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Environmental Control and Limnological Impacts of a Large Recurrent Spring Bloom in Lake Washington, USA

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ABSTRACT / A series of statistical analyses were used to identify temporal and spatial patterns in the phytoplankton and nutrient dynamics of Lake Washington, an mesotrophic lake in Washington State (USA). These analyses were based on fortnightly or monthly samples of water temperature, Secchi transparency, ammonium (NH_4), nitrate (NO_3), inorganic phosphorus (IP), total nitrogen (TN), total phosphorus (TP), dissolved oxygen (DO), pH and chlorophyll *a* (chl *a*) collected during 1995–2000 from 12 stations. Lake Washington has a very consistent and pronounced annual spring diatom bloom which occurs from March to May. During this bloom, epilimnetic chl *a* concentrations peak on average at 10 μg/L, which is 3 times higher than chl *a* concentrations typically seen during summer stratified conditions. The spring bloom on average comprised 62% diatoms, 21% chlorophytes and 8% cyanobacteria. During summer stratification, diatoms comprised 26% of the phytoplankton community, chlorophytes 37% and cyanobacteria 25%. Cryptophytes comprised approximately 8% of the community throughout the year. Overall, 6 phytoplankton genera (i.e., *Aulacoseira*, *Fragilaria*, *Cryptomonas*, *Asterionella*, *Stephanodiscus*, and *Ankistrodesmus*) cumulatively accounted for over 50% of the community. These analyses also suggest that the phytoplankton community strongly influences the seasonality of NO_3, IP, DO, pH and water clarity. According to a MANOVA, seasonal fluctuations explained 40% of the total variability for the major parameters, spatial heterogeneity explained 10% of variability, and the seasonal-spatial interaction explained 10% of variability. Distinctive patterns were identified between offshore and inshore sampling stations. The results of our analyses also suggest that spatial variability was substantial, but much smaller than temporal variability.

Lake algal blooms are controlled by physical (e.g., water column mixing, light, temperature and particle settling), chemical (e.g., nutrient availability and cycling) and biological (e.g., competition and grazing) processes. Much of what is known about seasonal phytoplankton community biomass and composition dynamics is based on a few classic case studies and especially the studies by Sommer and others (1986) and Lampert and others (1986). Lake Washington is temporally one of the most intensively sampled lakes in the world, and its famous rapid recovery from severe eutrophication due to wastewater diversion is well known to virtually all limnologists (Edmondson 1994). Lake Washington is also interesting because it has arguably the highest water quality of any lake located in the midst of a major urban area in the entire world, and economically important sockeye salmon (*Oncorhynchus nerka*) obtain some of the highest recorded juvenile growth rates throughout their range in this system (Eggers 1978; Edmondson 1994). Interestingly, despite the fact that Lake Washington has been systematically sampled at biweekly intervals for approximately 40 years and numerous studies of this lake have been published, no prior study has examined the typical seasonal dynamics of this system. This is somewhat ironic because Lake Washington has a very characteristic and consistent seasonal phytoplankton dynamic, which differs from the classic conceptual models of phytoplankton community dynamics (Sommer and others 1986, Marshall and Peters 1989). Because Lake Washington is one of the most well-known lakes in the limnological literature and because it has a pro-

KEY WORDS: Lake ecosystems; Heterogeneity; Lake Washington; Pattern; Plankton dynamics; Spring bloom

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*Author to whom correspondence should be addressed; *email:* georgea@u.washington.edu nounced seasonal phytoplankton dynamic, a detailed analysis of this lake's annual phytoplankton cycle could serve as an additional case study for the general limnological literature.

