The observations in 1971 and 1972 provide strong circumstantial evidence indicating that phosphorus is the key nutrient in the cultural eutrophication of Green Bay. During summer 1971, high phosphorus concentrations were present at the initiation of the blooms of *Aphanizomenon* and *Anabaena*. Both populations declined in abundance as the concentration of soluble phosphorus decreased. Although high levels of dissolved phosphorus preceding the *Aphanizomenon* bloom were not pronounced in summer 1972, blooms of the species did appear to decline with decreases in dissolved phosphorus. A contrast between phosphorus concentrations in 1971 and 1972 strongly suggests that phytoplankton standing crop responded proportionately to different phosphorus loadings each summer. The mean concentration of dissolved phosphorus at all sites in 1971 was 3 to 55 μg P/l. In 1972, however, mean values ranged from 35 to 81 μg P/l. The authors speculated that the higher phosphorus concentrations during the summer of 1972 were due to heavy rains before ground thaw in the spring, and to large amounts of phosphorus stored in the sediments and released into the surface water during summer.

The levels of dissolved phosphorus in the euphotic zone during each summer appear to be directly related to nitrogen-fixation rates. A plot of acetylene-reduction rates for the summers of 1971 and 1972 shows that fixation rates were higher in 1972 than in 1971 (Fig. 89). In addition, the size of *Aphanizomenon* blooms and their further extension north into the bay in 1972 suggests that phosphorus loadings were higher during summer 1972 than during summer 1971.

The data on acetylene-reduction rate and phytoplankton composition and abundance in Green Bay strongly suggest that heterocyst-forming blue-green algae (*Aphanizomenon* and *Anabaena*) or associated bacteria have the ability to fix atmospheric nitrogen. Although heterocysts of blue-green algae are suspected as the sites of fixation, conclusive proof has never been presented. The observations of Vanderhoef *et al.* (1972, 1974) are similar to those for Clear Lake, California (Horne and Goldman, 1972; Horne *et al.*, 1972), where nitrogen fixation is closely correlated with heterocyst production in blue-green algal populations. The observations in Green Bay also are similar to those of Ogawa and Carr (1969), who demonstrated that heterocyst production by *Anabaena* and *Aphanizomenon* in Lake Erie occurred when nitrate-nitrogen concentrations were low and inorganic phosphorus concentrations were high.

Recently, Lee (1974) considered the effect of an 80% reduction of phosphorus in waste water entering the bay. Assuming that recommendations proposed by the U. S. Department of the Interior (1968c) are adopted by treatment plants discharging into major tributaries of the bay, Lee estimated that the phosphorus content of southern Green Bay will be reduced by 50%, and there will be an approximate 40% decrease in the phosphorus content of the entire bay. Lee maintained that the mean concentration of orthophosphorus in Green Bay was on the order of 50 μg P/l, and that the 80% reduction in loading will result in average concentrations of about 20-30 μg P/l. Since such concentrations provide sufficient quantities of phosphorus for algal growth, it is unlikely that the regulation will result in significant improvements in the water quality of southern Green Bay. In order to reduce phosphorus input to the extent that nuisance blooms of algae do not occur in the bay, it would be

necessary to reduce loadings from diffuse sources, *e.g.* urban and agricultural runoff. Lee stated, however, that removing 80% of the phosphorus from point sources is a justifiable action. Although the water quality of the southern part of the bay may not improve significantly, the middle and upper parts of the bay and the open water of Lake Michigan will be protected from further deterioration.

SAMPLING PROBLEMS AND QUANTITATIVE PHYTOPLANKTON METHODS

An evaluation of the data in the section Floral Composition and Community Structure (p. 23) indicates that two problems are encountered when attempts are made to compare the results of phytoplankton investigations in Lake Michigan. The first is the difficulty of obtaining representative samples in the Lake. The second is that different quantitative methods are used to concentrate, enumerate, and express numerical data. These points are fundamental to an evaluation of studies conducted on Lake Michigan phytoplankton.

