

Phytoplankton in Lake Washington: long-term changes 1950-1999

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with 16 figures and 7 tables

Abstract: Phytoplankton communities and associated environmental conditions in Lake Washington, Seattle, U.S.A. are discussed mainly from the perspective of interannual variations. Three major eras are identified: "Eutrophication" (1941–1968); "Recovery from Eutrophication" (1969–1975); and "Daphnia Era" (1976–present). Each era is distinguished by distinctive species assemblages associated with unique physical and chemical conditions. Several statistical methods as well as subjective graphical analyses were explored as tools to organize the data into patterns. Phytoplankton species were initially aggregated into 41 taxonomic categories, and their occurrences by year and month were compared with environmental variables through clustering algorithms and correlations. Different analytical models further aggregated the phytoplankton into 7 or 8 super categories, but the composition of each category differed among models and no universal convergence emerged across aggregation methods. Among 17 environmental variables, the strongest linear correlations with phytoplankton biomass emerged for SECCHI transparency, pH, titration alkalinity, phosphate, and wind speed. The long-term study documented a significant, progressive increase in annual average epilimnetic temperatures during the past half century. Mechanistic theory based on nutrient competition for light, N, P, and Si, together with interaction with loss rates, provides a consistent framework for the dominance transitions between blue-greens and diatoms during recovery from eutrophication, as well as the diatom species transitions in later years. Key factors appear to be *Oscillatoria/Planktothrix* competitive abilities at low light levels, blue-green competitiveness in using ammonium at low TN:TP ratios and low loss rates from sinking, grazing, and water exchange. At elevated concentrations of nitrate, diatoms and green algae achieved dominance, and species composition assorted along Si:N or Si:P ratio gradients. Changes in grazer species appear to have contributed to the nutrient changes by promoting differential loss by sinking of particulate Si compared with N and P.

Key words: Phytoplankton community, community structure, interannual variation, nutrient availability, nutrient ratios.

Introduction

This paper describes and explores the long-term changes in the phytoplankton community of Lake Washington as it responded to cultural eutrophication, land development, watershed management, and other factors. Eutrophication stemmed from the input of treated sewage effluent from Seattle and its suburbs as they developed, but deforestation and changes in land use in the watershed both preceded and accompanied it (DAVIS 1973). The appearance of *Oscillatoria* in

1955 was a strong signal that the lake was close to producing nuisance conditions (EDMONDSON et al. 1956), and sewage effluent was diverted from the lake beginning in 1963, creating an excellent situation for a study of the lake as a quasi-experiment in lake fertilization (EDMONDSON 1993a). However, we found that other alterations in watershed conditions also affected the lake, so we actually had a series of quasi-experiments to evaluate.

Our general approach was to study specific events or changes in the plankton and then to search for coordination or correlation with conditions, either as causal factors or responses. To separate cause and effect from coincidence in explaining the changes, we found substitutes for experimental control and replication (EDMONDSON 1993a). For accounts of our theoretical precepts and references to detailed papers, see EDMONDSON (1991b, 1993b, 1994, 1997).

The main approach of the study was based on ecosystem concepts, defining an ecosystem as the integration of biological communities with the physical and chemical environment, sometimes emphasizing different aspects of the system, but always considering the context (see EDMONDSON 1991b: 58–59). For the phytoplankton, the scope of the study therefore includes the effects of concentrations of nutrients on phytoplankton growth as well as the effect of biological activity on nutrient concentrations. Other important parameters include stratification, solar radiation, and temperature changes. Zooplankton grazing also has had major impacts at various times throughout the period, but will be addressed only briefly in this paper.

The period of the study can be divided into three segments of time or “eras” based on conditions in the lake.

Eutrophication, 1941–1968

Before 1941, Lake Washington received raw sewage, but with increasing human population growth in the watershed, secondary sewage treatment plants were constructed, still discharging into the lake. ANDERSON (1954) found a prominent spring diatom bloom in 1950, followed by a clear period during the summer. *Oscillatoria agardhii* was present, but was not a conspicuous portion of the flora (COMITA & ANDERSON 1959; EDMONDSON 1991b). The lake was showing some chemical signals of change: phosphate concentrations were about twice as high as in 1933 and late-summer hypolimnetic oxygen concentrations were lower. Sampling began again in June 1955 after discovery that *Oscillatoria rubescens* was thriving (EDMONDSON et al. 1956; EDMONDSON 1991b), and the intensive study began in summer 1961 (Table 1). Sewage diversion from the lake began in early 1963, initially removing 16% of the effluent. In July 1965 an additional 21% was removed, followed by 6% more in April 1966. The biggest diversion, in March 1967, eliminated all but a fraction of a percent of the original input, with final diversion in February 1968.

Table 1. Generalized summary of sampling in Lake Washington. The years listed have complete coverage for each parameter. Other years were sampled partially or sporadically. Intervals between samples range from weekly to monthly, depending on the season and the focus of the study at that time. Sampling depths also varied, in summer usually every 5 to 10 m from the surface to the bottom for chemistry and phytoplankton. Zooplankton were sampled in 3 oblique sections.

Analyte:	Time periods:
Phosphorus	
Total P	1957-58, 1962-97
Total dissolved P	1957-58, 1962-97
Phosphate	
Unfiltered	1949-50, 1957-58, 1962-97
Filtered (SRP)	1963-97
Nitrogen	
Total reduced N	1957-58, 1962-82, 1989
Dissolved reduced N	1957-58, 1962-78
Nitrate	1950, 1957-58, 1962-97
Nitrite	1957-58, 1962-76
Ammonium	1957-58, 1962-76
Alkalinity	1949-50, 1957-58, 1962-97
pH	1950, 1957-58, 1962-97
Carbon dioxide (titration)	1950, 1957-58, 1962-76
Conductivity	1989-97
Oxygen	1949-50, 1957-58, 1962-97
Silicon	1957, 1976-97
Seston	1965-82
Particulate Iron	1970-82
Biology:	
Phytoplankton	
Abundance	1950, 1957-58, 1962-99
Chlorophyll	1949-50, 1957-58, 1962-99
Oxygen production	1957-58, 1963-79
Carbon-14 uptake	1963-66, 1970-80
Zooplankton abundance	1957-58, 1962-99
Benthos	1963-64, 1967-72, 1974-75
Periphyton	1964-75

Changes in the concentration of phosphate in the lake did not follow the sewage diversion sequence instantaneously or in direct proportion. However, there was a clear reduction of phosphate in the lake by 1965 (EDMONDSON & LEHMAN 1981). After final diversion, the lake continued to receive effluent occasionally from combined overflows from storm sewers, but this small amount had no discernable effect on phosphate concentrations (EDMONDSON & LEHMAN 1981).

Recovery, 1969-1975

By 1969, maximum summer biovolume of phytoplankton had decreased sharply, and *Oscillatoria* was no longer the main cyanobacterium present. *Oscillatoria*

continued to decrease in successive years until its abundance fell below detection limits in the middle of 1976, to be seen only rarely since. It made a small resurgence briefly in 1972, accompanied by a decrease in diatom abundance, probably as a consequence of a winter flood (EDMONDSON 1991a).

By 1975, the winter concentration of dissolved phosphorus had decreased to 66% of its 1968 value, and the lake appeared to be approaching "trophic equilibrium" (EDMONDSON 1977), a state in which it would be expected to vary from year to year in response to a variety of factors other than P inputs. Recovery from eutrophication did not mean that the lake was restored to its original condition. Changes in environmental factors other than sewage inputs had taken place in the lake and its watershed, and the lake signaled only briefly a possible trophic equilibrium condition in the phytoplankton before other factors came into effect.

***Daphnia* era, 1976–present**

In 1976, *Daphnia*, a genus of cladoceran zooplankton that had previously been infrequent and scarce, suddenly became dominant during late spring (EDMONDSON & LITT 1982; EDMONDSON 1985). It has dominated zooplankton biomass during summer ever since. The rise of *Daphnia* can be understood as a result of changes in two different factors: reduced populations of predators on *Daphnia* (EDMONDSON & ABELLA 1988) and the subsidence of *Oscillatoria*, which interferes with *Daphnia* feeding mechanics (INFANTE & ABELLA 1985). After 1975, phytoplankton populations were released from dominant control by "bottom up" (i.e., resource-controlled) nutritional conditions, because efficient grazing by *Daphnia* can have a large effect on the types and quantity of phytoplankton present (PORTER 1977; MCCAULEY & BRIAND 1979; LEHMAN & SANDGREN 1985; LAMPERT 1987).

In addition to the influence of *Daphnia*, Lake Washington has experienced various land use changes in the watershed. Our records show that the low alkalinity (acid neutralizing capacity) of Lake Washington waters has been increasing irregularly since the early 1960s. This long-term rise traces to anthropogenic development in the catchments, modified by hydrological input (EDMONDSON 1990, 1991a). The rise in alkalinity has been accompanied by subtle changes in the phytoplankton, including an increased proportion of coccoid cyanobacteria and the emergence of taxa new to the lake such as *Tabellaria fenestrata* and *Oocystis gigas*.

Methods

When an *Oscillatoria* bloom appeared in Lake Washington in 1955, there were still major uncertainties about the basic process of eutrophication (EDMONDSON 1969, 1972). We set up a sampling program (Table 1) based on the contemporaneous understanding of the relations among nutrient supplies and concentrations and the resulting types and quantities of planktonic organisms. Our purpose was to produce a detailed description of the chemical and biological conditions

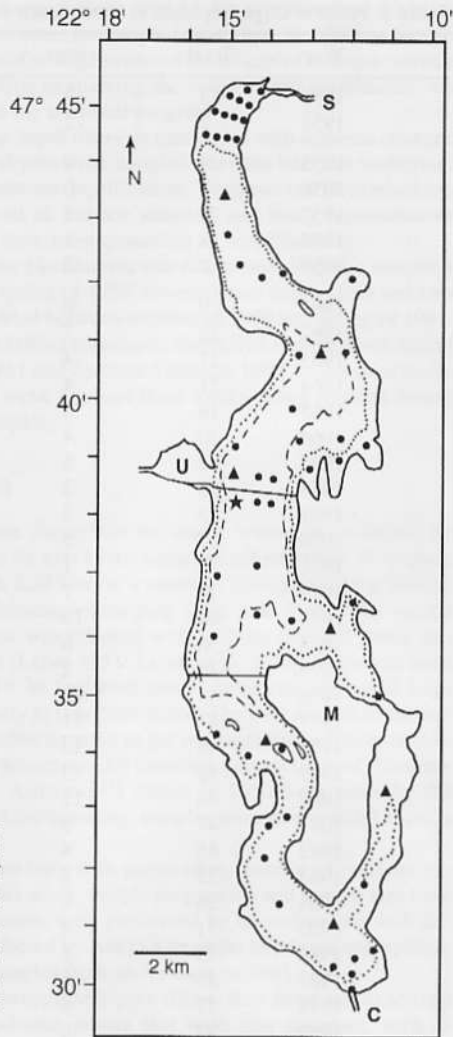


Fig. 1. Map of Lake Washington showing locations where phytoplankton has been sampled more than once. The main reference station off Madison Park is starred. Triangles show stations sampled repeatedly, especially during eutrophication and recovery. Dots show locations sampled for special purposes. S = Sammamish River; M = Mercer Island; C = Cedar River; U = Union Bay.

as they changed under the influence of increasing nutrient input. The record of the changes would provide data that could be used for testing ideas about controlling processes.

Earlier investigations (SCHEFFER & ROBINSON 1939) had sampled at three stations: one either end of the elongate lake plus one near its middle. Plankton, chemistry and seasonal change were similar at all three stations. The Department of Oceanography made measurements of some chemical and physical features (SECKEL & RATTRAY 1953; COLLIAS & SECKEL 1954) in connection with a salinity study. PETERSON (1955) measured surface temperature, chlorophyll, phosphate and nitrate at 26 stations distributed around the lake on 20 occasions between 9 July 1952 and 22 July 1953. He also found great similarity among stations. Shallow water stations tended to be less transparent, slightly warmer, and to have an earlier start on the spring phytoplankton bloom.

Because we initially emphasized seasonal and long-term changes in phytoplankton and chemistry, the most efficient and justifiable method was to concentrate sampling at one mid-lake

Table 2. Number of phytoplankton counts each year and their seasonal distribution.

Year	Total	winter	spring	summer	fall
1950	13	2	3	5	3
1951	2	2	0	0	0
1955	4	0	0	4	0
1956	7	0	3	3	1
1957	21	3	10	5	3
1958	8	1	4	2	1
1959	2	2	0	0	0
1961	9	0	0	5	4
1962	22	7	4	6	5
1963	27	4	7	10	6
1964	21	4	6	6	5
1965	18	4	5	4	5
1966	20	4	6	6	4
1967	23	5	8	5	5
1968	23	3	6	10	4
1969	23	3	5	9	6
1970	25	5	6	8	6
1971	28	7	7	8	6
1972	28	7	8	7	6
1973	44	13	11	10	10
1974	36	6	10	9	11
1975	36	7	10	10	9
1976	44	10	10	10	14
1977	47	11	13	11	12
1978	48	13	13	10	12
1979	52	13	13	13	13
1980	48	12	12	14	10
1981	47	8	13	14	12
1982	45	8	12	13	12
1983	32	8	11	7	6
1984	26	7	6	7	6
1985	31	8	8	8	7
1986	33	6	12	8	7
1987	35	6	9	13	7
1988	27	6	7	7	7
1989	33	6	10	10	7
1990	28	6	9	6	7
1991	28	7	7	7	7
1992	33	6	10	10	7
1993	31	5	10	10	6
1994	34	7	12	9	6
1995	42	8	11	13	10
1996	42	8	13	13	8
1997	26	6	9	5	6
1998	20	6	6	4	4
1999	18	3	5	5	5
Total	1290	273	360	359	298

reference station, located off Madison Park on the west shore (Fig. 1). We supplemented this with occasional synoptic trips to other locations. Over time, we sampled more than 30 different sites in the lake. This program continued after diversion of sewage to record the effects of reduced nutrient input. Later, as our emphasis shifted in the 1970s to studying the zooplankton populations, we intensified the biological sampling and reduced the chemical program.

We took samples through the water column at depth intervals that varied with seasonal changes in thermal stratification. Generally three to four depths were sampled when the lake was isothermal and 11 to 13 depths were sampled during full summer stratification. We preserved phytoplankton from many of the sampled depths. We analysed all surface samples, and many representative samples from the epilimnion and hypolimnion have been quantified as well (Table 2).

The lake was sampled four times in 1955 after *Oscillatoria* was discovered. Periodic sampling started late in 1956 and continued through the spring of 1959, covering two entire years and two partial years. Our sampling schedule was suspended between summer of 1959 and spring of 1961. The Washington Pollution Control Commission (1961) measured chlorophyll and nutrients during that hiatus. Our program started again in July 1961 and continued through 1999 on a regular basis. The interval between samples varied from one week to about three weeks, being shortest during seasons when conditions were changing most rapidly.

Phytoplankton counting methods

Counting methods remained essentially constant throughout the study. Water was collected by KEMMERER samplers during the 1950s, and then by VAN DORN samplers subsequently. From each collection, a 100 ml sample was preserved with acid LUGOL's solution, allowed to settle for one week, and then concentrated by aspiration. Subsamples ranging from 2 to 5 ml were settled overnight in counting chambers. Phytoplankton was counted with a ZEISS inverted phase microscope, using a modified UTERMÖHL method (LUND 1951; LUND et al. 1958). Transects were counted at magnifications of 125 \times and 312.5 \times to find both small, numerous algae and large infrequent algae that might contribute significantly to total biovolume. The goal of each count was to find at least 200 cells, but many more were often counted to get representation of rare species. The biovolume of filamentous organisms was determined by counting intersections of filaments with a standard WHIPPLE grid (OLSON 1950). ANDERSON's counts in 1950 were made by the LACKEY drop-transect method (LACKEY 1938). After counting, samples were stored with LUGOL's solution and formaldehyde for future reference.

The number of taxa detected in a sample can vary with preparation, amount of material examined, and the experience of the observer. In this study, sample preparation and sample size have been reasonably consistent throughout. Early counts were performed by several people with differing experience; since 1974, counts were conducted by ABELLA or under her direct supervision. To assess conformity, she has also recounted samples from as far back as 1961.

Beginning in 1974, 1 l of water was drawn through Millipore filters, then dried and examined microscopically for representatives of large colonial genera that were less abundant, such as *Anabaena*, *Aphanizomenon*, *Botryococcus* and *Microcystis*.