The objective of this study was to elucidate the typical season cycle for phytoplankton biomass and community composition, nutrient availability, water clarity, dissolved oxygen content and pH in Lake Washington. This study will utilize a database collected by a recent (1994–2000), spatially intensive (12 stations) limnological sampling program carried out by King County/Metro (KC Metro). Because the KC Metro monitoring program includes more sampling stations than most lake sampling programs, this database will also allow us to assess the extent to which the design of a sampling program influences our understanding of a lake's dynamics. One of the most critical questions that must be addressed by scientists or resource managers is how to design monitoring programs, and especially how to select the most appropriate spatial and temporal sampling scale, for sensitive systems like lakes or rivers with major anthropogenic stressors. Another basic question is how does the "scale" at which a system is sampled and conceptualized influence our understanding of how that system functions (Levin 1992, Fitz and others 1996)? Scale issues are one of the most vexing problems in environmental science and especially environmental modeling where it is almost always necessary to scale processes observed at a very fine scale to much larger systems of interest (Oreskes and others 1994, Pace 2001). With our analyses, we will be able to describe the typical seasonal patterns in Lake Washington, as well as determine the extent to which these patterns vary from one location to another in this lake.

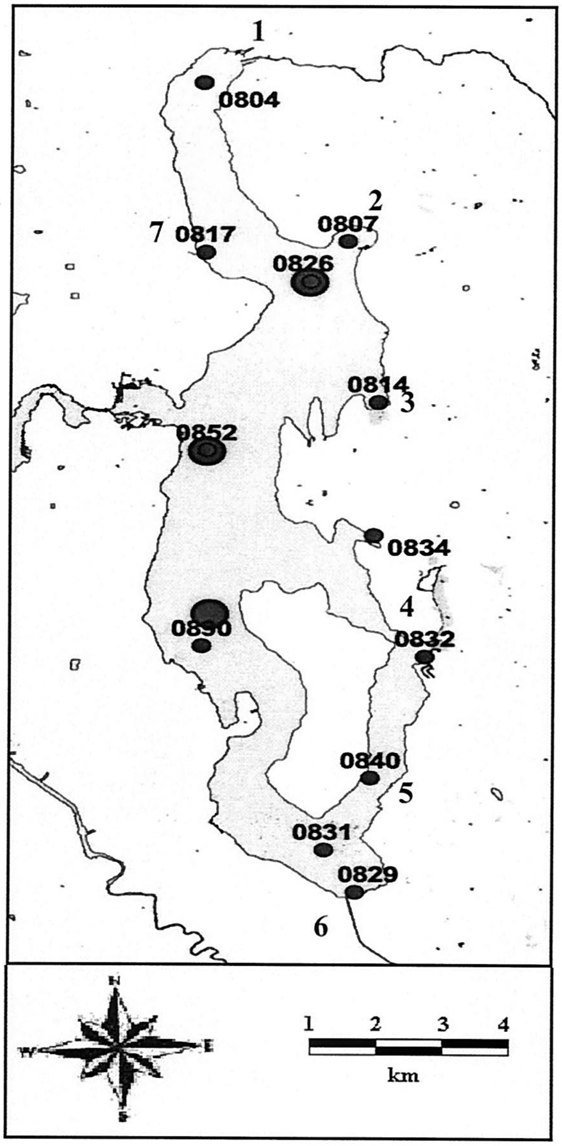

Figure 1. Map of Lake Washington indicating the sampling sites and the most significant neighboring streams (numbers 1–7).