SAMPLING PROBLEMS

Investigations of phytoplankton abundance and composition demonstrate that dramatic spatial and temporal variations can occur in Lake Michigan. Such variations appear to be more dramatic inshore than offshore. The size and composition of nearshore phytoplankton communities can be affected by plumes of nutrients entering the Lake from rivers, by the presence of a thermal bar, or by upwelling of nutrient-rich hypolimnetic water. The spatial distribution of phytoplankton also can be affected by wind, which causes dense concentrations of algae to pile up nearshore. These conditions, operating singly or in combination, can lead to extreme degrees of spatial heterogeneity. Ayers and Seibel (1973), for example, concluded that small-scale water masses, each with different biological characteristics, moved through their sampling grid at the Cook power plant at Benton Harbor. Intensive sampling over a small area was necessary to obtain accurate estimates of phytoplankton species abundance.

The offshore phytoplankton, although relatively more stable than nearshore communities, exhibits pronounced seasonal variations in abundance and composition, and can exhibit marked degrees of vertical heterogeneity. These phenomena are well illustrated in studies by Stoermer (1974), Stoermer and Kopczynska (1967), Huh *et al.* (1972), and Piala and Lamble (1971).

Collectively, phytoplankton studies in Lake Michigan indicate that it is difficult to obtain samples representative of large areas of the Lake. Intensive seasonal monitoring, including small-scale horizontal and vertical sampling, is necessary even to characterize phytoplankton assemblages at specific offshore and nearshore locations. Such sampling considerations are fundamental to the success of programs evaluating the effects of nutrient enrichment or thermal effluents on phytoplankton (*cf.* discussions by Huh *et al.*, 1972, and Ayers and Seibel, 1973).

QUANTITATIVE TECHNIQUES

When efforts are made to compare phytoplankton data, two problems normally are encountered: samples frequently are concentrated by different methods and data often are expressed in different quantitative units.

Concentration of Samples

Samples can be prepared for quantitative analysis by using one of several techniques--*e.g.* centrifugation, filtration through nets or onto Millipore filters, or natural settling (APHA, 1960; Margalef, 1969; and Wood *et al.*, 1969). Each method has been used in one form or another by Lake Michigan investigators. Griffith (1955), for example, concentrated algae by centrifugation, and Eddy (1927, 1934) used a plankton net. Techniques involving filtration of samples onto Millipore filters were employed by Holland (1969), Holland and Beeton (1972), Stoermer *et al.* (1971, 1972). Other investigators--*e.g.* Huh *et al.* (1972), Stoermer and Kopczynska (1967), and Cook and Risley (1963--unpublished)--utilized natural settling in Utermöhl-type chambers followed by direct examination using the Utermöhl technique (see Lund *et al.*, 1958). Parkos *et al.* (1969) employed natural settling in Imhoff cones, followed by counts in Sedgewick-Rafter cells (APHA, 1960).

The procedures used to concentrate Lake Michigan phytoplankton are so varied that they merit further discussion. Centrifugation does not result in complete capture of algal populations (*cf.* Hartman and Graffius, 1960; Tarapchak, 1973). Buoyant algae, especially blue-green algal populations, are lost in the flow water and delicate algae are damaged beyond recognition or are entirely destroyed by centrifugal force or impingement. Centrifugation generally results in underestimates of true population size. In samples from offshore regions in Lake Superior, for example, Tarapchak (1973) demonstrated that centrifugation underestimated phytoplankton abundance by a factor of two or more. Significant percentages of diatoms, chlorophytes, and chrysophytes also escaped capture, and delicate algae were either expelled with the flow water or damaged beyond recognition.

Another technique used to concentrate Lake Michigan phytoplankton is filtration through plankton nets with apertures of various sizes. This method was employed extensively by Eddy (1927, 1934). Concentration by such means results in gross underestimates of standing crop. Smaller algae (<50 μm in greatest dimension) are captured only if the pores of the net become clogged. Fortunately, this technique has not been used extensively in recent years.

The technique of membrane filtration, *i.e.* filtration onto Millipore filters, has been used widely in recent years. This method has the advantage of reducing sample volume and the space required for storage, but filters can obscure fine details of algal morphology. If samples are filtered under a moderately high vacuum, however, delicate algae can be destroyed or distorted (*cf.* Arthur and Rigler, 1967; Schindler and Holmgren, 1971). If the object of a study is to obtain accurate estimates of phytoplankton abundance, the use of filtration techniques can lead to serious errors. Holland (1969) and Holland and Beeton (1972) used membrane filtration to concentrate diatom samples. Since diatoms, unlike delicate flagellates, are relatively resistant to damage by filtration, the technique of membrane filtration can be employed successfully.