In this paper, cell volumes are expressed as μm^3 ; for filamentous cyanobacteria in which cells cannot be distinguished in the counting chambers volumes are reported as $\mu\text{m}^3/\text{mm}$ of filament length. Population sizes are expressed in terms of total biovolume (mm^3/l).

Individual cell volumes were calculated by measuring dimensions of individuals and relating them to simple geometrical shapes, without subtracting vacuolar volume. Some cells, such as *Stephanodiscus niagarae*, vary so much in volume that measurements of individuals were made for many dates (Table 4). Volumes of colonies that include a large vacant intercellular space such as *Coelosphaerium* were modified to exclude the space from the biovolume estimate.

Two taxa that had potential significance were not represented well by our counting methods. A colonial prokaryote tentatively identified as *Aphanothece clathrata* occurred sporadically from 1969 to 1979. In 1980, it became so abundant in summer that it interfered substantially in the counting process, providing a new meaning for the term "nuisance bloom." Because it grows in very irregular colonies of differing sizes and densities, we could not make precise measurements using our methods, and using a fluorescence method to examine filtered samples stained with

acridine orange proved cumbersome. Isolated colonies would not grow in culture, leaving us still unsure of its taxonomic status. Therefore, our estimates of *Aphanothece* biovolume are not included in this paper, but its fluctuating presence must be kept in mind for the years after 1980.

The second troublesome taxon is the dinoflagellate *Ceratium hirundinella*, which was found intermittently in the phytoplankton samples, but which often was a major constituent of the total biovolume when encountered because of its large cell size. Alternative estimates of its abundance were made from larger volume net hauls taken for zooplankton, and we found that the trends of occurrence in the zooplankton samples were similar to patterns observed in the phytoplankton counts.

During the study, a list of names was compiled that included nearly 400 taxa and counting categories. Names included confirmed species identifications as well as group designations for organisms that could not be identified precisely. With experience and study of live material, we were able to recognize some of these later on, and previous designations were adjusted where appropriate. The zooplankton samples were similar to patterns observed in the phytoplankton counts.

Results

Lake Washington phytoplankton before 1955

Lake Washington has been the focus of ecological studies for more than half a century (for a comprehensive list, see GREENBERG & SIBLEY 1994). A pathmark study of phytoplankton conducted by VICTOR B. SCHEFFER in 1933 (SCHEFFER 1936; SCHEFFER & ROBINSON 1939) tabulated seasonal occurrence of 72 taxa in net tows (Table 3), but biovolumes and relative abundance were not estimated. *Oscillatoria* occurred in summer and fall, but specimens were not identified to species level. *Aphanizomenon flos-aquae* appeared periodically throughout the year. Diatoms seemed to dominate the plankton through most of the year, with a large peak in spring and a lesser peak in the fall. Various green algae appeared from late spring through early fall, accompanied by coccoid colonial cyanobacteria. The mesh size of the net and the length of tows were not recorded, making it difficult to relate SCHEFFER's data to the current study beyond noting the identifications and relative occurrences of taxa. Small algae that could have escaped the net cannot be compared in any case.

In 1950, the lake was beginning to show chemical changes related to sewage inputs (ANDERSON 1954; COMITA & ANDERSON 1959), but the diatom flora inspected by G. ANDERSON was dominated by the same taxa found by SCHEFFER (Table 3). ANDERSON settled particulate material from water samples, then identified and counted the algae; he also produced biovolume estimates. He found that total biovolume of diatoms waned in midsummer and he identified fewer chlorophytes than did SCHEFFER. A large dinoflagellate, *Peridinium divergens*, was unusually abundant in one sample during August. *Oscillatoria agardhii* was present in small numbers during summer, but reached a peak in midwinter. *Aphanizomenon* was present, but rare. Coccoid blue-greens such as *Aphanocapsa* and *Microcystis* were abundant at the beginning of September.

Table 3. Phytoplankton found in Lake Washington during this study. The list of numbered names reports taxa treated in this paper. The numbers are used for identification in graphs and tables. Components of aggregated categories are indented and listed below the numbered category name. Some of the numbered taxa are groups of species joined by a "+". In the text, they will be referred to by the first name listed and a "+". Letters in parentheses refer to occurrences noted by SCHEFFER, 1936 (S) and ANDERSON, 1954 (A).

Taxon name	
Chlorophyceae	
1	<i>Oocystis gigas</i>
2	<i>Oocystis</i> spp.
	<i>O. borgei</i> (S, A)
	<i>O. lacustris</i>
	<i>O. parva</i> (S, A)
	<i>O. pusilla</i>
	<i>O. solitaria</i>
	<i>Oocystis</i> spp.
3	<i>Staurostrum paradoxum</i> (S, A)
4	Gelatinous green algae
	<i>Coelastrum microporum</i> (S, A)
	<i>Crucigenia</i> spp. (S, A)
	<i>Dictyosphaerium</i> spp. (S, A)
	<i>Elakatothrix</i> sp.
	<i>Eudorina</i> sp. (S)
	<i>Gloeocystis</i> sp.
	<i>Kirchneriella</i> spp. (S)
	<i>Nephrocytium</i> spp. (S)
	<i>Pandorina morum</i> (S)
	<i>Pseudosphaerocystis lundii</i>
	<i>Quadrigula</i> sp.
	<i>Selenastrum</i> spp.
	<i>Sphaerocystis schroeteri</i> (S, A)
	<i>Tetraspora</i> sp.
5	Acicular green algae
	<i>Ankistrodesmus</i> spp. (S, A)
	<i>Ankya judayi</i>
	<i>Monoraphidium contortum</i>
	<i>Monoraphidium</i> spp.
	<i>Schroederia</i> spp.
6	<i>Botryococcus</i> spp. (S, A)
7	Other green algae
	<i>Closteriopsis longissima</i>
	<i>Closterium</i> spp. (S)
	<i>Cosmarium</i> spp. (S, A)
	<i>Pediastrum duplex</i> (S)
	<i>Prasinoclamydomonas impressa</i>
	<i>Scenedesmus</i> spp. (S)
	<i>Ulothrix subconstricta</i> (S)
	other green algae
Bacillariophyceae	
8	<i>Asterionella formosa</i> (S, A)
9	<i>Cyclotella pseudostelligera</i> + <i>stelligera</i> + <i>glomerata</i>
10	<i>Cyclotella bodanica</i> + <i>comta</i> (S, A)
11	<i>Cyclotella ocellata</i> (S, A)

Table 3, continued.

Taxon name	
12	<i>Diatoma elongatum</i>
13	<i>Fragilaria crotonensis</i> (S, A)
14	<i>Aulacoseira subarctica</i> (S, A)
15	<i>Aulacoseira italica</i> var. <i>tenuissima</i> (S, A)
16	<i>Melosira varians</i> (S, A)
17	<i>Rhizosolenia eriensis</i> (S, A)
18	<i>Stephanodiscus neoastraea</i> + <i>minutula</i> (S, A)
19	<i>Stephanodiscus hantzschii</i> + <i>alpinus</i>
20	<i>Stephanodiscus niagarae</i> (S, A)
21	<i>Synedra</i> spp.
	<i>S. ulna</i> + <i>acus</i> + <i>delicatissima</i> (S, A)
	<i>S. radians</i>
	<i>S. rumpens</i>
	<i>Synedra</i> spp. (S)
22	<i>Synedra tenera</i>
23	<i>Tabellaria fenestrata</i> (S, A)
24	Other diatoms
	<i>Attheya zachariasii</i>
	<i>Aulacoseira distans</i>
	<i>Aulacoseira</i> spp.
	<i>Cyclotella</i> spp.
	<i>Fragilaria</i> spp.
	<i>Nitzschia acicularis</i>
	<i>Synedra cyclopum</i>
	other diatoms
Chrysophyceae	
25	<i>Mallomonas</i> spp.
	<i>M. producta</i> (S, A)
	<i>M. akrokomos</i>
	<i>M.</i> spp.
Cryptophyceae	
26	<i>Chroomonas minuta</i>
27	<i>Cryptomonas</i>
	<i>C. marssonii</i>
	<i>C.</i> spp.
Cyanobacteria	
28	<i>Anabaena</i> spp.
	<i>A. circinalis</i> (A)
	<i>A. flos-aquae</i>
	<i>A. utermohlii</i>
	<i>A.</i> spp. (S, A)
29	<i>Aphanizomenon flos-aquae</i> (S, A)
30	<i>Chroococcus limneticus</i> (S, A)
31	<i>Coelosphaerium</i> spp. (S, A)
32	<i>Microcystis aeruginosum</i> (S, A)
33	<i>Lyngbya limnetica</i>
34	<i>Oscillatoria agardhii</i> + <i>rubescens</i> + <i>prolifera</i>
35	<i>Pseudanabaena</i> sp.
36	Other colonial coccoid cyanobacteria
	<i>Anacystis</i> spp.

Table 3, continued.

Taxon name	
	<i>Aphanocapsa</i> spp. (S, A)
	<i>Gomphosphaeria</i> spp. (A)
	<i>Gloeocapsa</i> spp.
	other taxa
38	Other cyanobacteria
	<i>Oscillatoria limnetica</i>
Dinophyceae	
39	<i>Ceratium hirundinella</i> (A)
40	Other dinoflagellates
	<i>Gymnodinium helveticum</i>
	<i>Peridinium</i> spp. (A)
	<i>Glenodinium</i> spp.
	other dinoflagellates
Other algae	
41	Other algae
	<i>Cyanomonas</i> sp.
	2–3 μm unicells
	4–6 μm unicells
	7–10 μm unicells
	11–18 μm unicells
	> 18 μm unicells
	anything else not included in other categories

Lake Washington phytoplankton after 1955

Phytoplankton were grouped into four categories to examine major trends over time: (1) cyanobacteria other than *Oscillatoria*, (2) *Oscillatoria* itself, (3) diatoms, and (4) all others (Figs. 2, 3).

Phytoplankton biovolume was somewhat larger in 1957 than in 1950, and about half of the biovolume was represented by *Oscillatoria*. The dominance of *Oscillatoria* grew as phytoplankton abundance increased. Diatom populations continued to expand in spring, but they no longer dominated as they had in 1933 and 1950. The annual phytoplankton maximum was achieved in summer coincident with maximal development of *Oscillatoria*. This situation continued through the years of nutrient enrichment, with noticeable departure beginning only in 1968 as the last of the treated sewage was diverted from the lake. The year 1968 was striking because a species of *Anabaena* joined *Oscillatoria* to dominate the summer plankton, foreshadowing changes that would occur over the next several years. Beginning in 1969, relative proportions of the major groups changed in a systematic way. Cyanobacteria began a decline, and diatoms began a relative increase that would continue through 1975 (Fig. 4). The community realignments produced an accompanying progressive shift from summer to spring in the timing of maximum total biovolume. The **proportion** of diatoms began to increase in late

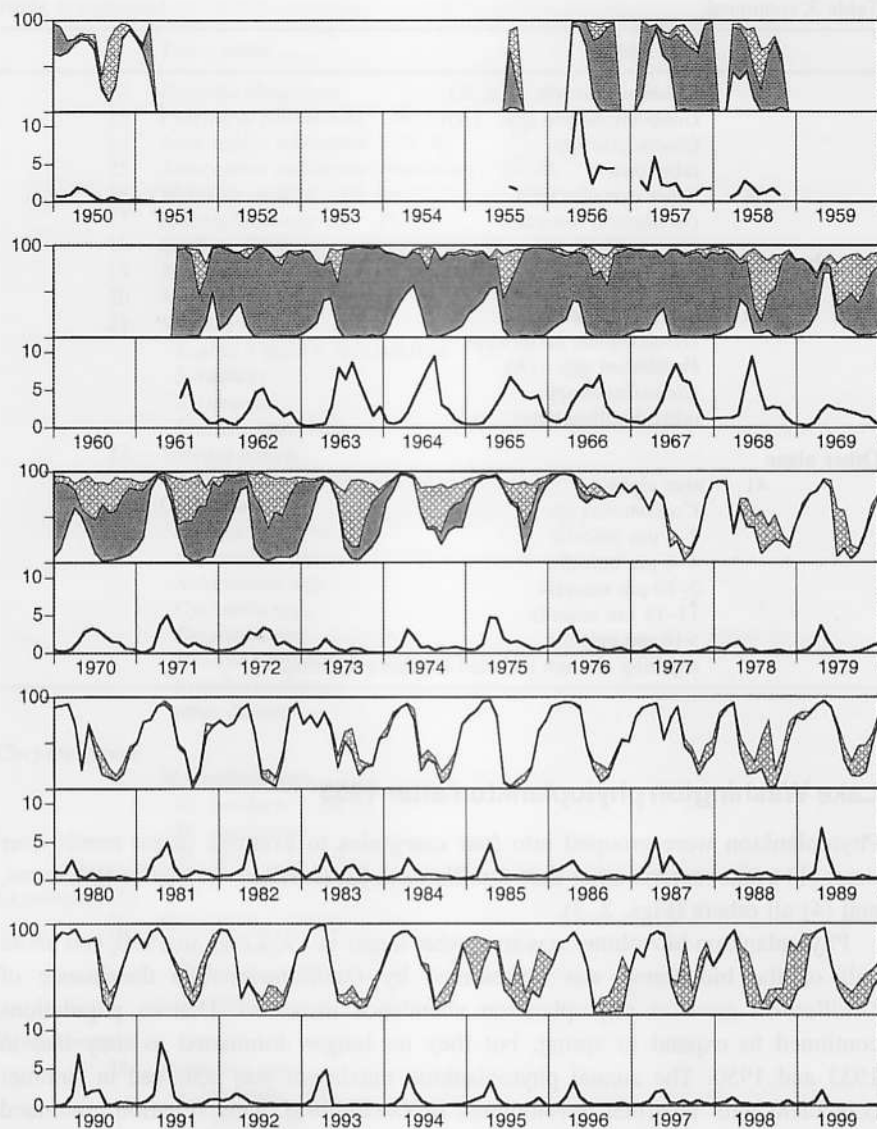


Fig. 2. Monthly average phytoplankton from 1950 to 1999 by decades. The lower panel within each of the five decade series reports the total biovolume of phytoplankton (mm^3/l) on a scale from 0 to 10. The upper panel in each series reports the percentage distribution of biovolume (scale = 0 to 100) among four categories: diatoms (white area at bottom), *Oscillatoria* (dark), all other cyanobacteria (hatched) and all other phytoplankton (white area at top).