Methodology

Study Area

Lake Washington is the second largest natural lake in the State of Washington, with a surface area of 87.6 km^2 and a total volume of 2.9 km^3 (Figure 1). The mean depth of the lake is 32.9 m (maximum depth 65.2 m), the summer epilimnion depth is typically 10 m and the epilimnion:hypolimnion volume ratio during the summer is 0.39. The retention time of the lake is on average 2.4 years (Edmondson 1991). The Lake Washington basin is a deep, narrow, glacial trough with steeply sloping sides sculpted by the Vashon ice sheet, the last continental glacier to move through the Seattle area (Edmondson 1994). The lake is 6.3 m above mean lower low tide in Puget Sound and is connected to Puget Sound via Lake Union and the Lake Washington Ship Canal which was constructed in 1916 (Edmondson 1994). Mercer Island lies in the southern half of the lake, separated from the east shore by a relatively shallow and narrow channel, and from the west shore by a much wider and deeper channel. Lake Washington's two major tributaries are the Cedar River (at its south end) which contributes about 57% of the annual hydraulic load and 25% of the phosphorus load, and the Sammamish River (at its north end) which contributes 27% of the hydraulic load and 41% of the phosphorus load. The majority of Lake Washington's immediate watershed (1274 km^2) is urbanized with 63% of the watershed surface area fully developed. Streams draining urban areas in the immediate watershed supply 14% of the phosphorus load and 4% of the water to Lake Washington (Brett and others 2002).

Lake Washington has been extensively studied and it is perhaps the best example in the world of successful lake restoration by wastewater diversion (Edmondson 1994). The lake received increasing amounts of secondary treated sewage between 1941 and 1963, which resulted in severe eutrophication and declining water quality. The phytoplankton community was dominated by cyanobacteria from 1955 to 1973. Sewage was diverted from the lake between 1963 and 1967, with discharge of wastewater treatment plant effluent (except for combined sewer overflows) eliminated by 1968. Rapid and predicted water quality improvements followed; cyanobacteria abundance has declined dramatically since 1976.

Currently, Lake Washington can be characterized as a mesotrophic ecosystem (Edmondson 1994). Furthermore, after more than 25 years during which several commercially valuable runs of salmon occurred, the number of adult sockeye salmon returning to the lake is decreasing and the reason for this change has not yet been determined (Fresh 1994).

Data-set

The data-set used for this study was assembled by the Major Lakes Monitoring Program of King County, Washington State, USA (KCWQR 2000). Data collection was carried out fortnightly (during the summer) and monthly (the rest of the year) sampling cruises from January 1995 to December 2000. Samples were collected from the 12 sampling stations shown in Figure 1. At each station samples were taken from 1 m below the surface of the lake to just above the lake bottom. Five stations ([0826], [0831], [0840], [0852], [0890]) were located in the deep central basin of the lake. The other seven sampling stations ([0804], [0807], [0814], [0817], [0829], [0832], and [0834]) are distributed around the shoreline of the lake, primarily off the mouths of influent streams. Soluble reactive phosphorus was determined according to the automated ascorbic acid method (SM4500-P F), total phosphorus was determined according to the automated ascorbic acid method after manual persulfate digestion (SM4500-P-B, E), nitrate + nitrite nitrogen was determined according to the automated cadmium reduction method (SM4500-NO_3-F), ammonium nitrogen was determined according to the automated phenate method (SM4500-NH_3-H), organic nitrogen was determined according to the block digestion and flow injection method (SM4500-N_{ORG}-D) and chlorophyll a according to the fluorometric method (SM10000-chlorophyll-H3).

Samples for the determination of phytoplankton taxa seasonal succession were also collected and were preserved with Lugol's Iodine, and counted using a Reichert-Jung Inverted Biological Microscope. These samples were enumerated in a semi-quantitative fashion with each taxa observed in each sample categorized as either dominant, common or present. To obtain an estimate of phytoplankton species composition from these semi-quantitative samples, we scored each category accordingly: dominant = 10, common = 3.33, present = 1, and absent = 0. We also tested two alternative weighting schemes to gauge the extent to which the final results were influenced by the weights used for our calculations. The alternative schemes considered were dominant = 3, common = 2, present = 1, and absent = 0; and dominant = 100, common = 10, present = 1, and absent = 0. Once weights were assigned to the semi-quantitative categories, we added up all the scores for each major taxonomic group (diatoms, cryptophtyes, chlorophytes, cyanophytes, and others) for each month and divided their respective sub-totals by this sum. To convert these percent composition estimates to actual biomass estimates for each grouping, we simply multiplied the percents by the overall seasonal cycle for chlorophyll concentrations. We used a similar approach to calculate which individual genera were most dominant within the specific taxonomic groupings. For example, for diatom genera we multiplied each observation by its respective score and then summed these values by genera and divided these sub-totals by the overall sum for diatoms.