One widely used method for quantifying phytoplankton is the Utermöhl technique (Utermöhl, 1958). Water samples are preserved in the field, later transferred to settling chambers, and counted using an inverted microscope. This procedure does not result in mechanical damage to cells, and if the samples are properly preserved, it allows precise counts to be made. Lund *et al.* (1958) give statistical information on the precision and accuracy of the method.

The Utermöhl technique has a distinct advantage over other methods primarily because delicate nannoplankters can be recognized and counted in analysis, and sample manipulation is minimal. There are, however, several problems. First, samples must be preserved and stored, a requirement that can pose logistical problems if the number of samples is large. Second, prolonged preservation in Lugol's solution can lead to deterioration of diatom cell walls. This phenomenon was observed in southern Lake Michigan by Stoermer and Kopczynska (1967) and at the Cook power plant by Ayers and Seibel (1973). The latter authors adopted the settle-freeze method of Sanford *et al.* (1969) to circumvent or reduce the magnitude of these errors.

The settle-freeze method of Sanford *et al.* (1969) is a modification of the Utermöhl technique. Water samples are placed in cylinders, settled onto microscope slides, frozen with dry ice, and fixed with alcohol vapor. Seibel and Ayers (1974) presented the results of a comparison between the settle-freeze method and the Utermöhl technique. The settle-freeze method yielded lower total cell counts than the Utermöhl method by factors ranging to 1.86, but the method gave statistically higher numbers of species than Utermöhl's method. Sanford *et al.* (1969) also noted statistically higher counts (by factors ranging to 1.3) with the Utermöhl technique. Although the settle-freeze method apparently underestimates total population size, the method can be used in studies where large numbers of samples are collected and a permanent record of phytoplankton is desired.

Sufficient evidence has accumulated in recent years to document the fact that nannoplankton (<60 μm in greatest dimension) can be an important component of phytoplankton in unproductive and moderately productive lakes (Munawar, 1973--unpublished; Munawar and Munawar, 1973--unpublished, 1975; Munawar and Nauwerck, 1971; Kristiansen, 1971; Pavoni, 1963; Schlindler and Holmgren, 1971; Kalff, 1972; Tarapchak, 1973). These observations, coupled with the fact that nannoplankton generally is more efficient photosynthetically than net plankton (Rodhe *et al.*, 1958; Kalff, 1972), strongly suggest that nannoplankton should not be ignored in Lake Michigan. None of the methods presently in use are entirely satisfactory for preserving, in recognizable condition, all of the phytoplankton species found in Lake Michigan. High priority should be placed on the development of more refined methods that will allow permanent preservation and recognition of all species.

Sample preservation can be related directly to problems of estimating phytoplankton abundance (*cf.* Davis, 1966). Solutions of alcohol or formalin generally preserve *rough* algae but damage nannoplankton, especially delicate flagellates. The most satisfactory preservatives are either Lugol's solution or gluteraldehyde (Vollenweider, 1969; Wood *et al.*, 1969). Both solutions minimize cell distortion, and they are the most common preservatives employed in phytoplankton studies today.

Units of Measurement

A second major problem in Lake Michigan phytoplankton research is that quantitative estimates are reported in different units. The seriousness of this problem has been discussed in detail by Vollenweider *et al.* (1974). Data on phytoplankton abundance in the Lake are presented in a variety of units (see Table 15) including: (*i*) individuals, *i.e.* organisms (*cf.* Parkos *et al.*, 1969; Eddy, 1927, 1934; Ayers and Seibel, 1973); (*ii*) cells (Holland and

Beeton, 1972; Stoermer and Kopczynska, 1967; Stoermer, 1974; Stoermer *et al.*, 1972); (*iii*) arbitrary units (Griffith, 1955; Piala and Lamble, 1971; Davis, 1966); and (*iv*) weight estimates (*cf.* Ayers and Seibel, 1973).