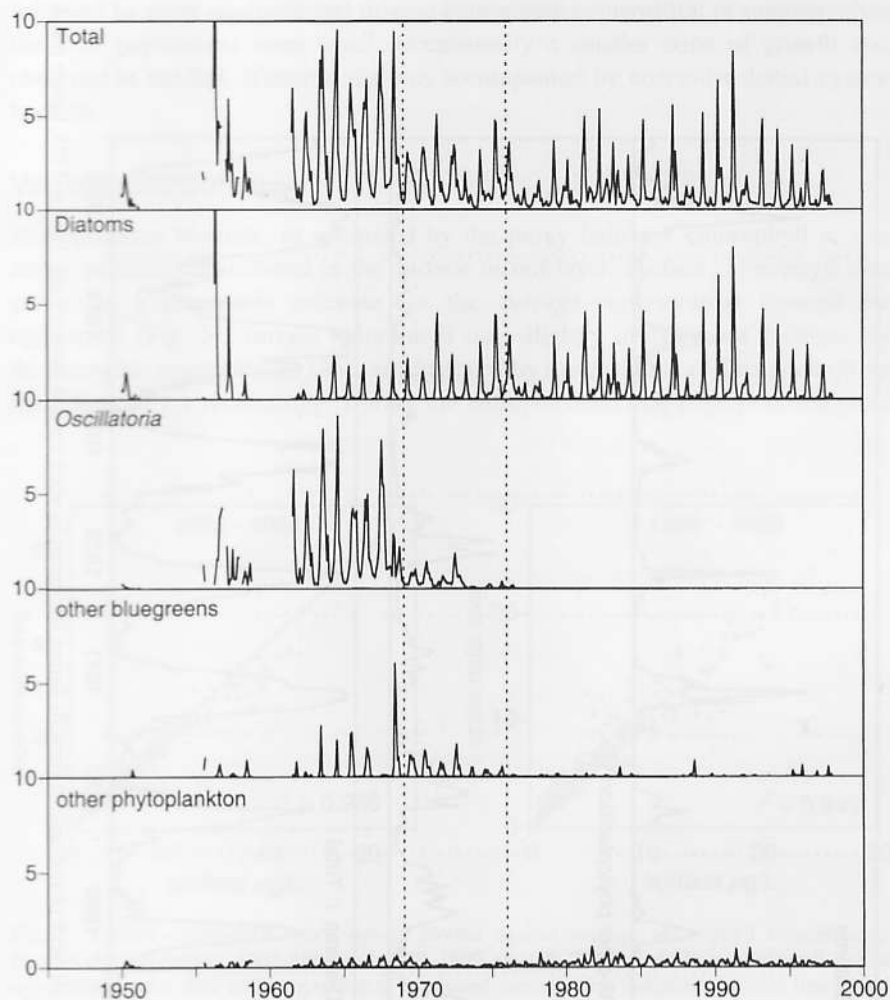


Fig. 3. Monthly average biovolume of phytoplankton by category as in Fig. 2 (mm^3/l) on a scale from 0 to 10. The three eras of (1) eutrophication, (2) recovery, and (3) post-recovery are separated by vertical dotted lines at 1969 and 1976.

fall and early winter, well in advance of the spring bloom each year. After 1970, the proportional increase in diatoms became evident even earlier each year, so that by 1975 it commenced in mid-August, well before the 1976 spring bloom. The shifting proportions were not caused by increases in diatom biovolume, but rather by declines in the rest of the phytoplankton. The phytoplankton seasonality in 1976 was unusual (Fig. 2) in that diatoms dominated throughout the year. This domination was not repeated subsequently. Instead, the basic pattern for annual succession of the phytoplankton featured domination by diatoms during spring,

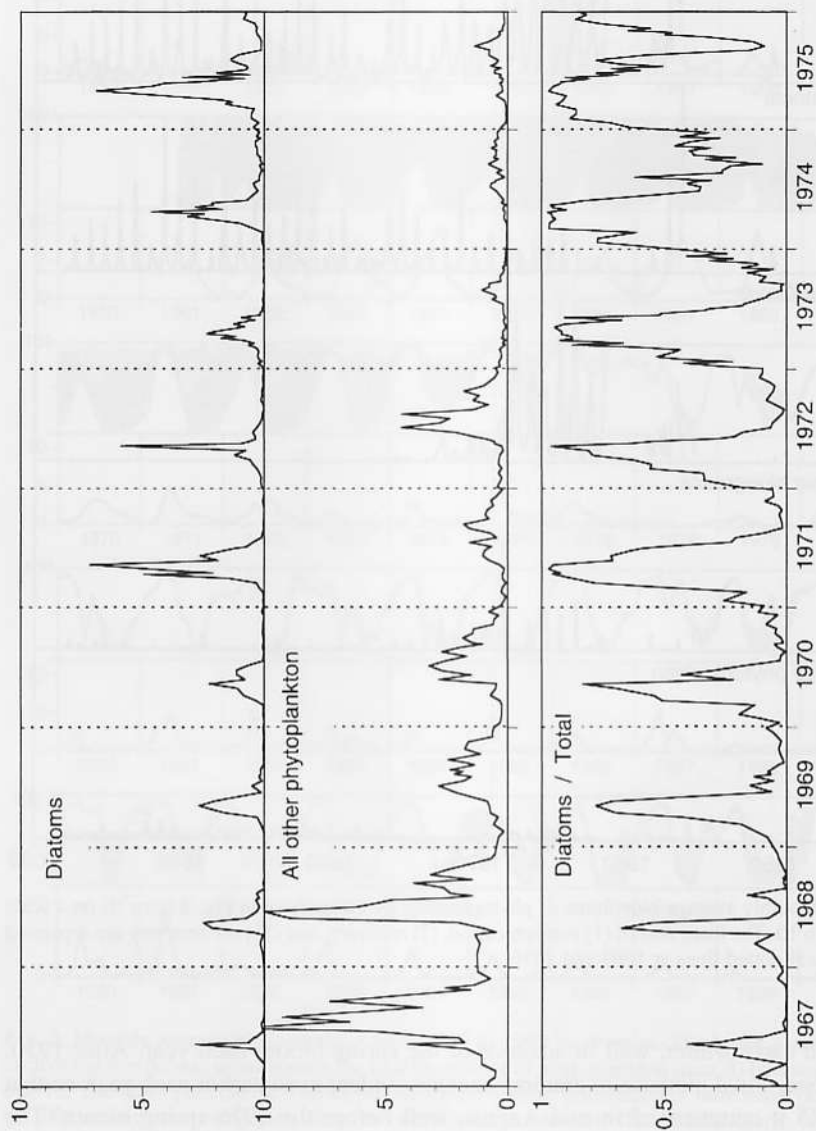


Fig. 4. Biovolume of diatoms compared with all other phytoplankton (mm^3/l) during late eutrophication era and recovery era, 1967 to 1975. Lower panel: ratio of diatom biovolume to total biovolume.

followed by more equitable and diverse community composition in summer when the total populations were small. Occasionally a smaller burst of growth was observed in the fall, featuring diatoms accompanied by coccoid colonial cyanobacteria.

Vertical distribution

Phytoplankton biomass, as estimated by the proxy indicator chlorophyll *a*, was rather uniformly distributed in the surface mixed layer. Surface chlorophyll thus serves as a reasonable estimate for the average concentration through the epilimnion (Fig. 5). Surface chlorophyll may slightly overestimate biomass for the eutrophic years 1962 to 1968, as illustrated by the deviation of data points from the reference 1:1 relationship. During the eutrophication era, phytoplankton were

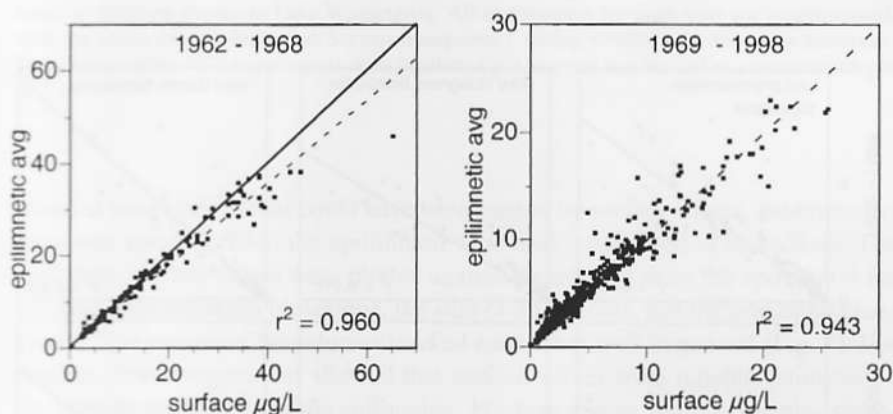


Fig. 5. Surface chlorophyll concentration plotted against average chlorophyll concentration through the epilimnion, 1962–1968 and 1969–1999, in $\mu\text{g/L}$. The dashed lines are best fit linear regressions to the data with proportion of explained variance (r^2) indicated. A solid line of 1:1 slope is shown for reference.

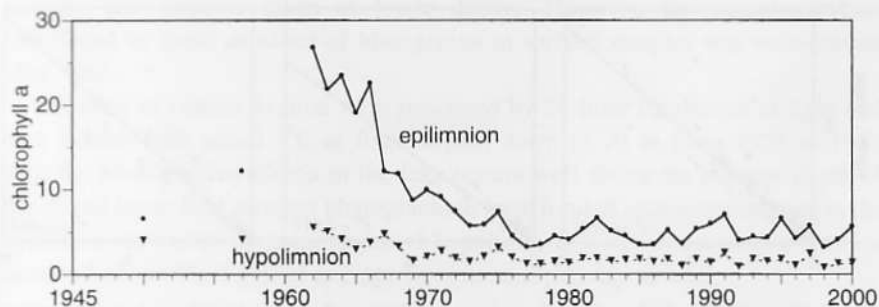


Fig. 6. Average chlorophyll ($\mu\text{g/L}$) from April to October within the epilimnion and hypolimnion at Madison Park.

less evenly distributed through the epilimnion when blooms of buoyant blue-greens floated to the surface, which is illustrated by the points below the 1:1 line at the higher values of chlorophyll. However, for years during and after recovery, the slope of the regression is not distinguishable from 1.0.

Chlorophyll concentrations in the epilimnion were consistently greater than in the hypolimnion during thermal stratification, thus most phytoplankton occurred above the thermocline (Fig. 6). There is no evidence for development of metalimnetic phytoplankton blooms in Lake Washington. Neither chlorophyll data nor vertical distribution counts of phytoplankton show any increases through or below the thermocline. Rather, there is a sharp decline in chlorophyll below the mixing depth after stratification is established each year.

Vertical series of phytoplankton samples were counted at intervals from 1962 through 1988 to check the reliability of surface samples in representing the phytoplankton communities of the lake. No large populations of any species were

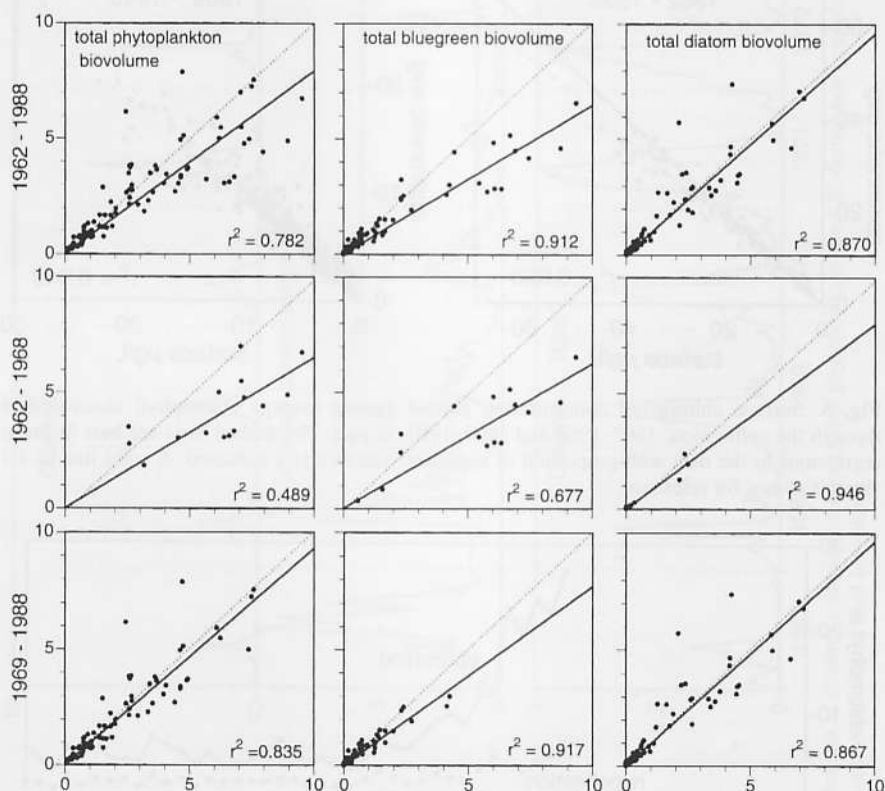


Fig. 7. Plots of phytoplankton biovolume in mm^3/l from surface samples (X-axis) against average biovolume within the epilimnion (Y-axis) from 1962 through 1988. The solid line represents a 1:1 relationship while the dashed line represents the best fit linear regression through the points.

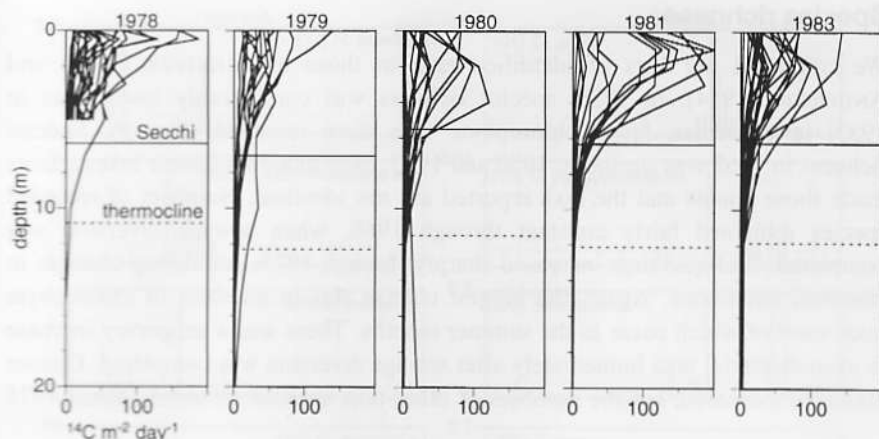


Fig. 8. Net ^{14}C fixation in $\text{mg C m}^{-2} \text{ day}^{-1}$ calculated from light and dark bottles incubated for 24 hours at different depths in Lake Washington. All experiments for each year are superimposed, with the mean mixing depth and SECCHI transparency during stratification shown as horizontal lines. Many of the 1978 experiments were incubated at a site that was limited to a maximum depth of 5 m.

found at lower depths that could have been missed by surface counts. Additionally, most rare species within the epilimnion were also represented at the surface. For each date, surface values were plotted against the average from the epilimnion for the total phytoplankton biovolume, the sum of all diatoms, and the sum of all blue-greens. The measured biovolumes tracked each other well in general (Fig. 7). For diatoms, linear regressions showed that surface values were reliable estimates of the biovolume throughout the epilimnion. For blue-greens, surface samples sometimes overestimated mean biovolume because of buoyancy, and its interaction with wind, which could redistribute algae both vertically and horizontally. When biovolume data for all taxa were combined, the large populations of blue-greens present during eutrophication affected the aggregate relationship between surface samples and samples taken at lower depths. However, the occasional bias introduced by large densities of blue-greens in surface samples was unimportant after 1968.

Net rates of carbon fixation were measured by 24-hour incubation of light and dark bottles with added ^{14}C at fixed depths down to 20 m from 1978 to 1983 (Fig. 8). Most photosynthesis in the lake occurs well above the average depth of the mixed layer; thus summer phytoplankton have limited access to nutrients in the hypolimnion, except by entrainment of hypolimnetic water. Most carbon fixation occurred above the depth of average SECCHI transparency as well.

Species richness

We compared our lists of identified taxa to those of SCHEFFER (1936) and ANDERSON (1954). In 1950, species richness was considerably lower than in 1933; in particular, fewer chlorophyte taxa were recorded (Fig. 9). Species richness in 1962 was similar to 1950 and 1957, even though different investigators made those counts and the taxa reported are not identical. Numbers of recorded species remained fairly constant through 1968, when sewage diversion was completed. Richness then increased sharply through 1975, paralleling changes in chemical conditions. Again, the biggest change was in numbers of chlorophyte taxa, most of which occur in the summer months. There was a temporary increase in cyanobacterial taxa immediately after sewage diversion was completed. Diatom taxa also increased, but the numbers of other taxa showed no trends. Since 1975

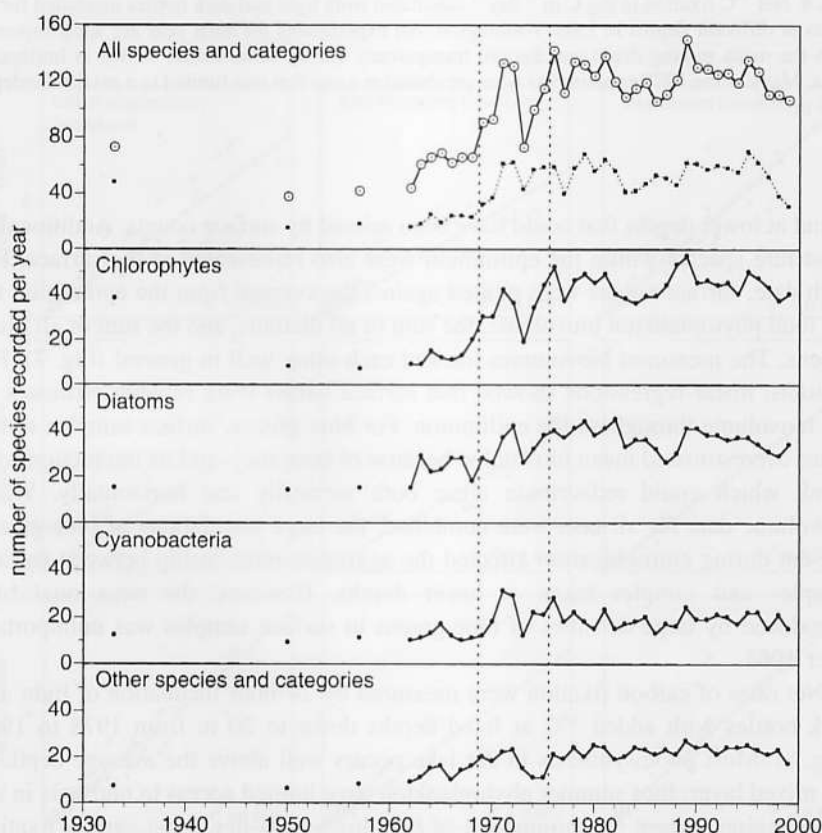


Fig. 9. Species richness expressed as number of taxa recorded each year. In the uppermost panel, the top line represents all taxon records including single occurrences, and the lower line represents the number of taxa that appeared at least five times in the counts for that year. The four lower panels report species richness by major algal groups.