Statistical Analysis

Statistical Methods and Data Manipulation. The various lake stations were not sampled in a comparative fashion along the vertical dimension, since the shoreline sites were for the most part shallow and did not exhibit thermal stratification during the summer period. Therefore, a full 3-D statistical analysis was not feasible and data from the hypolimnetic depths of the offshore sites were excluded prior to the analyses. The relations among the variables were examined by calculating both standard and partial correlation coefficients. Pearson's correlation coefficient is a measure of the linear association between two variables, whereas partial correlation also takes into account potential interactions of other variables on the two in question (Zar 1999). Examination of the interactions of chlorophyll a versus the other water quality parameters was done by cross-correlation (lag correlation), which is a method to simultaneously analyze oscillations for two

Table 1. Statistics variables in Lake Washington during 1995-2000

Variables[a]	MAV	SD	CV (%)
Water temperature	12.43	7.83	62.93
Secchi transparency	3.91	1.15	29.48
Ammonium	24.84	10.48	42.17
Nitrate	220.44	8.81	39.95
Inorganic phosphorus[b]	9.05	4.74	52.48
Total nitrogen	360.00	100.88	28.02
Total phosphorus	18.27	10.18	55.71
TN:TP	49.99	17.35	34.71
Dissolved oxygen	9.85	1.66	16.84
pH	7.66	0.43	5.56
Chlorophyll *a*	4.52	3.98	88.08

[a] MAV: mean annual values; SD: standard deviation; CV: coefficient of variation

[b] All the filterable molybdate-reactive P

series, differing by a distance of k units in time (Legendre and Legendre 1983). Statistical analyses designed to detect significant differences in the spatial and temporal scale were carried out using Multivariate Analysis of Variance (MANOVA). This method considers the correlation among multiple variables, which separate ANOVAs cannot do, and therefore provides more powerful testing if variables are correlated (Zar 1999). Moreover, the distribution of the spatial heterogeneity was further quantified using a Hierarchical Analysis of Variance. The designation of this method was based on the presumption that the stations constituted a factor nested within another "dummy" factor, characterizing the deep and shallow sections of the lake. All the above methods were applied to mean monthly values of the variables, which means that all the sampling units (values of the variables) for each combination of station, month and year were averaged over the epilimnion depths to form the new database. Multidimensional scaling (MDS) was used as a data reduction technique to identify a small number of factors and form a 2-D conceptual space that explains most of the variance observed in the much larger set of variables. Data were standardized to zero mean and unit variance in order to exclude bias due to the different measurement scales of the various variables (Legendre and Legendre 1983).