Obviously, the use of dissimilar counting units leads to different numerical values. Algae are unicellular--*i.e.* an organism consists of a single cell, or groups of cells can form colonies or filaments consisting of a few to hundreds of cells. Counts based on cells or organisms per unit volume of lake water are fundamentally satisfactory for descriptive studies of seasonal succession patterns or regional investigations of species distribution; however, the use of different units detracts from the accuracy of quantitative comparisons among stations, locations, and different studies. Quantitative estimates based on cells, for example, yield higher values than counts based on individuals, because many planktonic organisms are colonial or filamentous.

This problem is compounded even further by the use of various *unit* measures. Griffith (1955), for example, used the arbitrary counting method of Wright (1955): four cells of the green alga *Scenedesmus* and a cell of the diatom *Stephanodiscus* represent one unit, and a 300 μm filament length of *Aphanizomenon* and *Melosira* represents a unit. Studies by Nalco Chemical Company (Piala and Lamble, 1971; Gulo and Lamble, 1971; and Huh *et al.*, 1972) use a different *unit* method: unicellar organisms and diatom frustules are one counting unit, a 100 μm length of filament is a unit, and four cells of a colonial alga are a unit (except for certain colonial blue-green algae which are counted as 50 cells per unit). In addition to these inconsistencies, the long-term studies at the Chicago and Milwaukee water filtration plants were based on different counting units during various time periods (Damann, 1966).

If the results of phytoplankton investigations in Lake Michigan are to be compared with one another and with data from other lakes, it is necessary to standardize counting units and the method of numerical expression. Estimates based on biomass not only provide one of the least ambiguous expressions but allow phytoplankton standing crop to be expressed as a fresh weight value, thereby providing a basis for estimating carbon content and its turnover rate in phytoplankton populations (*cf.* Strickland and Parsons, 1968; Schindler and Holmgren, 1971; Vollenweider *et al.*, 1974). In addition, biomass estimates can be used as an expression of trophic state (*cf.* Vollenweider, 1971; Vollenweider *et al.*, 1974).

GENERAL SUMMARY

Phytoplankton occupy a unique position in the aquatic ecosystem of Lake Michigan. Algal populations not only represent the interface between the physicochemical environment and biological communities at higher trophic levels, but they generally respond quickly to environmental disturbances. Although the Lake's phytoplankton has been studied since the turn of the century, most data relating to man's effects on water quality have been generated during the last decade.

This report summarizes published information on phytoplankton research ranging from algal systematics and variations in phytoplankton standing crop and composition to primary productivity, limiting-nutrient interactions, and trophic-state evaluations of Lake Michigan. The report has six major

sections: (*i*) a historical synopsis of phytoplankton research and review of literature, (*ii*) spatial and temporal variations in phytoplankton abundance and species composition, (*iii*) spatial and temporal variations of primary productivity, (*iv*) an examination of the phosphorus-silica-eutrophication hypothesis in relation to nutrient concentrations and loading rates of phosphorus, silica, and nitrogen, including a discussion of the comparative trophic state of Lake Michigan, (*v*) dynamics of phytoplankton succession in Green Bay and the ecological significance of nitrogen-fixation by plankton, and (*vi*) a general account of sampling problems and the limitations and advantages of selected quantitative methods.

HISTORICAL SYNOPSIS OF PHYTOPLANKTON INVESTIGATIONS

Phytoplankton research in Lake Michigan began in the late 1800's. The initial investigations were purely taxonomic in nature, but during the period 1932-1950, several quantitative nearshore studies were undertaken. With the development of the radiocarbon technique for measuring primary productivity, a new dimension of research opened in the 1950's. Studies in the 1960's and early 1970's focused on (*i*) describing seasonal variations in phytoplankton abundance, (*ii*) describing regional distribution patterns of important species, and (*iii*) experimental studies of phytoplankton nutrient limitation. These studies have led to a general understanding of the effects of cultural eutrophication on phytoplankton in Lake Michigan, and have provided insights into the factors that regulate species distribution and seasonal succession.

FLORAL COMPOSITION AND COMMUNITY STRUCTURE

A large body of data on phytoplankton flora is available. The reports published since 1900 indicate that over 2000 species, varieties, and forms of algae have been recorded in the plankton. About 1300 are diatoms, and 700 to 800 species are either green and blue-green algae, or dinoflagellates, golden-brown algae, and euglenophytes. Although the flora appears to be relatively well-documented, additional studies are needed to resolve taxonomic problems, to investigate the composition of winter assemblages, and to identify small, delicate nannoplankton species, especially phytoflagellates and rare species.