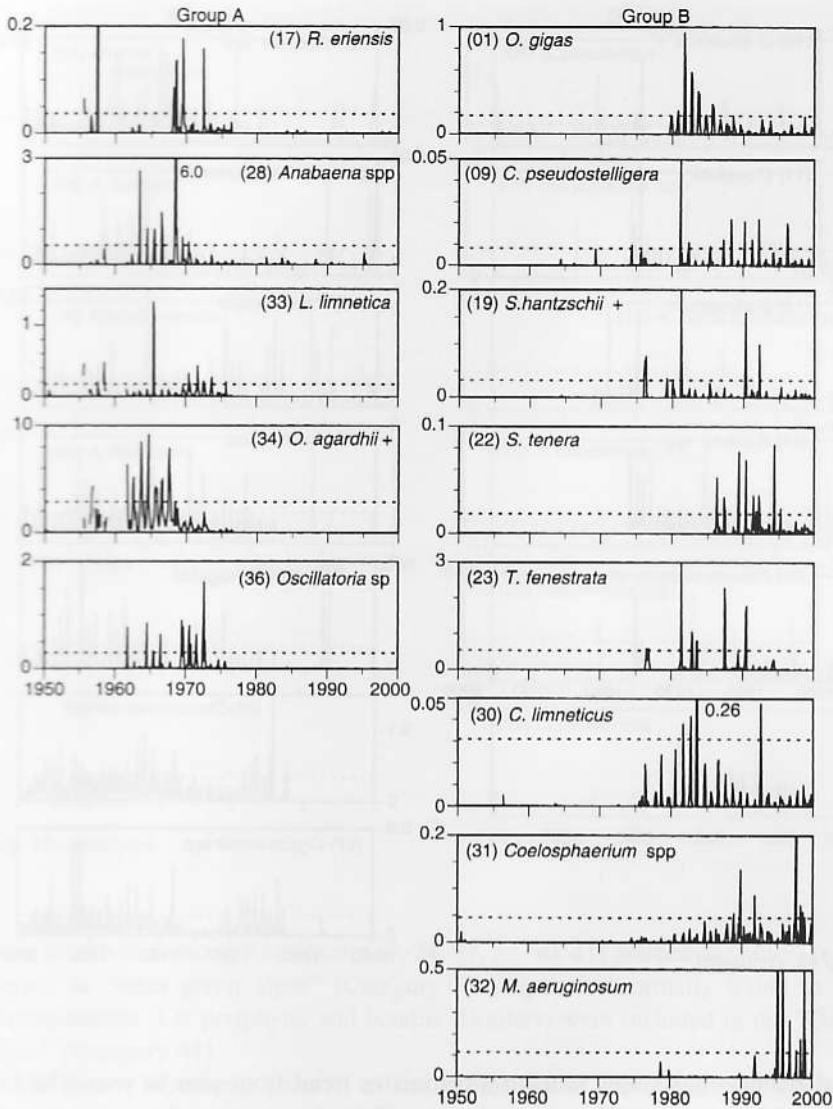


Fig. 10. Monthly mean biovolume in mm^3/l for 1950–1999, arranged in groups A to G as defined in the text. Note that the vertical scales differ to maximize visibility of variation for each species. For occasional peaks that exceed the Y-axis maximum, the peak value is printed to the right of the truncated peak. A horizontal line in each panel represents 1 standard deviation above the mean of all non-zero occurrences.

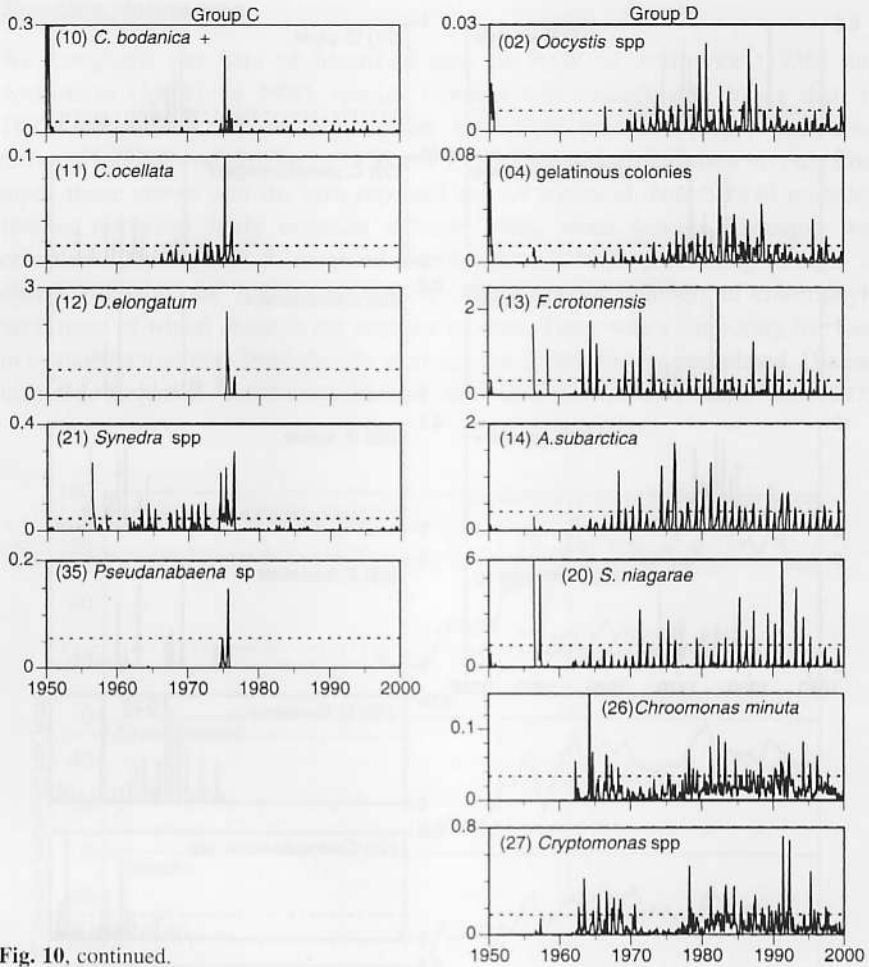


Fig. 10, continued.

total richness has varied without a distinctive trend from year to year. The low point of richness in 1973 seems to be an artifact of a one-year change in counting personnel.

Grouping taxa and years

We classified all of the phytoplankton into 41 categories (Table 3) that include 33 distinct genera and species. Two categories include chlorophytes grouped by morphologies that could affect zooplankton grazing: colonial green algae that have a polysaccharide matrix as protection (Category 4: Gelatinous green algae), and small algae with a needle shape (Category 5: Acicular green algae). Rare taxa

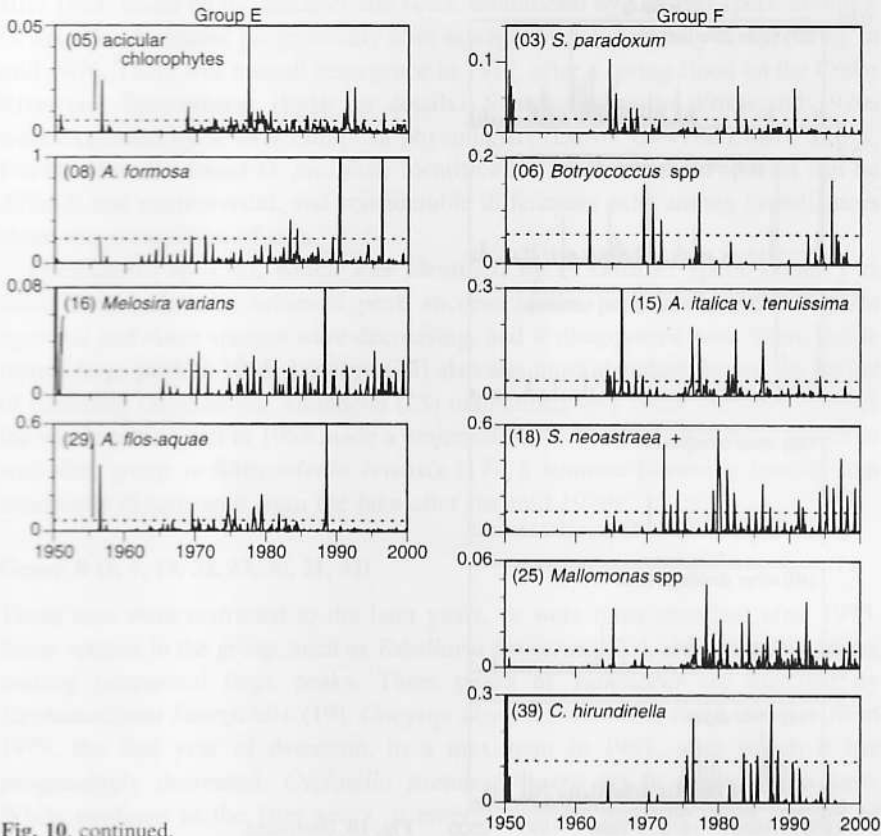


Fig. 10, continued.

were distributed among 6 categories (7, 24, 37, 38, 40, 41) marked as "other", e.g., *Volvox* in "other green algae" (Category 7). Algae not normally found in the phytoplankton (i.e. periphytic and benthic dwellers) were included in the "Other algae" (Category 41).

We regard biovolume (mm^3/l) as the expression of the quantity of environmental resources used or occupied by a species, and therefore not available to other organisms. Maximum and mean biovolumes for all occurrences were tabulated for each taxon category (Table 4), documenting a wide range of frequency, abundance and timing in population maxima. Some categories such as *Diatoma elongatum* (12) and *Pseudanabaena* sp. (35) were distinctive because they were abundant, but very limited in distribution. Others were noteworthy because they were present most years, but rarely became abundant, such as *Aphanizomenon*, inconspicuous most years except for 1988 when it made a large population (EDMONDSON 1997).

EDMONDSON established 7 groups of taxa with common population characteristics, based on perceptions gained through study of graphical patterns of variation

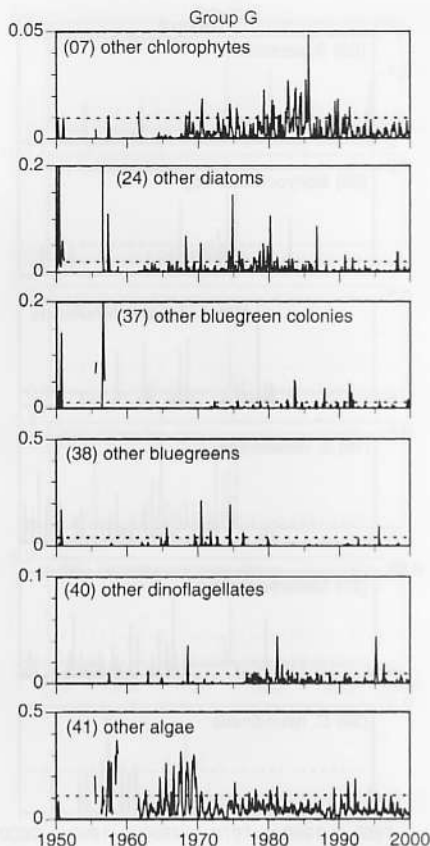


Fig. 10, continued.

of monthly average biovolumes (Fig. 10), with special attention paid to the years 1962 to 1999. Criteria included the years of occurrence, timing and peak values of maximum development, and year to year fluctuations. Of course, some assignments were not clear cut, and a few decisions were difficult. Each group name is followed by the assigned number of each taxon included in the group (Table 3).

Group A (17, 28, 33, 34, 36)

These taxa were present only before 1976 or were very scarce after that year. *Oscillatoria agardhii* and sister species (34) dominate the group. The species of *Oscillatoria* that we consider here are included in the proposed genus *Planktothrix* (ANAGNOSTIDIS & KOMÁREK 1988), but here we retain the old name found in many limnological papers. It is interesting that the first *Oscillatoria* to become conspicuous in Lake Washington was *O. rubescens*, which indicated cultural eutrophication was taking place because of its history in Swiss lakes (HASLER 1947). *O. rubescens* was more abundant than *O. agardhii* in the 1950s, but was not found

after 1968, based on its characteristic color, established by DROUET (pers. comm.). *O. agardhii* decreased progressively after sewage diversion, finally disappearing in mid-1976. There was a small resurgence in 1972, after a spring flood on the Cedar River (see EDMONDSON 1991b for details). Samples from the 1960s and 1970s were examined by several European phycologists (LUND, CANTER-LUND, SKUJA, FOTT), who also found *O. prolifica*. Identification of *Oscillatoria* species can be difficult and controversial, and considerable differences exist among investigators about the recognition of taxa.

Oscillatoria sp. (36), which was identified by F. DROUET (pers. comm.) as *Schizothrix calcicola*, achieved peak success in the period when *Oscillatoria agardhii* and sister species were decreasing, and it disappeared with them. Aside from a large peak in 1965, *Lyngbya* (33) also was most abundant during the period of declining *Oscillatoria*. *Anabaena* (28) maintained very small numbers through the whole period, but in 1968 made a major outburst. The only diatom to associate with this group is *Rhizosolenia eriensis* (17), a summer-blooming species that essentially disappeared from the lake after the mid 1970s.

Group B (1, 9, 19, 22, 23, 30, 31, 32)

These taxa were restricted to the later years, or were most abundant after 1975. Some species in the group, such as *Tabellaria fenestrata* (23), are generally scarce, making occasional large peaks. Three peaks of *Tabellaria* are matched by *Stephanodiscus hantzschii*+ (19). *Oocystis gigas* (1) showed a rapid increase from 1979, the first year of detection, to a maximum in 1981, after which it has progressively decreased. *Cyclotella pseudostelligera* (9) is a borderline case. While confined to the later years, it emerged earlier than the other species of the group. Four other members of this group have their maximum peaks in 1981.

Group C (10, 11, 12, 21, 35)

These taxa have periods of abundance centered on 1975, three of them quite limited in time. *Diatoma elongatum* (12) developed a very large population in the spring of 1975 and a smaller one in 1976, but has rarely been found in the lake otherwise. The maximum of *Cyclotella ocellata* (11) was preceded by a ten-year period of small populations. *C. bodanica*+ (10) was abundant in 1950 and had a few small occurrences after its peak in 1976. Planktonic *Synedra* species (21) were abundant in one of the few samples from 1956, but achieved their maximum annual mean in 1975, whereas their maximum monthly mean occurred in 1976. *Pseudanabaena* (35) is noteworthy because it is the only filamentous cyanobacterium not assigned to Group A.