Results

Results of the statistical analyses of the physical, chemical and biological properties of Lake Washington are given in Table 1. In addition, temporal variation is represented graphically in Figure 2, where the graph dots correspond to the mean monthly values and the respective perpendicular lines on the X axis describe their ranges. Water temperature in Lake Washington fluctuated regularly with time presenting its maxima in August (≈20°C) and the minimum in February (≈8°C). The greater variation in March and August should be attributed to the interannual variability, since the temperature distribution over the lake was rather uniform during the annual cycle. Moreover, the variability of the vertical profiles of temperature over the annual cycle is presented in the 3-D graph of Figure 3. Secchi transparency was lowest in the spring (3.0–3.5 m), fluctuated around 3.8 m most of the year, and had a maximum value of 4.7 m. Ammonium was notable for its lack of any consistent fluctuation with time, and had a mean annual value of 24.84 μg/l, a uniformly distributed variation of ±10 μg/l and a coefficient of variation of about 42%. However, nitrate concentrations were about nine times higher 220 μg/l, constituting the dominant fraction of the total nitrogen stock 360 μg/l. Therefore, the nitrate and total nitrogen annual patterns (Figures 2d and 2f) were almost identical, having a rather regular sequence of maxima in the winter followed by minima in the summer. The ratio of total phosphorus to inorganic phosphorus was about two and the annual cycles of both parameters were characterized by winter highs and summer lows (Figures 2e and 2g). Dissolved oxygen and pH varied from 8 mg/l (September-November) to 12 mg/l (April) and 7.2 (December-January) to 8.2 (May), respectively. The DO and pH maxima coincided with a major annual diatom bloom (≈10 μg/l) during the spring (April and May). Algal biomass was fairly constant during the rest annual cycle, varying from 2 to 4 μg/L. The high value of the chlorophyll *a* coefficient of variation (88%) possibly results from the tripling or quadrupling during April and May and the moderate differences in the timing and progress of the spring bloom between years, since the interannual variations of the rest of the months and the differences among the stations were rather small. Finally, the total N: total P atomic ratio was consistently above 16:1 during the entire annual cycle, with a mean of 49.99, suggesting that phosphorus was the limiting nutrient for phytoplanktonic growth in Lake Washington.

Figure 4 shows the composition of the phytoplankton community over the annual cycle. During the peak of the spring bloom, diatoms comprised on average 62% of the phytoplankton community, chlorophytes 21% and cyanobacteria 8%. During the period of summer stratification from July to October, diatoms comprised 26% of the phytoplankton community, chlorophytes 37% and cyanobacteria 25%. Cryptophytes comprised a quite consistent 8 ± 2% (±1 SD of