The cultural eutrophication of Lake Michigan has affected the species composition of the phytoplankton. An investigation by Stoermer (1967) indicates that there has been an increase in the number of littoral and benthic diatoms found in open water. This phenomenon occurs primarily in the southern basin and can be attributed to nutrient enrichment. Several investigations also show that relatively distinct indicator species exist in the Lake (*cf.* Stoermer and Yang, 1969, 1970; Holland, 1968, 1969). These studies, based on regional and seasonal distribution patterns, show that nutrient enrichment of inshore and open water of the southern basin favors development of eutrophic algal species (*e.g. Fragilaria capucina, F. capucina* v. *mesolepta, Melosira granulata, Stephanodiscus binderanus, Stephanodiscus tenuis, Stephanodiscus subtilis, Diatoma tenue* v. *elongatum, Nitzschia dissipata,* and *Coscinodiscus subsalsus*). These algae have displaced species with oligotrophic affinities (*e.g. Cyclotella comta, Cyclotella kuetzingiana, Cyclotella ocellata, Cyclotella stelligera,* and *Melosira distans*) characteristic of low-nutrient water in the northern basin. In Lake Michigan, pollution-tolerant diatoms and other algal species adapted to high-nutrient conditions are either absent or present in low percentages in the northern basin and in Grand Traverse Bay. The maximum

abundance and growth rates of eutrophic diatoms occur in southern Green Bay and at inshore locations, particularly in the southern basin and near large rivers that carry substantial loads of phosphorus.

The species diversity of diatom and total phytoplankton assemblages indicates that structural properties of algal communities appear to have limited values as indicators of water quality. Diatom diversity is low in oligotrophic environments and in polluted harbors and high in regions of moderate enrichment. Measurements of phytoplankton community structure of total phytoplankton assemblages indicate that diversity varies seasonally, and that index values are not necessarily higher in low-nutrient offshore regions.

Investigations of phytoplankton abundance in Lake Michigan are based either on diatoms or on the total assemblage. The most detailed seasonal studies on diatoms are in central Lake Michigan and Green Bay (*cf.* Holland, 1968, 1969; Holland and Beeton, 1972; Holland and Claflin, 1975), and in the southwestern region near the Waukegan Generating Station (*cf.* Huh *et al.*, 1972). These studies show that differences in abundance between inshore and offshore water are dramatic, particularly in the southern basin, and that species characteristic of nutrient-enriched water are consistently more abundant in nearshore water. The abundance and growth rates of diatoms on the average are higher in water receiving nutrient loadings directly from polluted tributaries.

Studies on phytoplankton abundance have been made in different regions by different investigators. Although numerous data are available for nearshore areas, reliable estimates on abundance of offshore phytoplankton have been generated only during the last decade. Unfortunately, many studies have utilized different units of enumeration; therefore, precise comparisons among data sets are difficult to make. Studies on the Lake's phytoplankton can be grouped conveniently into three major categories: (*i*) early nearshore studies in southern Lake Michigan, (*ii*) long-term monitoring studies at water treatment plants at Chicago and Milwaukee, and (*iii*) recent investigations conducted in different regions or at different stations in the Lake.

Observations by Daily (1938) and Damann (1941) at the breakwater near Chicago indicated that diatoms were the major phytoplankton component and that marked annual variations in phytoplankton abundance can occur from year to year. Griffith's (1955) observations at the same station differed from those of Daily and Damann; her results indicated that the phytoplankton was dominated by blue-green algae instead of diatoms.

Long-term studies at the water treatment plants in Chicago and Milwaukee (Damann, 1945, 1960, 1966) indicate that nutrient enrichment of inshore water near Chicago caused a progressive increase in plankton abundance, and that diatoms normally associated with advanced stages of cultural eutrophication (*e.g. Stephanodiscus binderanus*) are present at water-intake sites. Data on water temperature and seasonal patterns of plankton abundance show that a unimodal curve with peak abundance in summer occurs in the Milwaukee region, and a bimodal curve, with peaks in spring and fall, occurs in nearshore water of the southern basin. Water temperature near 10°C appears to be correlated with optimum conditions for algal growth.