Group D (2, 4, 13, 14, 20, 26, 27)

These taxa occurred through the whole period with considerable annual fluctuations, several becoming most prominent after eutrophication. *Cryptomonas* (27)

Table 4. Abundance and occurrence of phytoplankton by category in Lake Washington, 1962-1994. The maximum and mean volumes are expressed as mm^3/l . Cell volumes are in μm^3 , but the entry was left blank where it varied widely. Means include non-zero values only. Percent of population is the portion of total community biovolume made by a given taxon. See Fig. 10 and associated text. Presence is the percentage of time the category was present, based on interpolated

Name	Cell volume	maximum	Volume		
			order	mean	order
Chlorophyceae					
<i>Botryococcus</i> spp.		0.401	22	0.068	13
* <i>Oocystis gigas</i>	4500	1.269	13	0.115	9
<i>Oocystis</i> spp.		0.090	35	0.005	33
<i>Staurastrum paradoxum</i>	5880	0.223	27	0.015	25
gelatinous colonial chlorophyceae		0.122	34	0.003	35
acicular chlorophyceae		0.181	32	0.068	12
Bacillariophyceae					
<i>Asterionella formosa</i>	620	5.619	5	0.054	15
* <i>Aulacoseira subarctica</i>	1510	2.228	10	0.190	5
<i>A. italica</i> var. <i>tenuissima</i>	565	0.555	17	0.024	19
<i>Cyclotella ocellata</i>	300	0.220	28	0.007	32
<i>C. pseudostelligera</i>	30	0.188	31	0.003	34
<i>C. bodanica</i> +	3150	0.359	23	0.019	22
* <i>Diatoma elongatum</i>	1060	3.233	7	0.408	3
* <i>Fragilaria crotonensis</i>	340	4.248	6	0.132	7
<i>Melosira varians</i>	3500	0.476	19	0.023	20
<i>Rhizosolenia eriensis</i>	275	0.280	26	0.014	28
* <i>Stephanodiscus niagarae</i>		14.048	1	0.782	2
<i>S. neoastraea</i> +	11800	1.390	11	0.060	14
<i>S. hantzschii</i> +	250	0.514	18	0.017	24
<i>Synedra</i> spp.		0.600	15	0.019	21
<i>Synedra tenera</i>	250	0.212	30	0.015	26
<i>Tabellaria fenestrata</i>	5400	5.686	4	0.331	4
Chrysophyceae					
<i>Mallomonas</i> spp.	1000	0.166	33	0.008	31
Cryptophyceae					
<i>Chroomonas minuta</i>	125	0.423	21	0.017	23
* <i>Cryptomonas</i> spp.	2100	1.370	12	0.078	11
Dinophyceae					
<i>Ceratium hirundinella</i>	106500	0.587	16	0.149	6
Cyanobacteria					
<i>Anabaena</i> spp.	65	8.360	3	0.108	10
<i>Aphanizomenon flos-aquae</i>		1.201	14	0.030	17
<i>Chroococcus limneticus</i>	268	0.438	20	0.014	27
<i>Coelosphaerium</i> spp.		0.212	29	0.011	29
<i>Microcystis aeruginosa</i>	33	0.339	24	0.010	30
* <i>Lyngbya limnetica</i>		2.566	9	0.041	16
* <i>Oscillatoria agardhii</i> +		12.619	2	1.084	1
<i>Pseudanabaena</i> sp.		0.334	25	0.028	18
* <i>Schizothrix calcicola</i>		3.046	8	0.122	8
Grouped phytoplankton					
other chlorophyceae		0.058		0.006	
other bacillariophyceae		0.213		0.009	
other colonial cyanobacteria		0.102		0.004	
other cyanobacteria		0.405		0.013	
other dinophyceae		0.118		0.007	
other algae		0.468		0.057	

daily values. For each list, the order of each category by volume is given. For example, the category with the largest maximum volume is *Stephanodiscus niagarae*; it has the second largest mean based on non-zero abundance data, but is sixteenth in the presence list. Asterisks mark a group of conspicuous taxa (see Fig. 10).

	maximum	Percent order	mean	order	Occurrence present	order
Chlorophyceae						
<i>Botryococcus</i> spp.	61.9	16	9.4	7	6.5	32
* <i>Oocystis gigas</i>	92.1	5	17.9	5	29.5	23
<i>Oocystis</i> spp.	42.0	23	0.4	32	43.3	15
<i>Staurastrum paradoxum</i>	43.8	22	0.9	29	25.7	26
gelatinous colonial chlorophyceae	33.9	25	0.7	30	64.2	9
acicular chlorophyceae	76.2	10	0.3	34	79.1	5
Bacillariophyceae						
<i>Asterionella formosa</i>	52.2	18	3.7	14	70.4	7
* <i>Aulacoseira subarctica</i>	84.1	8	14.1	6	79.4	4
<i>A. italica</i> var. <i>tenuissima</i>	23.2	31	1.5	20	60.7	11
<i>Cyclotella ocellata</i>	6.6	34	0.4	33	34.2	21
<i>C. pseudostelligera</i>	6.3	35	0.2	35	38.8	18
<i>C. bodanica</i> +	29.6	28	1.8	19	14.8	31
* <i>Diatoma elongatum</i>	87.5	6	22.0	4	6.0	34
* <i>Fragilaria crotonensis</i>	92.5	4	8.5	8	82.3	3
<i>Melosira varians</i>	62.1	15	1.1	26	15.6	30
<i>Rhizosolenia eriensis</i>	66.3	13	1.0	28	33.9	22
* <i>Stephanodiscus niagarae</i>	92.8	3	38.1	2	41.4	16
<i>S. neoastraea</i> +	50.2	20	4.2	13	47.5	13
<i>S. hantzschii</i> +	11.4	32	1.0	27	28.8	24
<i>Synedra</i> spp.	28.8	29	1.1	24	76.9	6
<i>Synedra tenera</i>	10.5	33	1.1	25	19.2	29
* <i>Tabellaria fenestrata</i>	93.5	2	26.9	3	26.8	25
Chrysophyceae						
<i>Mallomonas</i> spp.	30.7	26	0.6	31	39.2	17
Cryptophyceae						
<i>Chroomonas minuta</i>	30.5	27	1.3	22	96.3	1
* <i>Cryptomonas</i> spp.	73.1	11	5.4	12	96.1	2
Dinophyceae						
<i>Ceratium hirundinella</i>	56.5	17	8.2	9	6.3	33
Cyanobacteria						
<i>Anabaena</i> spp.	83.2	9	6.6	11	65.2	8
<i>Aphanizomenon flos-aquae</i>	85.3	7	2.6	15	60.9	10
<i>Chroococcus limneticus</i>	24.1	30	2.3	16	20.3	27
<i>Coelosphaerium</i> spp.	44.9	21	1.1	23	37.7	19
<i>Microcystis aeruginosa</i>	63.2	14	1.4	21	19.4	28
* <i>Lyngbya limnetica</i>	52.0	19	2.1	17	51.3	12
* <i>Oscillatoria agardhii</i> +	98.9	1	50.8	1	46.1	14
<i>Pseudanabaena</i> sp.	38.1	24	1.8	18	4.1	35
* <i>Schizothrix calcicola</i>	68.8	12	7.1	10	35.9	20
Grouped phytoplankton						
other chlorophyceae	27.7		4.0		72.5	
other bacillariophyceae	40.3		1.1		90.2	
other colonial cyanobacteria	28.6		0.7		46.5	
other cyanobacteria	36.4		0.6		32.0	
other dinophyceae	31.8		0.6		34.8	
other algae	81.8		0.5		100.0	

and *Chroomonas* (26) are distinguished by somewhat bimodal long-term distributions, with relative scarcity in the 1970s. *Oocystis* spp. (2) and gelatinous greens (4) tended to be more abundant in later years. *Fragilaria crotonensis* (13) was more prominent during eutrophication than other taxa in this group and was somewhat erratic after diversion of the nutrient effluent. *Aulacoseira subarctica* (14) has been present every year, but made an especially important contribution to the spring flora in 1976. When *Stephanodiscus niagarae* (20) appears, it always dominates the phytoplankton because of its large cell size.

Group E (5, 8, 16, 29)

Inter-annual fluctuation of mean biovolumes are less pronounced than for Group D, but the two categories are similar other than in degree of variation. *Asterionella* (8) stands out for its large maxima in 1990 and 1996, quite different from its typical annual distribution. *Aphanizomenon* (29) also made an unusual burst of growth in 1988, and was the subject of a separate paper (EDMONDSON 1997).

Group F (3, 6, 15, 18, 25, 39)

These taxa have distributions that do not conform with other groups, exhibiting scattered peaks through the years of the study. *Aulacoseira italica* var. *tenuissima* (15) showed four periods of maximum abundance, decreasing in population size from 1966 to 1987. *Botryococcus* (6) and *Ceratium* (39) may be poorly estimated by the sampling methods because of their large sizes and numerical rarity.

Group G (7, 24, 37, 38, 40, 41)

This group includes all the "other" categories that are not represented by genus names. They do not have common patterns of occurrence, but are included as a group for completeness. Summed together, these taxa range from 1.3% in 1963 to 7.6% in 1979 of the total phytoplankton annually by volume.

Alternative grouping algorithms

We also examined the distributions and relationships among our original 41 taxonomic categories using various mathematical techniques, of which we will discuss two. The TWINSpan algorithm (HILL 1979) classifies data into a two-dimensional array, clustering species and samples by ordination of ranked taxa within the data set. Successive ordinations are performed by reciprocal averaging of percentage annual biovolume, and the results are divided into two groups each time (GAUCH 1982). Six groups were produced at the third division (Table 5). TWINSpan makes three groups that agree well with EDMONDSON's graphically-perceived Groups A, B and C, with some small variations. However, the other three TWINSpan divisions did not conform closely with the visual groupings, and separated the members of EDMONDSON's Groups D, E and F. Some taxa remained

Table 5. Comparisons among groups produced by visual inspection of graphs (WTE: see results section), TWINSpan and VARCLUS. Taxa marked by asterisk in the VARCLUS groups indicate a relatively poor fit with that group.

35 categories: names	#	WTE	TWINSpan		VARCLUS	
<i>Rhizosolenia eriensies</i>	17	A	33	A	17	A
<i>Anabaena</i> spp.	28	A	34	A	20	D
<i>Lyngbya limnetica</i>	33	A	36	A	28	A *
<i>Oscillatoria agardhii</i> +	34	A			33	A
<i>Oscillatoria</i> sp.	36	A	1	B	34	A
			19	B	36	A
<i>Oocystis gigas</i>	1	B	22	B		
<i>Cyclotella pseudostelligera</i> +	9	B	23	B	18	F
<i>Stephanodiscus hantzschii</i> +	19	B	30	B	22	B
<i>Synedra tenera</i>	22	B	31	B	31	B
<i>Tabellaria fenestrata</i>	23	B	32	B	32	B *
<i>Chroococcus limneticus</i>	30	B				
<i>Coelosphaerium</i> spp.	31	B	11	C	8	E
<i>Microcystis aeruginosa</i>	32	B	17	A	19	B
			21	C	23	B
<i>Cyclotella bodanica</i> +	10	C	35	C		
<i>Cyclotella ocellata</i>	11	C			10	C
<i>Diatoma elongatum</i>	12	C	2	D	11	C
<i>Synedra</i> spp.	21	C	5	E	12	C
<i>Pseudanabaena</i> sp.	35	C	6	F	21	C
			12	C	35	C
<i>Oocystis</i> spp.	2	D	14	D		
gelatinous chlorophytes	4	D	16	E	1	B *
<i>Fragilaria crotonensis</i>	13	D	18	F		
<i>Aulacoseira subarctica</i>	14	D	26	D	26	D
<i>Stephanodiscus niagarae</i>	20	D	27	D	27	D
<i>Chroomonas minuta</i>	26	D	28	A	30	B *
<i>Cryptomonas</i> spp.	27	D				
			3	F	2	D
acicular chlorophytes	5	E	4	D	5	E
<i>Asterionella formosa</i>	8	E	8	E	6	F
<i>Melosira varians</i>	16	E	13	D	13	D *
<i>Aphanizomenon flos-aquae</i>	29	E	15	F	14	D
			20	D	15	F
<i>Staurastrum paradoxum</i>	3	F	29	E		
<i>Botryococcus</i> spp.	6	F			3	F *
<i>Aulacoseira italica</i> var. <i>tenuissima</i>	15	F	9	B	4	D
<i>Stephanodiscus neostraea</i> +	18	F	10	C	9	B
<i>Mallomonas</i> spp.	25	F	25	F	16	E
<i>Ceratium hirundinella</i>	39	F	39	F	29	E
					39	F

together, such as 2, 14, 26, and 27, but others were classified very differently by the TWINSpan multivariate analysis.

Principal component cluster analysis (VARCLUS, JOYNER 1985) splits clusters progressively using the goodness of fit of members within a cluster produced by grouping taxa along axes defined by correlation. At 7 clusters, an estimated 57% of the variation was explained. There was little gained by additional splitting. The defined groups again were somewhat different from graphical and TWINSpan analysis (Table 5). Visual Groups A and C were again separated consistently, but EDMONDSON's Group B was split into different clusters. There was no strong coherence within groups D, E, and F, similar to results by TWINSpan.

Each of these three methods categorized the same data differently and produced different groupings, yet there were some similarities among results. To some extent they represent extremes in the ways that the biovolume data could be compared (e.g., by correlation coefficients or by fraction of total). Disparities trace in part to the subjectivity and flexibility (hence, non-linearity) of EDMONDSON's visual assessments and judgments about the extent and importance of long periods of erratic occurrences of small populations, whereas the formal statistical methods we used are more rigid and circumscribed, but they are not so responsive to non-linear patterns.

Grouping years by phytoplankton patterns

Limnologists who conduct long-term limnological studies will remember certain years as outstanding because of floods or unusual weather conditions. Similar years can become grouped together in memory. Likewise, some years are memorable because of unusual conditions in the plankton. In the preceding section, we showed that algal species could be categorized variously according to their temporal occurrence. By the same token, years can also be grouped by reference to phytoplankton communities.

We used the same statistical methods, TWINSpan and VARCLUS, to group years by comparing phytoplankton populations, and each produced 8 clusters (Table 6). The clusters and their component years are ordered chronologically where possible. Both methods segregated out the years 1962 to 1970 in sequence, although the years were somewhat differently aggregated. After that, years or blocks of years are segregated differently and assigned to various groups by the two algorithms. After the appearance of *Daphnia*, clusters of years are no longer sequential. The years 1976, 1981–83, 1987, and 1990 appear to belong together, as do 1977–78 with 1980, 1988, and 1992. When graphs of phytoplankton percent biovolumes for each year are placed in groups defined by TWINSpan (Fig. 11), the similarities of key categories that define the groups can easily be seen.

ERAS		TWINSPAN		VARCLUS				
#	year	#	year	#	year			
1	1962	1	1962	1	1962			
	1963		1963		1963			
	1964		1964		1964			
	1965		1965		1965			
	1966		1966		1966			
	1967		1967		1967			
	1968		1968		1968			
		2	1968		1969			
2	1969	3	1969	2	1970			
	1970				1972			
	1971		4		1970	3	1973	
	1972				1971		1975	
	1973				1972			
	1974				1973			
	1975				5	1974	4	1977
			1975			1978		
	1976	1988						
		1992						
3	1976	6	1977	5	1971			
	1977		1981		1985			
	1978		1982		1986			
	1979		1983		1989			
	1980		1986		1991			
	1981		1987		1993			
	1982		1989		1994			
	1983		1990		1995			
	1984		1991					
	1985		1992		6	1976		
	1986		1993			1981		
	1987		1994			1982		
	1988					1983		
	1989		7		1978		1987	
	1990				1979	1990		
	1991				1980			
	1992				1984	7	1974	
	1993				1985		1979	
	1994				1988		1980	
	1995				1995		1984	
	1996				1996	1997		
	1997		1997		1999			
	1998		1998					
	1999		1999		8	1996		
		1998						

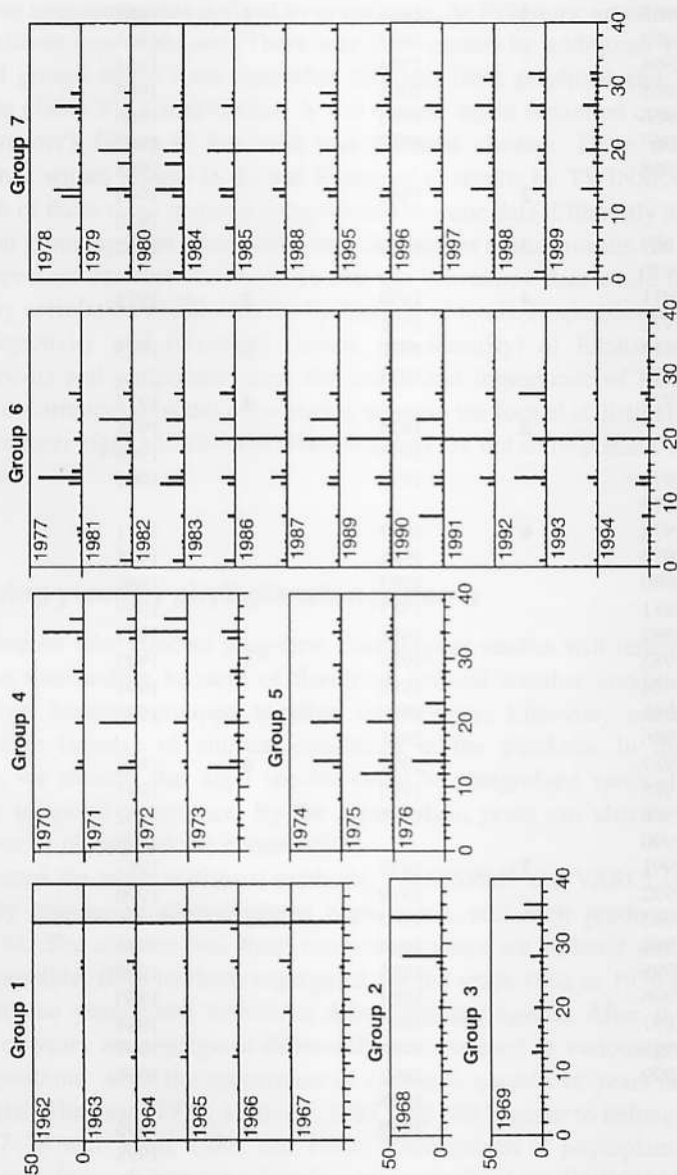


Fig. 11. Annual percent abundance of 35 independent phytoplankton taxa (i.e., taxa identified in Table 7), arranged by groups from TWINSpan analysis. Each panel represents a year, with the identifying category number on the X-axis and the percent abundance represented by the Y-axis.