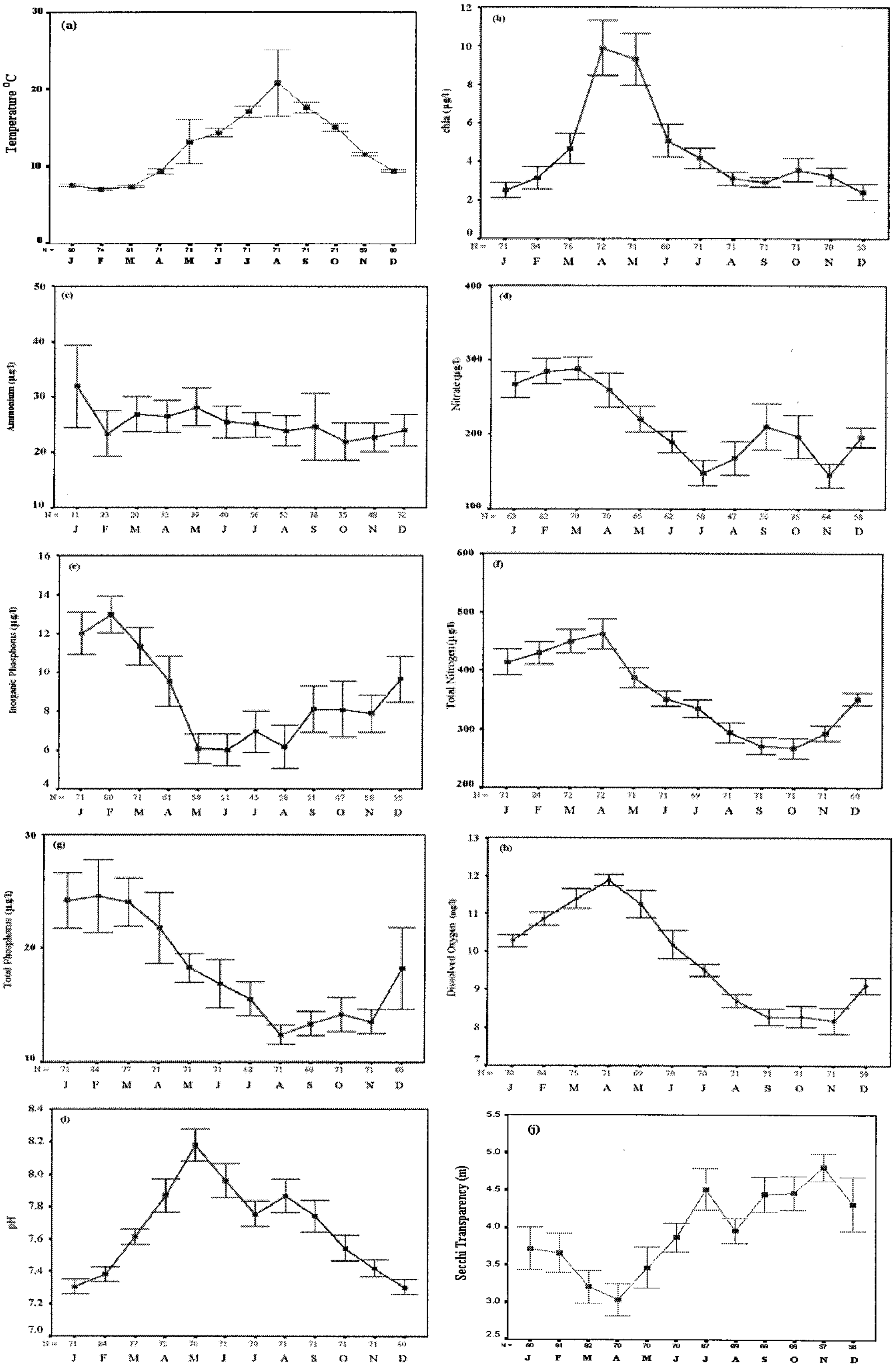

Figure 2. Annual patterns of (**a**) water temperature, (**b**) chlorophyll *a*, (**c**) ammonium, (**d**) nitrate, (**e**) inorganic phosphorus, (**f**) total nitrogen, (**g**) total phosphorus, (**h**) dissolved oxygen, (**i**) pH and (**j**) Secchi transparency in Lake Washington. (The error bars and N represent the range and sample size of monthly parameter values and include all the stations and years of the study.)

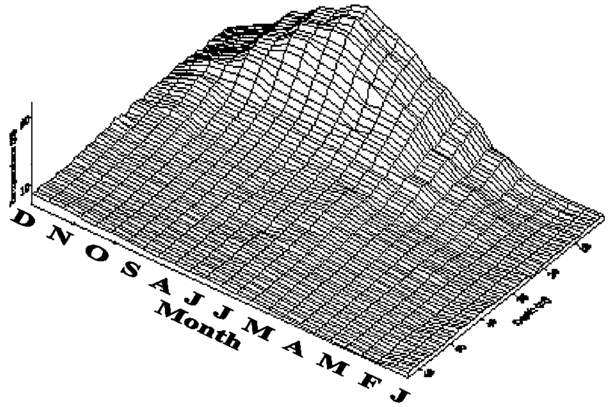

Figure 3. Annual variability of the vertical profiles of temperature in Lake Washington.