Since 1960, several studies have been conducted in different locations in the Lake. The most intensively studied region of Lake Michigan is the southern basin. Investigations by Stoermer and Kopcyznska (1967) and Stoermer (1974) demonstrated that diatoms dominate the phytoplankton in the southern basin but that blue-green algae now dominate the assemblage during summer and early fall. These studies also show that water temperature is correlated with progressive plankton pulses which begin in nearshore water and gradually move out into offshore water. Stoermer's study suggests that temperature and high-nutrient conditions interact to produce a bimodal phytoplankton abundance curve in the southern basin.

Investigations undertaken by Schelske *et al.* (1971) in eastern Lake Michigan demonstrate the effect of upwelling on phytoplankton abundance, and studies conducted by the U. S. Department of the Interior (1968a) and by Parkos *et al.* (1969) demonstrate the magnitude of regional differences in phytoplankton abundance. Investigations conducted at the Cook power plant (*cf.* Ayers and Seibel, 1973) and near the Waukegan Generating Station (*cf.* Huh *et al.*, 1972) illustrate the effects of localized nutrient enrichment on phytoplankton, and also demonstrate the extreme degrees of patchiness occurring in Lake Michigan phytoplankton distribution. The effects of localized nutrient enrichment also are apparent in Grand Traverse Bay, where nutrient-rich water from the Boardman River results in larger phytoplankton standing crops than in the open bay (Stoermer *et al.*, 1972), and near Milwaukee and in southern Green Bay, where eutrophic diatom populations are abundant (Holland, 1968, 1969; Holland and Beeton, 1972; Holland and Claflin, 1975). These studies indicate that phytoplankton abundance is higher in nearshore water, especially in regions close to urbanized and agricultural areas. Until recently, the Lake has been dominated by diatoms; however, nutrient loadings to the Lake have reached a point sufficient to allow blue-green and green algae to become dominant components of the open-water plankton in the southern basin. This shift in species composition apparently occurred during the 1960's.

PRIMARY PRODUCTIVITY

Several studies provide data on primary productivity in the Lake. All of the estimates, except those of Fee (1973a), Rousar (1973), and Saunders *et al.* (1962), are based on production rates per cubic meter. Investigations by Schelske and Callender (1970), Parkos *et al.* (1969), and Stoermer *et al.* (1972) indicate that inshore regions, especially in the southern basin and in Green Bay, exhibit higher photosynthetic rates than offshore locations. In southern Green Bay near the mouth of the Fox River, levels of primary productivity are an order of magnitude higher than in any other region of Lake Michigan.

Recent investigations by Fee (1973a), using a model and an experimental incubator, provided the first estimates of annual primary production for the euphotic zone of Lake Michigan. Based on observations at five stations in central Lake Michigan, his data show that production exhibits a bimodal curve, with maximum productivity occurring during spring and fall. Mid-summer productivity levels at nearshore stations are approximately twice as high as offshore production rates.

PHOSPHORUS, SILICA, AND EUTROPHICATION

The observation that inshore water in some regions of Lake Michigan exhibits conditions of advanced eutrophication prompts two questions. Has

the offshore water of the Lake been affected adversely by nutrient inputs? What nutrient or nutrients have the potential to cause artificial eutrophication of the deep-water, offshore environment of the Lake? Schelske and Stoermer (1971, 1972) provided evidence showing that significant alterations in phytoplankton have occurred recently in the Lake, and that this phenomenon can be attributed directly to changes in nutrient concentrations. The data and arguments presented by these authors suggest that serious disturbances have occurred in the offshore water of Lake Michigan, especially in the southern basin. They predicted that continued inputs of phosphorus at present-day loading rates will lead to more pronounced degrees of cultural eutrophication in the near future.

Schelske and Stoermer contended that phosphorus is the element controlling the rate of eutrophication of Lake Michigan. They maintained that increased inputs of this element have resulted in substantial increases in diatom abundance. Since silica is a major nutrient required for diatom growth, the available pool of this nutrient in the euphotic zone is being depleted. They predicted that continued inputs of phosphorus will result in progressively larger annual diatom standing crops, until dissolved silica concentrations are reduced to limiting levels. Once diatoms are removed as competitors, they predicted that green and blue-green algae will become dominant components of the phytoplankton. This will occur first in the open water of the southern basin and then in the northern basin when nutrient concentrations become high enough.