Peak populations

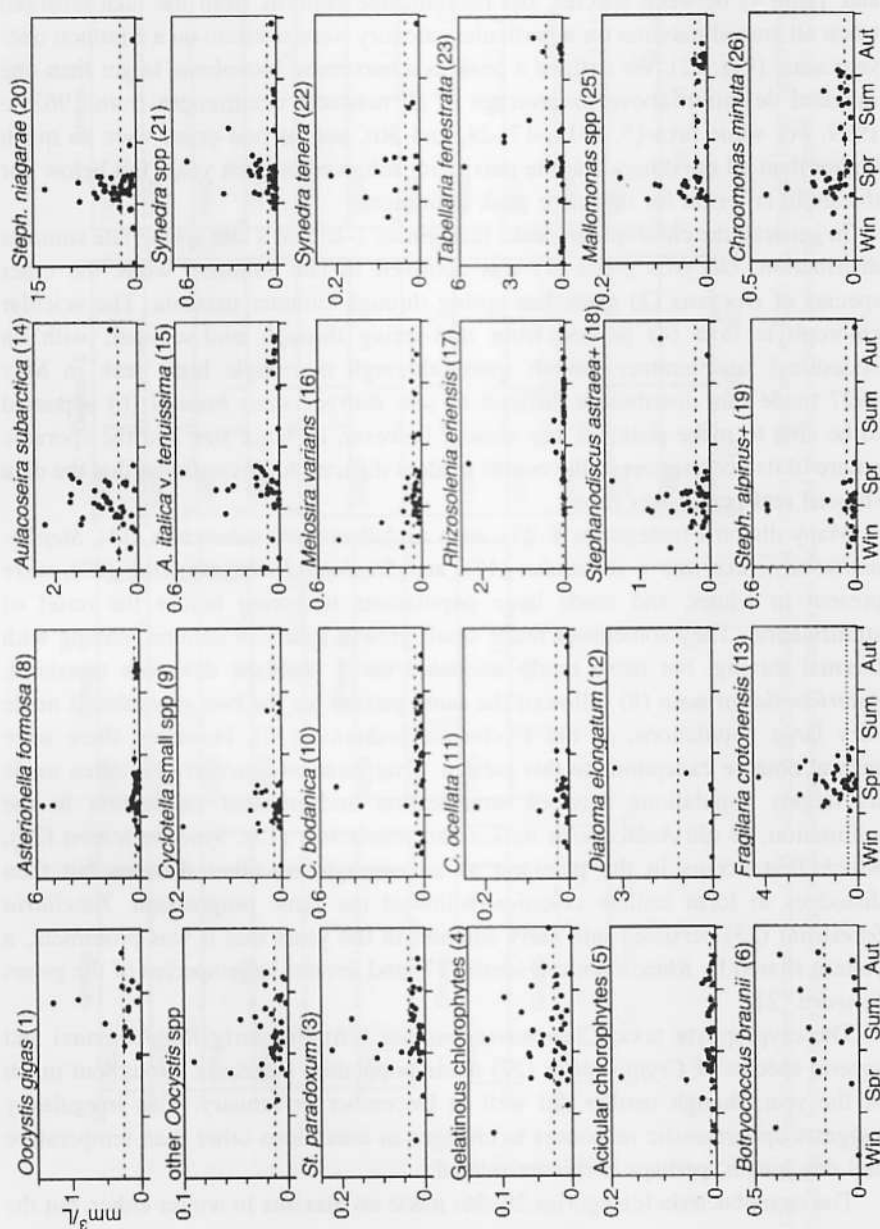
Many species have an annual peak in abundance, often seasonally predictable (Fig. 10), indicating a high growth rate, a prolonged period of slower growth, or both, but which always suggests favorable conditions for that species before the maximum. Maximal biovolumes differed greatly in size and timing (see Fig. 10 and Table 4) between species, but recognizable patterns from the lake emerged when all annual maxima for a particular category were overlain on a common one-year scale (Fig. 12). We defined a peak as a maximum biovolume larger than one standard deviation above the average of all non-zero occurrences from 1962 to 1999. For some taxa (5, 8–11, 17, 28, and 30), one or two years were so much higher than all the others that the maximum achieved in most years fell below our threshold criterion for objective peak definition.

In general, the chlorophyte peaks (categories 1–6) had a late spring/late summer distribution. *Oocystis gigas* (1) was confined to late summer, while the other species of *Oocystis* (2) made late spring through summer maxima. The acicular chlorophyte taxa (4) peaked from mid-spring through mid-summer, with an occasional late summer growth spurt, although the single high peak in May 1977 made this distribution difficult to see. *Botryococcus braunii* (6) appeared to be able to make peaks in any season; however, its large size and the sporadic nature of its occurrences in the counts made it difficult to be confident that the data showed real peaks over time.

Many diatoms (categories 8–23), such as *Aulacoseira subarctica* (14), *Stephanodiscus neoastraea* + *minutulus* (18), and *Stephanodiscus niagarae* (20), were present in winter, and made large populations in spring before the onset of stratification. They sometimes made small growth spurts in autumn, ending with thermal mixing, but these rarely exceeded the 1 standard deviation threshold. *Asterionella formosa* (8) followed the same pattern for the two years that it made very large populations, as did *Cyclotella bodanica* (10). However, there were several notable exceptions to this pattern. *Fragilaria crotonensis* (14) often made its largest populations between stratification and nutrient exhaustion in the epilimnion, as did *Aulacoseira italica* var. *tenuissima* (15). *Synedra tenera* (22), which first occurs in the plankton as an epiphyte on other diatoms but then dislodges to form stellate colonies, followed the same progression. *Tabellaria fenestrata* (23) persisted into early summer in the years that it was prominent, a pattern shared by *Rhizosolenia eriensis* (17) and several large species of the genus *Synedra* (21).

The cryptophyte taxa, *Chroomonas minuta* (26) (formerly *Rhodomonas*) and several species of *Cryptomonas* (27) made population increases throughout much of the year, though neither did well in December or January. This irregularity suggests opportunistic responses to changes in conditions other than temperature and day length, perhaps herbivore-related.

The cyanobacteria (categories 28–36) made no maxima in winter either, but the



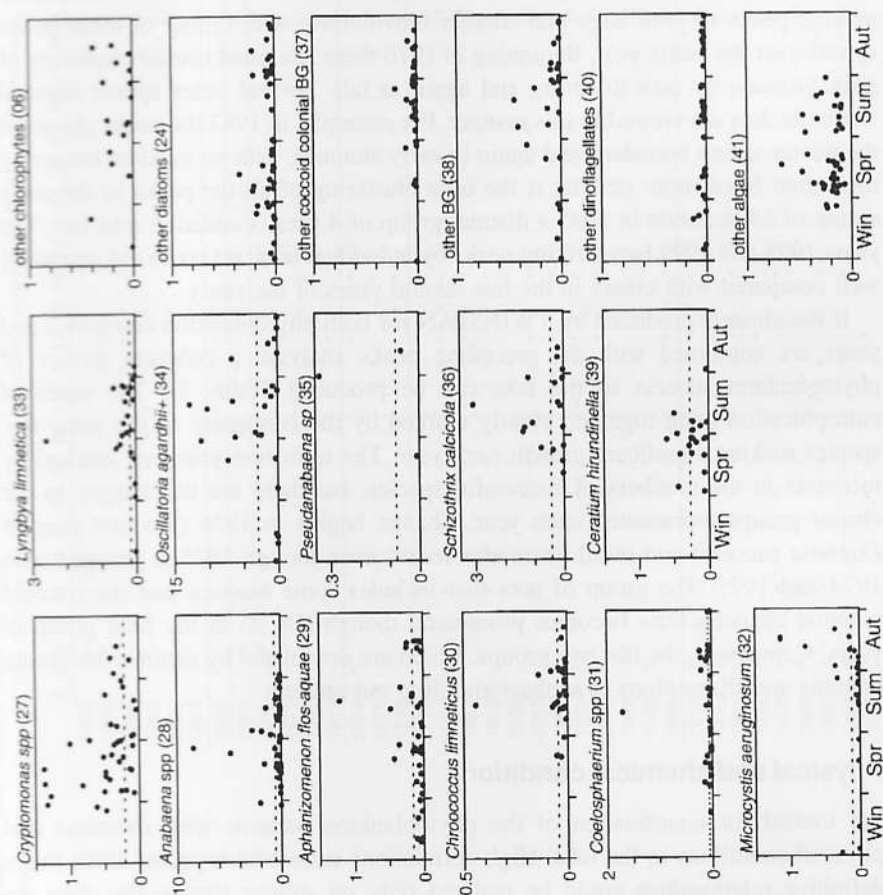


Fig. 12. Maximum annual abundances of 41 individual taxa and aggregations expressed in mm^3/l plotted by the day of the year on which each annual maximum was achieved. "Win" = Jan to Mar; "Spr" = Apr to Jun; "Sum" = Jul to Sep; "Aut" = Oct to Dec. The dotted horizontal line is 1 standard deviation above the mean of all occurrences.

largest populations occurred in summer, except for *Microcystis aeruginosa* (32) which made sizeable populations in mid to late fall just before thermal mixing. The timing of the peak *Oscillatoria* populations actually varied a great deal from year to year anytime from May (1968) to late October (1965). However, some of this variation could be due to the buoyancy of the filaments and wind conditions just before sampling.

Ceratium hirundinella, the lone dinoflagellate to make sizeable populations in Lake Washington, made maximal populations in late spring to early summer, approximately the same period of time as *Fragilaria crotonensis*.

Another way to look at the success of the different taxa is to group the data by years to show the magnitudes and seasonal distribution of peak productivity by different taxa over time (Fig. 13), using a logarithmic scale. When this is done, the years of eutrophication are seen to have had relatively few species able to make large populations, and these population peaks occurred in late spring through summer. All the species identified had the ability to make very large biovolumes. In the years following diversion, larger numbers of taxa were successful, making peaks of both large and smaller biovolumes, with timing of these peaks spread over the entire year. Beginning in 1976 there is a trend toward clustering of peak biomass by taxa in spring and again in fall. Several years appear unusual when the data are viewed in this manner. For example, in 1983 the peaks cluster at the winter-spring boundary and again in early summer, with no maxima occurring thereafter. Even more striking is the tight clustering of all the peaks in the early spring of 1994, while in 1995 a distinct group of 4 taxa is added in mid-fall. The years 1998 and 1999 lack striking peaks by individual taxa; no taxon did unusually well compared with others in the last several years of the study.

If the clusters produced by TWINSpan for both phytoplankton categories and years are combined with the preceding peaks analysis, a coherent picture of phytoplankton success in the lake can be produced (Table 7). The years of eutrophication hang together, clearly marked by the continuity of the same few species making significant growth each year. The transition years are marked by increases in the numbers of successful species, but there are no changes in the cluster groups represented each year. Change begins in 1976 (the first year of *Daphnia* success) and in all years afterwards, even though 1976 is grouped with 1974 and 1975. The group of taxa that includes some diatoms and the coccoid colonial cyanobacteria becomes prominent, though less so in the final group of years. Conversely, the last two groups, which are dominated by summer-blooming diatoms and filamentous cyanobacteria, drop out entirely.

Physical and chemical conditions

We looked for coordination of the phytoplankton patterns with chemical and physical conditions in the lake. High correlations cannot be expected since many definitive relationships could be realized only on shorter time scales than we

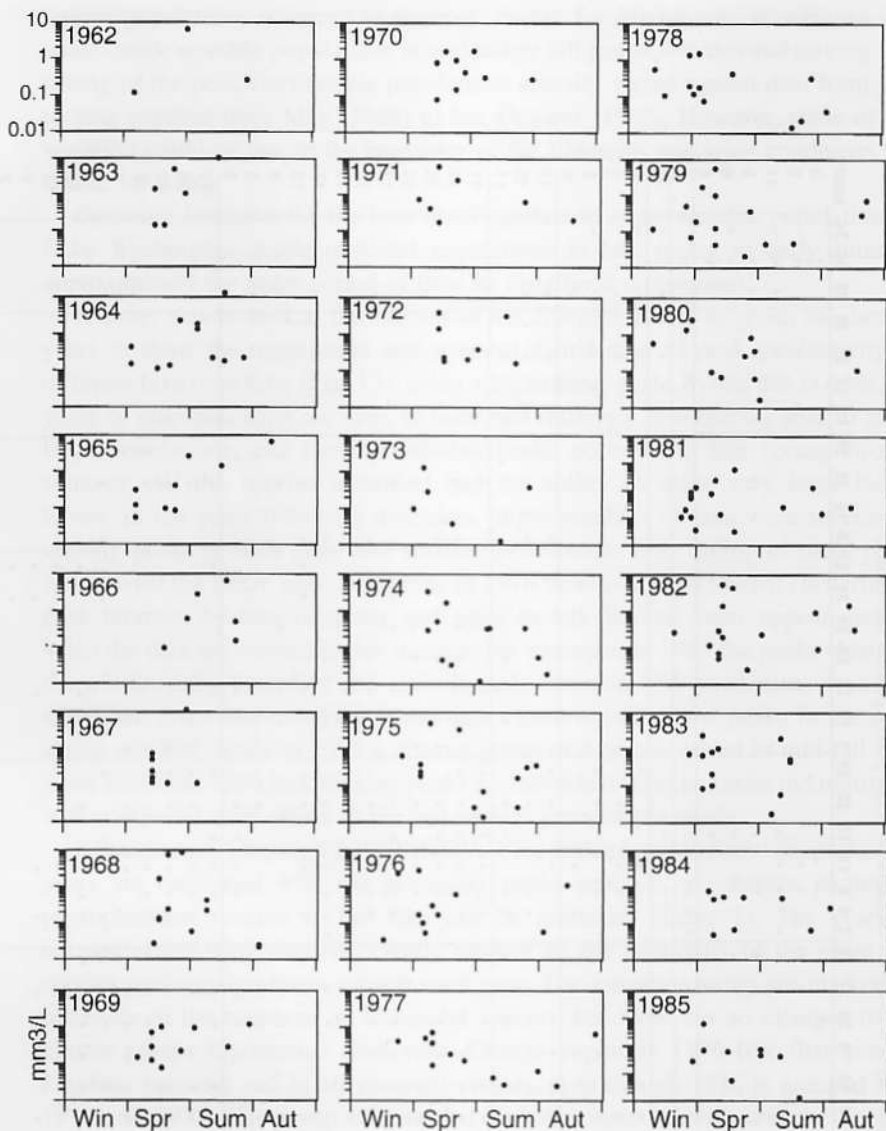


Fig. 13. Biovolume maxima for taxa that exhibited maximal abundance more than 1 standard deviation above their long-term mean (see Fig. 12). Data are shown by year according to the date in any given year when a maximum was attained. "Win" = Jan to Mar; "Spr" = Apr to Jun; "Sum" = Jul to Sep; "Aut" = Oct to Dec. The Y-axis is in mm³/L on a logarithmic scale.