monthly averages) of the community throughout the year, while other taxa (chrysophytes, dinoflagellates, and euglenoids), on average, only comprised 3 ± 2% of the phytoplankton. Over 90% of the diatom community was composed of just six genera of 15 detected; these were (in descending order of importance): *Aulacoseira* (AKA *Melosira*), *Fragilaria, Asterionella, Stephanodiscus, Diatoma* and *Tabellaria.* Five genera of 12 detected comprised over 95% of the cyanobacteria community; these were *Microcystis, Anabaena, Aphanizomenon, Anacystis* and *Chroococcus. Oscillatoria*, which was formerly the single most dominant phytoplankton genus in Lake Washington, comprised only 0.5% of the cyanobacteria assemblage during 1995–2000. The chlorophyte community was considerably more diverse than either the diatoms or cyanobacteria. It took 11 chlorophyte taxa of the 28 detected to comprise 90% of the chlorophyte assemblage; these taxa were *Ankistrodesmus, Actinastrum, Oocystis, Ulothrix, Sphaerocystis, Staurastrum, Pediastrum, Cosmarium, Crucigenia, Coelosphaerium* and *Scenedesmus.* Cryptophytes were almost all identified to the genus *Cryptomonas*, but were most likely a mixture of *Cryptomonas* and *Rhodomonas.* Overall, 15 phytoplankton genera individually accounted for at least 2% of the overall community, and cumulatively over 80% of the community. These taxa were *Aulacoseira, Fragilaria, Cryptomonas, Asterionella, Stephanodiscus, Ankistrodesmus, Actinastrum, Microcystis, Oocystis, Ulothrix, Anabaena, Aphanizomenon, Anacystis, Diatoma* and *Sphaerocystis.*

Surprisingly, the weights used to convert the semi-quantitative categories to community composition estimates only had a small impact on these results. The three weighting schemes provided highly (non-linearly) correlated percent composition estimates for the 65 genera assessed ($r^2 = 0.97 - 1.0$). The scheme employing weights of 100, 10 and 1 gave a 34% greater proportional representation for the two genera that comprise greater than 9% of the community, 17% smaller proportional representation for the 10 genera that comprised between 3–10% of the community, and a 45% smaller representation for the 53 genera that comprised less than 3% of the community compared with the 3, 2 and 1 weighting scheme. Qualitatively, each scheme gave the same list of 15 most common genera (see above), although the relative ranking within these lists varied slightly. These results suggest that although this procedure could not provide truly quantitative estimates, because of the large number of samples summarized it probably gave a good estimate of the most dominant phytoplankton genera in Lake Washington.

Simple linear and partial correlations among the various water quality parameters are presented in Table 2. Time series relationships of chlorophyll *a* versus the other physical and chemical parameters were also computed, using cross correlations (Figure 5), in an attempt to interpret the previous mentioned seasonal fluctuations. Ammonium was excluded from these analyses, since its concentration was not related to seasonality and moreover it constituted a small portion of the inorganic nitrogen pool. The cross-correlogram of Figure 5a shows that temporal variability of chlorophyll *a* was associated with temperature. All the combinations fluctuated regularly with time, having a statistically significant dominant oscillation on the order of 12 months and a lag phase of 2 months. The partial correlation coefficient was not significant (0.011) because of the existence of the lag phase between this pair of parameters.

On the other hand, the negative significance (−0.125) of the simple coefficient should be considered as an "artifact" of the analysis, since this type of correlation does not take into account the possible interactions of any of the other variables on this pair. In contrast, the combination of chlorophyll *a* and Secchi transparency did not have a lag phase, having a highly significant negative cross-correlation at lag number equal to zero and a dominant oscillation on the order of 12 months. Simple and partial correlation coefficients were in agreement with these results (−0.354 and −0.233, respectively). Cross-correlograms of chlorophyll *a* with nitrate and inorganic phosphorus were quite similar (Figure 5 c–d); these patterns show that there is dependence between these nutrients and primary production. The significant cross-correlation coefficients at lag numbers from 1 to 3 months correspond to the processes of nutrient accumulation in the lake during the winter period and the subsequent nutrient uptake during the spring phytoplanktonic