The authors assembled data from their own observations and experiments and drew on information generated in other investigations. There are four lines of evidence indicating that Lake Michigan is undergoing serious cultural eutrophication: (*i*) changes have occurred recently in phytoplankton composition and abundance, (*ii*) concentrations of dissolved silica have decreased on a lake-wide basis, (*iii*) diatoms utilize silica in the euphotic zone of the Lake and reduce concentrations to limiting levels, and (*iv*) nutrient-enrichment experiments indicate that phosphorus and silica are the principal limiting nutrients. The contention that phosphorus is the key element in the eutrophication process also is supported by observations on correlations between particulate phosphorus and primary productivity, and by the ratio of silica to phosphorus concentrations in tributaries.

The fact that blue-green and green algae have become dominant components of the summer phytoplankton community in the southern basin is highly significant. This shift is generally characteristic of north-temperate lakes undergoing accelerated eutrophication. Since many blue-green and mucilaginous green algae are not grazed appreciably by many herbivorous zooplankton (*cf.* Porter, 1972, 1973), it is possible that zooplankton species composition may change appreciably in the near future. These changes could eventually affect the entire food web, including fish which are of economic and recreational value.

The trophic state of Lake Michigan can be assessed and compared with the other Great Lakes by evaluating phosphorus loading rates and by considering several parameters that reflect trophic conditions. Several estimates have been made of phosphorus loading into Lake Michigan. Each estimate is below the dangerous level proposed by Vollenweider (1968, 1975). Although this observation suggests that the Lake is not in serious danger of becoming highly

eutrophic, the computed loadings are for the whole of Lake Michigan. Inshore regions in the southern basin, near Milwaukee, and in Green Bay presently exhibit clear signs of advanced eutrophication; these regions receive large supplies of phosphorus directly from polluted tributaries. Based on concentrations of chlorophyll *a*, total phosphorus, primary productivity, and Secchi-disc transparency, Lake Michigan as a whole can be judged as mesotrophic. Its water quality is intermediate between Lakes Superior and Erie. On the basis of Lee's (1974) preliminary calculations, an 80% reduction in phosphorus loading to the Lake should result in significant improvements in nearshore and, eventually, offshore water quality. This general prediction is in agreement with the predictions of Schindler (1974) regarding phosphorus control and water quality improvements in the Great Lakes.

PHYTOPLANKTON ECOLOGY IN GREEN BAY

The southern part of Green Bay is regarded generally as a region showing symptoms of advanced stages of cultural eutrophication. The characteristics of the phytoplankton in the bay are in direct contrast to the open water of Lake Michigan. The physical and chemical characteristics of the bay and levels of primary productivity indicate that conditions in the bay are considerably more eutrophic than in the Lake as a whole. In southern Green Bay, severe oxygen depletion usually develops in the hypolimnion during summer (*cf.* Howmiller and Beeton, 1973). Schelske and Callender (1970) have shown that Secchi-disc transparency generally is less than 3.0 m in the southern portion of the bay and that concentrations of dissolved silica, nitrate-nitrogen, and ammonia in the epilimnion are severely depleted by algal growth during summer.

Studies on nitrogen fixation by phytoplankton in Green Bay have been conducted by Vanderhoef *et al.* (1972, 1974). The studies were designed to relate atmospheric nitrogen fixation to specific algal populations and to variations in the physical and chemical environment, and also to estimate the input of atmospheric nitrogen as part of the nitrogen budget of the bay. Studies were carried out at sites along a transect from the extreme southern part of the bay to a northernmost site near Sturgeon Bay.

The authors drew several conclusions pertinent to an understanding of phytoplankton dynamics in the bay. They demonstrated that nitrogen fixation can be attributed to *Aphanizomenon* and *Anabaena* or to associated bacterial populations, and that algal populations are limited principally by phosphorus. Species such as *Microcystis* and *Coelosphaerium* appear to have a competitive advantage over other blue-green algae when concentrations of inorganic nitrogen are low or reach limiting levels. Significant amounts of nitrogen (40% of the total budget) are fixed biologically by the plankton. The overall effect of atmospheric nitrogen fixation is to produce even more drastic symptoms of advanced eutrophication.