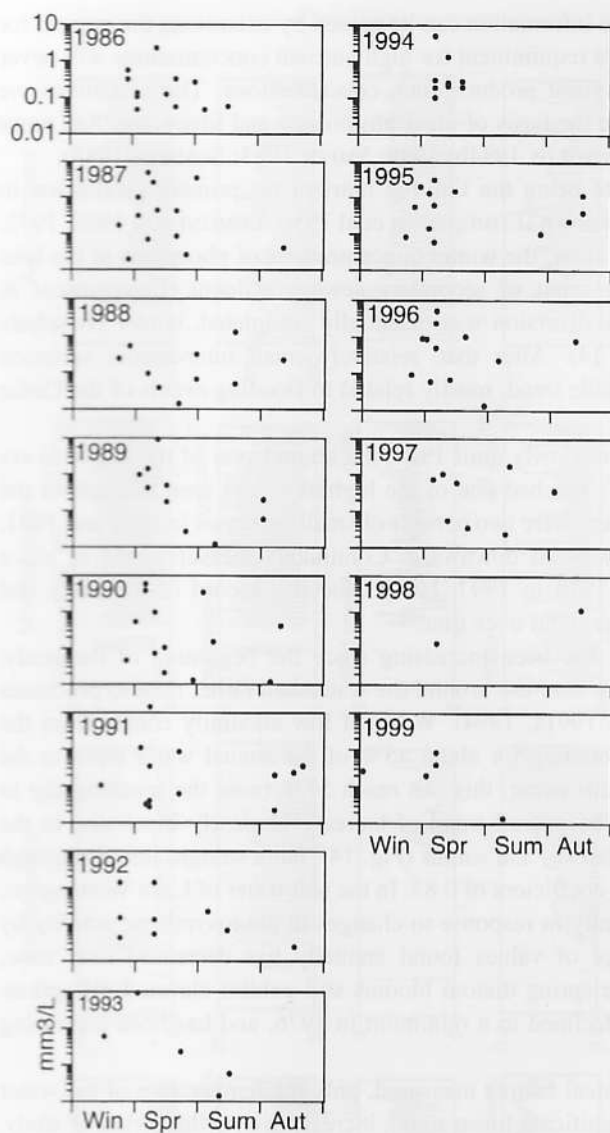


Fig. 13, continued.

measured. However, some information can be gained by examining the record; for example, organisms with a requirement for high nutrient concentrations will never thrive in a lake that does not produce such concentrations. The conditions we examined were chosen on the basis of algal physiology and lifecycles (AHLGREN 1977; KILHAM 1986; REYNOLDS 1984b, 1989; SMITH 1983; SOMMER 1988).

The case for phosphate being the limiting nutrient for primary production in Lake Washington is well known (EDMONDSON et al 1956; EDMONDSON 1969, 1972, 1991b). During eutrophication, the winter concentrations of phosphate in the lake depended largely on the input of secondary sewage effluent (EDMONDSON & LEHMAN 1981) and, once diversion was essentially completed, winter phosphate decreased quickly (Fig. 14). After that, relatively small inter-annual variation occurred with no discernable trend, mostly related to flooding events of the Cedar River.

Nitrates decreased more slowly until 1977, the second year of the *Daphnia* era when cladoceran numbers reached one of the highest values seen throughout the whole study. After that there were two periods of small increases in 1982 and 1991, but the trend overall continued downward. Continuous measurements of silica were available only for 1978 to 1997, but produced a record of increases and decreases with no obvious trend over time.

Alkalinity in the lake has been increasing since the beginning of the study, related more to changes in land use around the watershed rather than to processes in the lake (EDMONDSON 1991a, 1994). Water of low alkalinity comes from the Cedar River, usually accounting for about 45% of the annual water input to the lake. However, when floods occur, this can reach 57% (note the resulting dip in alkalinity in 1990–91). The overall trend of increase is clearly illustrated in the annual plot, with some plateaus and surges (Fig. 14), but a straight line fit through the data had a correlation coefficient of 0.83. In the soft water of Lake Washington, surface pH varies seasonally in response to changes in photosynthetic activity by phytoplankton. The range of values found annually has decreased over time, although years with large spring diatom blooms still exhibit elevated pH spikes. The annual average pH declined to a minimum in 1976, and has been increasing slowly since.

Of all the various physical factors measured, only the temperature of the water at 5 m depth showed a significant linear trend, increasing over the period of study. The linear regression had a correlation coefficient of 0.49. The value at 5 m was considered representative of epilimnetic water temperature. Other variables showed year to year variation, but no trends. Solar radiation data in the last years of the study may be underestimated due to equipment problems at the UW Atmospheric Sciences Department where it was measured. The lower wind velocities in 1965–68 affected thermal mixing and had biological consequences (EDMONDSON 1988). Wind velocity was also lower during the outburst of *Aphanizomenon* in 1988 (EDMONDSON 1997).

The most easily observed coordination occurs between the high concentrations

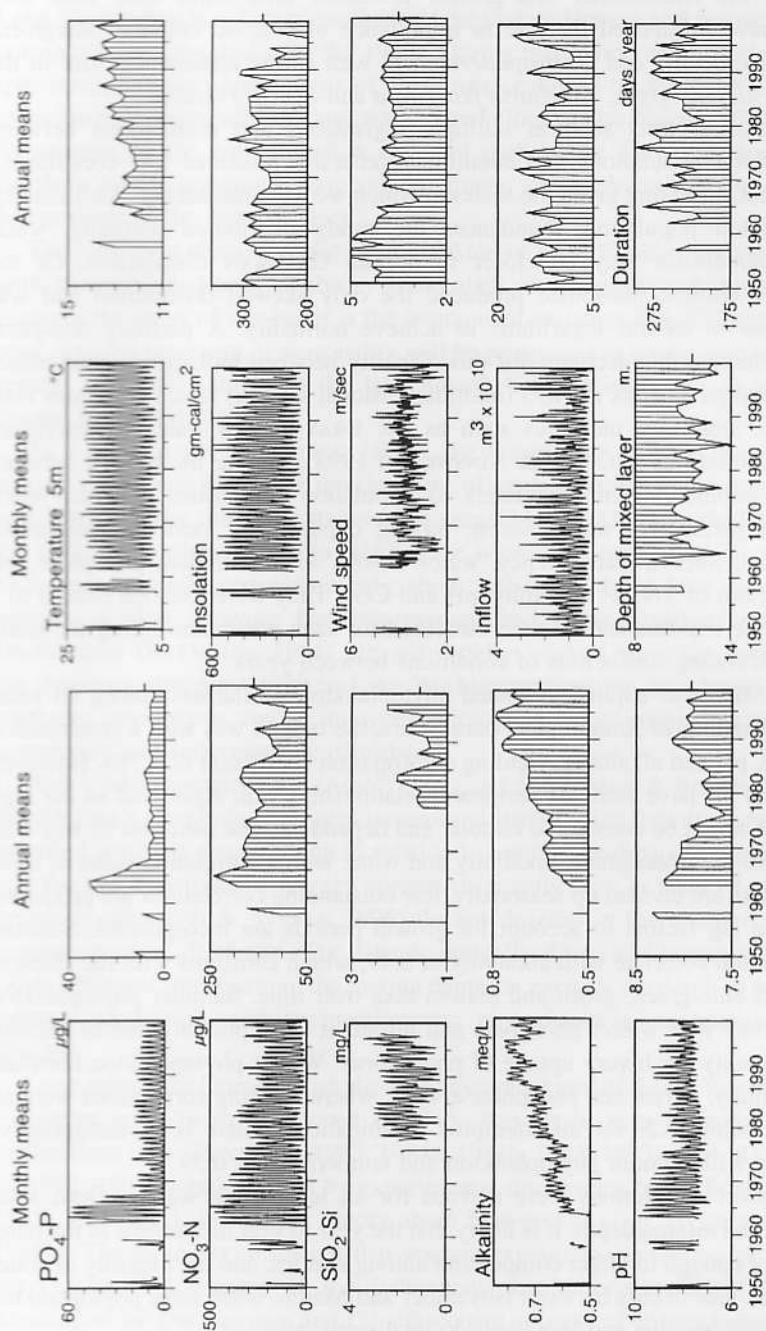


Fig. 14. Chemical and physical data plotted as monthly and annual averages, except for depth of the mixed layer and its duration, which are both annual values. The horizontal ties to the right of each annual plot mark the average for the period 1962–1999. Units of measure are given above the monthly graphs.

of phosphate in the eutrophication era and EDMONDSON's algal Group A, in particular the filamentous blue-greens. Increased alkalinities over time may perhaps have influenced the rise in importance of coccoid colonial bluegreens such as *Microcystis* and *Coelosphaerium*, as well as the appearances late in the study of *Oocystis gigas*, *Tabellaria fenestrata* and *Synedra tenera*.

Mathematical tests such as multiple regressions and correlations between phytoplankton populations and conditions generally produced low coefficients, which is not surprising given the scales at which we were measuring. Additionally, phytoplankton population abundances are rarely distributed normally, while physical conditions may be closer to normal GAUSSIAN distribution. Of the parameters chosen, phosphate produced the only skewed distribution and was transformed to natural logarithms to achieve normality. A partially non-parametric technique that accounts for this disparity between biological communities and physical parameters is MDS (multidimensional scaling) which correlates non-parametric similarity measures such as the BRAY-CURTIS index to Euclidean distance similarities (CLARKE & AINSWORTH 1993), finding the best fit between various combinations of parameters to population similarities between years. Seventeen parameters were chosen: mixing depth, wind velocity, epilimnetic temperature, SECCHI transparency, water inflow, solar radiation, phosphate, nitrate, the ratio of TN:TP, alkalinity, pH and CO₂. They were rescaled from 0 to 1 based on the maxima and minima measured for each parameter during the study before calculating similarities of conditions between years.

When MDS was applied to annual phytoplankton similarities among all years and combinations of limnological parameters, the best fit was with a combination of SECCHI, pH and alkalinity, yielding a correlation coefficient of 0.784. However, SECCHI and pH have complex reciprocal relationships with algae, and so the high correlation might be considered circular and dependent. The next best fit was with a combination of phosphate, alkalinity and wind, with a correlation value of 0.48.

If the data are divided up seasonally, few outstanding correlations are produced, even when lag factors to account for growth periods are incorporated. Summer phytoplankton correlate with alkalinity at 0.49, which conforms with the changes in coccoid blue-green, green and diatom taxa over time. Summer phytoplankton also correlate with winter phosphate and nitrate at 0.56, possibly due to *Oscillatoria*'s capacity for luxury uptake of phosphorus. Winter phytoplankton correlate with alkalinity, nitrate and phosphate at 0.42, whereas spring correlations were all very low, below 0.20 for all attempted combinations. There is an unimpressive correlation with autumn phytoplankton and temperature at 0.39.

Low direct correlations were derived for all tests using water inflow, solar radiation, and mixing depth. It is likely that the year to year differences in the latter two are not enough to affect competition among species, and the majority of water input to the lake occurs between November and March, when most phytoplankton are relatively inactive and less likely to be directly affected.

Discussion

Lake Washington is a diatom-producing lake that underwent and recovered from a eutrophication episode during the 1960s. During that temporary episode, its native (pre-eutrophication) populations of algae were eclipsed by mass development of cyanobacteria, especially shallow-water populations of *Oscillatoria* (*Planktothrix*). Subsequent to the eutrophication era, and particularly after the emergence of *Daphnia* as an important zooplankton grazer, chlorophytes became important components of the summer flora.

The long-term changes in the phytoplankton of Lake Washington are consistent with an established body of theory about algal communities and their dynamics. Because the focus of this paper is the interannual variation and differences among eras, detailed treatment of seasonality will be postponed to a later report, but some regular seasonal features of the lake nonetheless are important to review and discuss at this time.

As a deep, warm monomictic lake, Lake Washington exhibits ice-free winter mixing conditions that favor development of centric diatoms, and these diatoms typically comprise the initial stages of its vernal bloom. Although the lake receives the bulk of its tributary flushing during the winter mixing period, the water load each year typically constitutes only about one-third of the lake volume. Thus inocula of slow growing but loss-resistant and photo-adaptive taxa such as *Oscillatoria* (REYNOLDS 1994) are not rapidly washed from the lake. Instead, the dynamics that played out in Lake Washington over the decades of this study represent interactions among autogenic biological forces resonating to physical seasonality and anthropogenic disturbance.

With a lake geometry ratio ($\text{Area}^{0.25}/Z_{\text{max}} = 1.5$; GORHAM & BOYCE 1989) Lake Washington's morphology ensures its seasonal stratification, but the duration of the stratified period is short enough in relation to nutrient loading and productivity so that the low hypolimnetic oxygen conditions usually seen in lakes of comparable geometry (HONDZO & STEFAN 1996) do not develop in the absence of anthropogenic nutrient discharge. The lake is optically deep, as illustrated by Fig. 8. During thermal stratification, the mixing depth far exceeds the depth of positive net primary production, and so metalimnetic phytoplankton communities do not develop.

Long-term developments within the phytoplankton of Lake Washington are consistent with theory developed by C. S. REYNOLDS in a series of insightful publications (e.g., REYNOLDS 1983, 1984a, 1984b, 1988, 1993, 1994; REYNOLDS et al. 1982, 1993) supplemented by experimental discoveries by U. SOMMER (1983, 1985, 1988, 1991) and recent theory about blue-greens (e.g., HYENSTRAND et al. 1998b). The basic circumstances that warrant explanation in theory for this paper are (1) variable success of the indigenous diatom community, (2) episodic domination by *Oscillatoria*, and (3) subsequent success of chlorophytes.

Diatoms

Lake Washington's perennial diatoms, *Aulacoseira subarctica*, *Stephanodiscus niagarae*, and *Fragilaria crotonensis* are prototypical members of what REYNOLDS (1984b) originally classified as "Group II" species (later termed "R" species; REYNOLDS 1988), which are characterized by large individual cells or colonies, elongated in one or two axial dimensions, and well tolerant of strong physical mixing. They are successful at low light and low temperature (TALLING 1957; WILLÉN 1991), thus accounting for their persistence through the winter and their emergence as dominant species at the start of each year (Fig. 4). However, these diatoms are susceptible to rapid elimination in the late spring owing to diminution of the thermal mixed layer, combined with accelerated sinking losses caused by aggregation and photoinhibition (REYNOLDS 1989).

Other diatoms of significance in the lake fall into two categories based on their temporal occurrence: (1) those that exhibited success during the eutrophication and recovery eras (*Rhizosolenia eriensis*, *Cyclotella bodanica*, *Cyclotella ocellata*, *Diatoma elongatum*, and *Synedra* spp.), and (2) those that emerged after recovery from eutrophication and at about the time of establishment of *Daphnia* in the lake (*Cyclotella pseudostelligera*, *Stephanodiscus hantzschii*, *Synedra tenera*, and *Tabellaria fenestrata*). All, except for *Tabellaria* and *Synedra tenera*, occur as single cells and they are smaller and appear less heavily silicified than the perennial winter diatoms. They persist well into the period of thermal stratification and they thus experience the twin stresses of nutrient limitation and zooplankton grazing.

Although the biomass-limiting nutrient for Lake Washington was firmly established as phosphorus (EDMONDSON 1969, 1970, 1972), the relative and changing proportions of other elements, such as N and Si, may have had profound influences on species composition of the developing biomass annually. During the eutrophication era, the ratio of Total N to Total P fell to values of 10 or lower by mass (Fig. 15), or well within the range that SMITH (1983) identified as conducive to cyanobacterial dominance. Of equal importance, there is evidence of modern differential depletion of SRSi with respect to both $\text{NO}_3\text{-N}$ and SRP each spring (Fig. 15). Si:P ratios now regularly fall below 200 (by mass or by moles) on a seasonal basis, which is well into the range that SOMMER (1988) identified experimentally as placing most diatoms at a competitive disadvantage with respect to chlorophytes.