SAMPLING PROBLEMS AND QUANTITATIVE PHYTOPLANKTON METHODS

An evaluation of quantitative phytoplankton data indicates that two problems are encountered when attempts are made to compare the results of different investigations. The first involves difficulties in obtaining representative samples from the Lake. The second is that different methods have been used to concentrate, enumerate, and express quantitative data. Most studies demonstrate that seasonal variations in phytoplankton abundance are

pronounced, especially in nearshore water, and that phytoplankton populations frequently exhibit extreme degrees of patchiness. Suitable sampling schemes must be employed to obtain representative and accurate measurements of population size. These considerations are imperative in attempting to assess the effects of point-source nutrient discharges or the effects of heated effluents on the phytoplankton of Lake Michigan. Most quantitative data generated on phytoplankton cannot be compared directly because different quantitative methods and numerical expressions have been used. A standard quantitative technique and counting unit must be adopted in the future.

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The initial literature survey on which this volume is based was completed in summer 1973, and an initial draft of the manuscript was completed in early 1974. Since that time numerous papers containing information on Lake Michigan phytoplankton have appeared in a variety of journals and reports. Where possible, an effort has been made to incorporate data into the volume or to add significant information by using footnotes. Several reports appearing in 1975 and 1976 are important information or data sources. The *Directory of Great Lakes Research and Related Activities* for 1976, prepared by the Great Lakes Research Advisory Board (1976), presents a synopsis of current research projects on the Great Lakes. Several reports provide significant information on phosphorus loadings to the Great Lakes. The reports (and appendices) to the International Joint Commission for 1974 and 1975 (Great Lakes Water Quality Board, 1975, 1976a, 1976b) and the Environmental Protection Agency's *Report on Inputs of Phosphorus from Precipitation to Lake Michigan* (Murphy and Doskey, 1975) contain estimates of phosphorus loadings. A two-volume report on the *Limnology of Grand Traverse Bay, Lake Michigan* (Auer *et al.*, 1976a, 1976b) gives a detailed treatment on phytoplankton composition and variations in standing crop in addition to nutrient concentrations and nutrient loadings from rivers entering the bay. A study by Kopczynska (1973) provides detailed information on species occurrence and seasonal patterns of abundance and correlations of species abundance with selected physical and chemical parameters in the vicinity of a major river outlet. Recently, Stoermer and Ladewski (1976) published parameterized temperature distributions for a number of phytoplankton species occurring in Lake Michigan.

APPENDIX OF METRIC/ENGLISH EQUIVALENTS

Metric Unit	*Abbreviation*	*Approximate U. S. equivalent*
kilometer	km	0.6214 mile
kilometer	km	0.5400 nautical mile
meter	m	3.2808 feet
centimeter	cm	0.3937 inch
square kilometer	km^2	0.3861 square mile
square meter	m^2	10.7640 square feet
cubic meter	m^3	1.3079 cubic yards
cubic meter	m^3	35.3140 cubic feet
liter	l	1.0568 quarts
liter	l	0.2642 gallon
metric ton	MT	1.1023 short tons
kilogram	kg	0.0011 short ton
kilogram	kg	2.2046 pounds
gram	g	0.0353 ounce
degrees Celsius	°C	°Fahrenheit = 9/5 °C + 32

English Unit	*Abbreviation*	*Approximate metric equivalent*
mile	mi	1.6093 kilometers
nautical mile		1.8520 kilometers
foot	ft	0.3048 meter
inch	in.	2.5400 centimeters
square mile	mi^2	2.5900 square kilometers
square foot	ft^2	0.0929 square meter
cubic yard	yd^3	0.7646 cubic meter
cubic foot	ft^3	0.0283 cubic meter
gallon	gal	3.7853 liters
quart	qt	0.9463 liter
short ton (2000 lb)	t	0.9072 metric ton
pound	lb	4.5359×10^{-4} metric tons
pound	lb	0.4536 kilogram
ounce	oz	28.3500 grams
degrees Fahrenheit	°F	°Celsius = 5/9 (°F - 32)

NOTE: The following units are used interchangeably in this manuscript:
mg/l = ppm (milligrams per liter = parts per million);
μg/l = ppb (micrograms per liter = parts per billion).

CREDITS

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7 p. 5 (*Fig. 2*)

8 p. 21 (*Fig. 15*)

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11 p. 17 (*Fig. 12*)

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