Routine measurements of SRSi did not commence until 1978, so concentrations during eutrophication and recovery are not documented directly. Peak diatom biomass during the eutrophication era was lower than in most subsequent years (Fig. 4) despite elevated phytoplankton biomass overall. It is likely therefore that differential depletion of SRSi with respect to N and P was less extreme during eutrophication than in recent years. This proposition is consistent with the chemical determinations conducted by J. SHAPIRO in 1957 and 1958 during

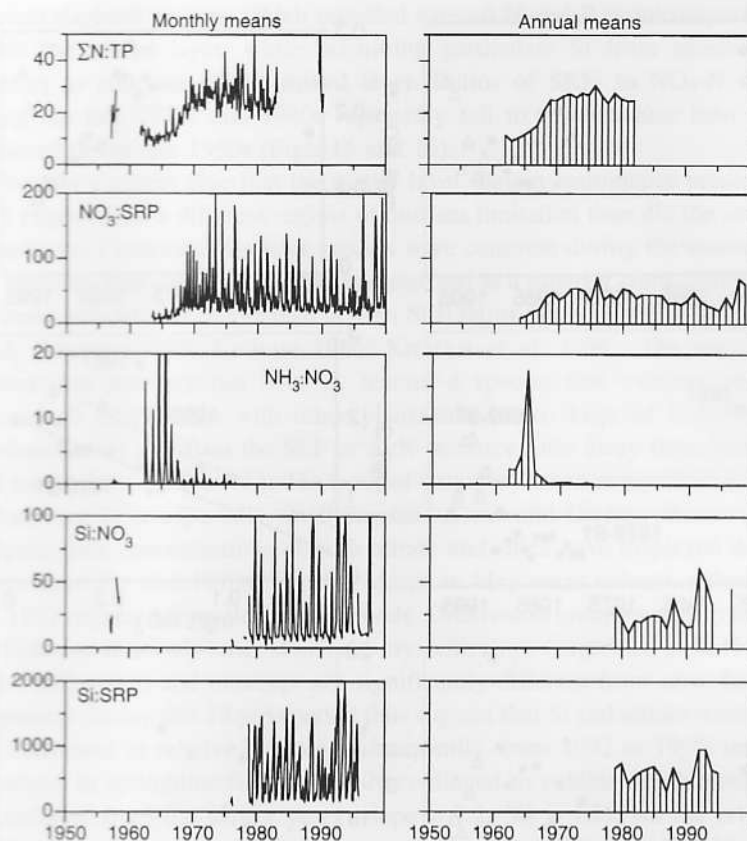


Fig. 15. Ratios of some chemical parameters plotted in the same fashion as Fig. 14. Analytical zeros for parameters in the denominator were set to the minimum detection level to calculate the ratio. ΣN is the sum of total Kjeldahl nitrogen and NO_3^- .

eutrophication. At that time, the lowest $\text{SRSi:NO}_3\text{-N}$ ratio encountered was 9 by mass, but ratios typically ranged from 40 to 140 during thermal stratification. SRP was not yet being measured in those years. Comparison with data in Figs. 15 and 16 illustrates that silica depletion relative to N was not a plausible concern at that time, and SRSi levels remained above 2 mg/l during the spring. Indeed, SHAPIRO's findings were the logical basis for originally excluding SRSi from the suite of measured lake parameters during the eutrophication era.

With the rise of *Daphnia* as an important planktonic herbivore in the mid-1970s it might seem reasonable to expect conspicuous changes in the diatom community resulting from grazing. However, cell sizes of diatom taxa that persisted in the thermal mixed layer during eutrophication and recovery compared with those that replaced them after 1975 are not consistent with an hypothesis that size-selective

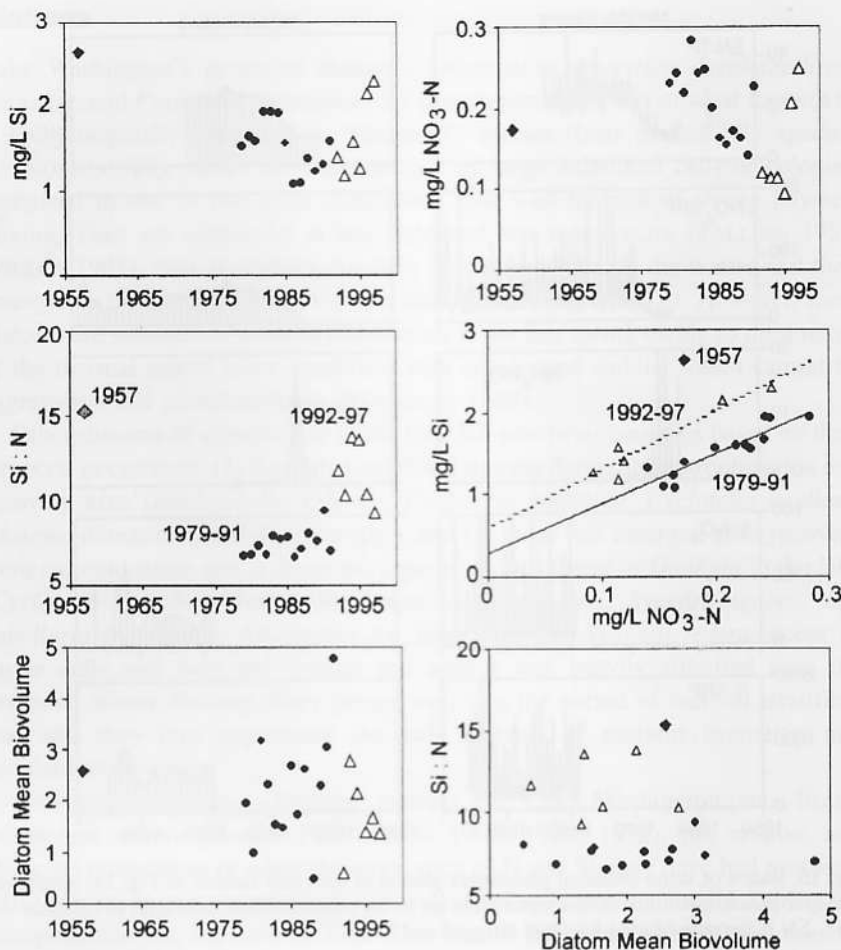


Fig. 16. Mean values from March to May of surface soluble reactive silica as Si (mg/l), NO₃-N (mg/l), and their ratio by mass compared with diatom biovolume (mm³/l). Symbols represent 3 time periods: 1957, 1979–91, and 1992–97. A: mean SRSi by year. B: mean NO₃-N by year. C: mass ratio Si:N by year. D: SRSi plotted against NO₃-N for each year with regression lines drawn through 1979–91 ($r^2 = 0.83$) and 1992–97 ($r^2 = 0.92$). E: diatom mean biovolume by year. F: Si:N plotted against diatom mean biovolume for each year.

grazing was the operative mechanism for community change. Many single-celled taxa of sizes presumed to be accessible to herbivorous zooplankton persisted with the change in grazers. Rather, the species replacements are more consistent with the idea that wholesale diatom community replacement during stratification occurred along Si:P or Si:N temporal gradients. Accelerated depletion of epilimnetic SRSi probably commenced during the recovery from eutrophication, as diatom biomass rebounded. Silica depletion then culminated with the rise of

efficient daphnid grazers, which recycled egested N and P as uncompacted feces within the mixed layer, while permitting particulate Si from egested diatom frustules to sink out of the mixed layer. Ratios of SRSi to $\text{NO}_3\text{-N}$ measured during the late 1970s and 1980s repeatedly fell to lower values than anything measured in the late 1950s (Figs. 15 and 16).

There is a potent clue that the mixed layer diatom community present before 1975 experienced a different regime of nutrient limitation than did the subsequent assemblage. Planktonic *Synedra* species were common during the eutrophication and recovery eras. *Synedra* is well-characterized as a superior competitor for P, and a prime candidate for dominance at high Si/P ratios (TILMAN 1981; TILMAN et al. 1982; SOMMER 1985; KILHAM 1986; KILHAM et al. 1986). The only *Synedra* present post-recovery has been *S. tenera*, a species that exhibits an unusual commensal relationship with other planktonic forms. Loss of *Synedra* spp. is consistent with a shift in the Si:P or Si:N resource ratio away from favoring the best competitors for P or N and in favor of stronger diatom competitors for Si such as *Asterionella* or especially small *Stephanodiscus* and *Cyclostephanos* species.

Springtime concentrations of both nitrate and silica have displayed downward trends since the mid-1970s (Fig. 16, March to May mean values), although 1996 and 1997 departed from the overall trends. Differences among years from 1979 to 1991 obeyed relatively strict stoichiometry, with slope (expressed as Si:N by mass) of 6.1 (SE = 0.8) and intercept not significantly different from zero. Interannual differences during this 13 year period thus suggest that Si and nitrate were supplied and consumed in relative balance. Subsequently, from 1992 to 1997, interannual variations in springtime Si and $\text{NO}_3\text{-N}$ continued to exhibit stoichiometry indistinguishable from the earlier years (slope = 7.2, SE = 1.1), but the relationship exhibited a significant positive intercept (0.56 mg/l Si, SE = 0.17). This suggests the re-emergence of a situation in which Si concentrations remain in relative excess of nitrate during peak spring bloom conditions. The years 1992 to 1997 are characterized by elevated Si:N ratios compared with 1979 to 1991, and in this respect lake conditions are becoming more similar to 1957. This situation may portend further changes in the diatom species assemblage toward species with greater efficiency of nitrate utilization.

Cyanobacteria

Long-term changes in the cyanobacteria community of Lake Washington are the main cause of this lake's reputation in the annals of eutrophication problem-solving. It is particularly noteworthy that the dominant taxon during eutrophication was *Oscillatoria agardhii*, not itself an acknowledged N-fixer, although *Anabaena* species were subdominant and abundant (Fig. 10). After the emergence of *Daphnia* in 1976, globose colonies of *Chroococcus limneticus* and *Coelosphaerium* established themselves during summer, albeit at low absolute biomass levels, and they have been joined occasionally by *Microcystis aeruginosa*.

Colonial coccoid cyanobacteria (Chroococcales) do not produce heterocysts, although non-heterocystous cyanobacteria, including *Oscillatoria*, can fix N in the dark when there is no production of nitrogenase-disabling O_2 by photosynthesis, or in the light by spatial separation between aerobic and anerobic portions of colonies or by temporal separation of photosynthesis and N fixation in different phases of the cell cycle (CARPENTER & PRICE 1976; STAL & KRUMBEIN 1985; MITSUI et al. 1986).

Presence of cyanobacteria in Lake Washington, and especially the presence of N-fixing *Anabaena* during eutrophication, are fully consistent with the low ratios of TN:TP present year round in the lake at that time (Fig. 15). Modern theory about factors which determine success of cyanobacteria (HYENSTRAND et al. 1998b) identifies nine different elements that each may contribute to observed patterns. Following HYENSTRAND et al., these are:

1. cyanobacteria are favored at low ratios of TN to TP;
2. cyanobacteria have competitive advantages at low light intensities;
3. cyanobacteria have competitive advantages at high pH and low concentrations of dissolved CO_2 ;
4. some cyanobacteria exploit their ability to regulate buoyancy by means of gas vacuoles to achieve competitive success in stable water columns;
5. some cyanobacteria gain metabolic advantages at elevated water temperatures;
6. many cyanobacteria are resistant to zooplankton grazing;
7. cyanobacteria that colonize water columns from sedimentary resting stages bring with them a nutrient storage surplus that enhances their success in the plankton;
8. non N-fixing cyanobacteria benefit from inorganic N in the form of ammonium, but they are inefficient competitors with eukaryotes when N is available mainly as nitrate;
9. cyanobacteria have high requirements for trace elements compared with most eukaryotes.

Empirical evidence for the utility of TN:TP ratio in predicting potential blue-green dominance regardless of species has been indisputable since the original demonstration by SMITH (1983), although explanatory theory had previously focused on N-fixation by specific taxa as the only clear mechanism (SCHINDLER 1977; FLETT et al. 1980). The reason that non N-fixers likewise succeed at low TN:TP but not at high ratios has only recently been recognized as a physiological consequence of differences between prokaryotic and eukaryotic nitrate reductase, with the consequence that eukaryotes, especially fast growing chlorophytes, outcompete blue-greens when nitrate is a plentiful source of inorganic N (HYENSTRAND et al. 1998a, 1998b). Experimental evidence for the ability of the chlorophyte *Selenastrum* to outgrow *Oscillatoria agardhii* at elevated nitrate concentrations has existed, in fact, for decades (AHLGREN 1977).

Epilimnetic ratios of NO_3 -N to SRP increased by over 10-fold on average during the recovery era (Fig. 15), because P-rich effluent was diverted from the lake. Moreover, the reduced loading of anthropogenic P into the lake caused

reduction in the mixed layer biomass, resulting in enhanced water column transparency and less severe light limitation during stratification. Epilimnetic pH declined coincident with decreased primary production, and dissolved CO_2 concentrations increased. *Oscillatoria* and allied cyanobacteria thus lost competitiveness on points 1, 2, 3, and 8. To the extent that unmeasured trace elements were diverted along with the sewage effluent, the blue-greens could have suffered from item 9, as well.

Extirpation of *Oscillatoria agardhii* or *O. rubescens* populations after reductions in nutrient loading appears to be a general occurrence (LEPISTO et al. 1999; TEUBNER 2000), as is the observation that in the absence of *Oscillatoria*/*Planktothrix*, the taxa *Aphanizomenon* and *Microcystis* enjoy success when N:P ratios decline (TEUBNER et al. 1999). The commonality of algal community response to elevated TN:TP reveals a more complex shift in relative availability of reduced and oxidized inorganic nitrogen species. Non N-fixing blue-greens are supposed to rely on ammonium more so than nitrate (HYENSTRAND et al. 1998a, 1998b). During the eutrophication era, dissolved inorganic nitrogen ($\text{DIN} = \text{NH}_4 + \text{NO}_2 + \text{NO}_3$) levels regularly fell to near-undetectable concentrations during summer (Fig. 16). The recurrent small pool of DIN each summer was dominated by ammonium rather than nitrate (Fig. 16). After 1967, DIN never fell quite as low as it did from 1962 to 1967, but whenever DIN is at its lowest concentration, the pool is dominated by ammonium. Only so long as DIN concentrations remain above about $30 \mu\text{g/l}$, or roughly $2 \mu\text{M}$, does nitrate remain the dominant chemical species.

Oscillatoria dominated Lake Washington during conditions of low TN:TP, low average mixed layer light intensity, and low concentrations of summer DIN with ammonium as the main nitrogen source. As nutrient diversion and dilution by fluvial flushing eliminated these conditions and established higher TN:TP, *Oscillatoria* disappeared from the lake.

Despite elimination of the extreme conditions that favored *Oscillatoria*, summer TN:TP ratio by mass continued to fall below 30:1, sometimes to as low as 20:1, documented until regular monitoring for TN was discontinued in 1982. These ratios are associated with the presence of both N-fixing and non N-fixing blue-greens in other lakes, and hence it is no surprise that taxa such as *Aphanizomenon flos-aquae*, *Chroococcus*, *Coelosphaerium*, and *Microcystis* have continued to make modest contributions to the flora each summer.

Colonial greens and cyanobacteria

The emergence of large colonial green and blue-green species after establishment of the grazer *Daphnia* is best understood in the context of REYNOLD's (1984, 1988) characterization of these colonies as Type III, "S", or slow-growing, stress-tolerant species that are resistant to grazing loss and sedimentation. These taxa include the greens *Oocystis gigas* and other *Oocystis* species, gelatinous green colonies, and coccoid colonial cyanobacteria. Emergence of *Microcystis* in more recent years

may indicate that the progressive warming of Lake Washington during the second half of the 20th century (Fig. 14) is leading to more physically stable conditions in which *Microcystis* can profitably exploit its buoyancy-regulating capabilities.

Summary

The aim of this paper has been to outline the scope of the study and to describe the long-term changes in phytoplankton and environmental conditions. Detailed analyses of seasonal dynamics of individual taxa in relation to environmental factors will be addressed in future reports. We have shown that the empirical changes in Lake Washington phytoplankton over 45 years of continuous record are consistent with established theory, and that they suggest additional falsifiable hypotheses. For example, we hypothesize that the mixed layer diatoms present after recovery from eutrophication are more competitive for low SRSi than those species present before 1976. We also demonstrate that environmental conditions continue to favor episodic presence of cyanobacteria among the plankton community. We intend to present further refinements and evaluation of mechanistic theory about light effects, vertical mixing, and grazer interactions in the near future.

The key factors promoting dominance by *Oscillatoria*/*Planktothrix* during the eutrophication era appear to be its competitive abilities at low light levels, competitiveness in using ammonium at low TN:TP ratios, and low loss rates from sinking, grazing, and water exchange. In the presence of adequate nitrate, Lake Washington produces mainly diatoms which appear to vary in species composition along Si:N or Si:P ratio gradients. One of the influential consequences of *Daphnia* dominance over *Diaptomus* since the mid-1970s may have been a transition in nutrient recycling dynamics that affected these gradients through differential loss by sinking of particulate Si compared with N and P. During the mid- to late 1990s, the lake started to exhibit a reversal of the trend in Si:N established after recovery from eutrophication, and so future changes in diatom composition might be anticipated.

Analyses of Lake Washington phytoplankton communities by different objective statistical clustering criteria failed to converge on a common set of species categories. This observation suggests that the interplay between environmental factors and species success is characterized by thresholds, feed-backs, and other nonlinear features that are outside the a priori constraints of the statistical models. Application of our long-term experience with Lake Washington to other lakes implies that hunting for patterns in the absence of mechanistic theory and ideas about causality will not be meaningful because even with a massive data set the statistical results will vary with the assumptions behind the methods as much or more so than with any natural processes that the methods are imagined to elucidate. Theory based on competition for light and nutrients, and incorporating interaction with loss rates, seems to provide a powerful and consistent explanatory

framework for the major changes in phytoplankton of Lake Washington during a half century of observation. At the interannual temporal scale of this report, the effects of grazers on community composition seem to be inextricably linked to changes in the nutrient dynamics of the lake.

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