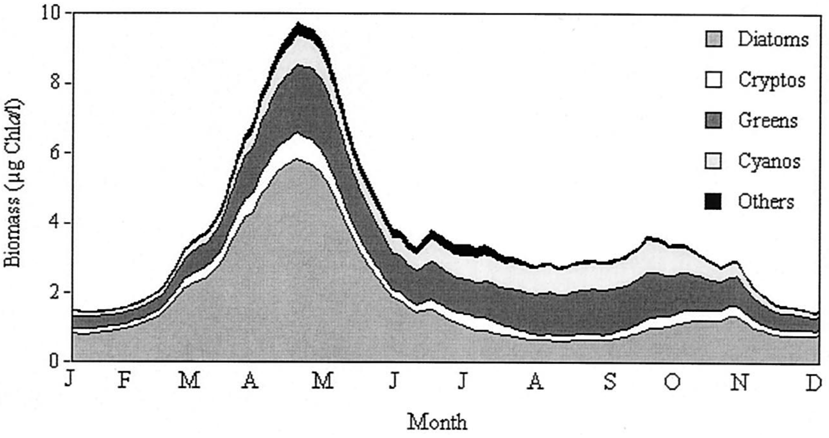

Figure 4. Lake Washington seasonal phytoplankton succession.

Table 2. Simple linear (lower triangle) and partial (upper triangle) correlation coefficients among the various water quality parameters

Temperature	Secchi transparency	Nitrate	Inorganic phosphorus	Total nitrogen	Total phosphorus	Dissolved oxygen	pH	Chlorophyll *a*
	−0.106*	−0.174**	−0.105*	0.064	−0.036	−0.600**	0.217**	0.011
	(477)	(477)	(477)	(477)	(477)	(477)	(477)	(477)
0.237**		−0.151*	0.021	−0.006	−0.433**	−0.203**	−0.001	−0.233**
(738)		(477)	(477)	(477)	(477)	(477)	(477)	(477)
−0.531**	−0.298**		0.292**	0.694**	−0.240**	−0.051	−0.242**	−0.054
(616)	(690)		(477)	(477)	(477)	(477)	(477)	(477)
−0.415**	−0.151**	0.567**		0.237**	0.265**	0.011	−0.209**	−0.083
(610)	(688)	(617)		(477)	(477)	(477)	(477)	(477)
−0.587**	−0.406**	0.746**	0.464**		0.317**	0.214**	0.106*	0.085
(752)	(825)	(715)	(705)		(477)	(477)	(477)	(477)
−0.333**	−0.461**	0.375**	0.417**	0.507**		−0.062	−0.034	−0.076
(743)	(818)	(710)	(693)	(838)		(477)	(477)	(477)
−0.533**	−0.436**	0.230**	0.063	0.469**	0.253**		0.410**	0.106*
(749)	(822)	(700)	(691)	(838)	(829)		(477)	(477)
0.278**	−0.232**	−0.390**	−0.457**	−0.211**	−0.152**	0.318**		0.410**
(756)	(829)	(707)	(697)	(845)	(836)	(851)		(477)
−0.125**	−0.354**	−0.136**	−0.241**	0.163**	0.056	0.444**	0.524**	
(744)	(818)	(709)	(693)	(840)	(840)	(830)	(837)	

*Correlation is significant at the 5% level.

**Correlation is significant at the 1% level.

bloom. Moreover, the role of inorganic phosphorus as a limiting factor for this ecosystem is indicated in the statistical significance of the partial correlation coefficient and the correlogram for a zero lag phase. Figures 3e and 3f show that both total nitrogen and phosphorus in combination with chlorophyll *a* had an irregular fluctuation with time.

The existence of significant cross-correlation coefficients for certain lag phases should be attributed to the respective statistical trends of nitrate and inorganic phosphorus, since these nutrient forms constitute the dominant fraction of the total nitrogen and phosphorus stock. This statement is in agreement with the significant values of the partial and simple correlation coefficients relating total phosphorus to inorganic phosphorus and total nitrogen to nitrate. Regular variations of chlorophyll *a* with dissolved oxygen and pH were revealed by the respective cross-correlograms. The dominant oscillations of these combinations were on the order of 12 months with no lag phase, indicating the regulatory role of photosynthetic activity in the carbon cycling processes. Simple and partial correlation coefficients between these parameters were also significant, verifying this trend.

However, the pattern of pH was not entirely clear, having significant values only in the zone of the ±1

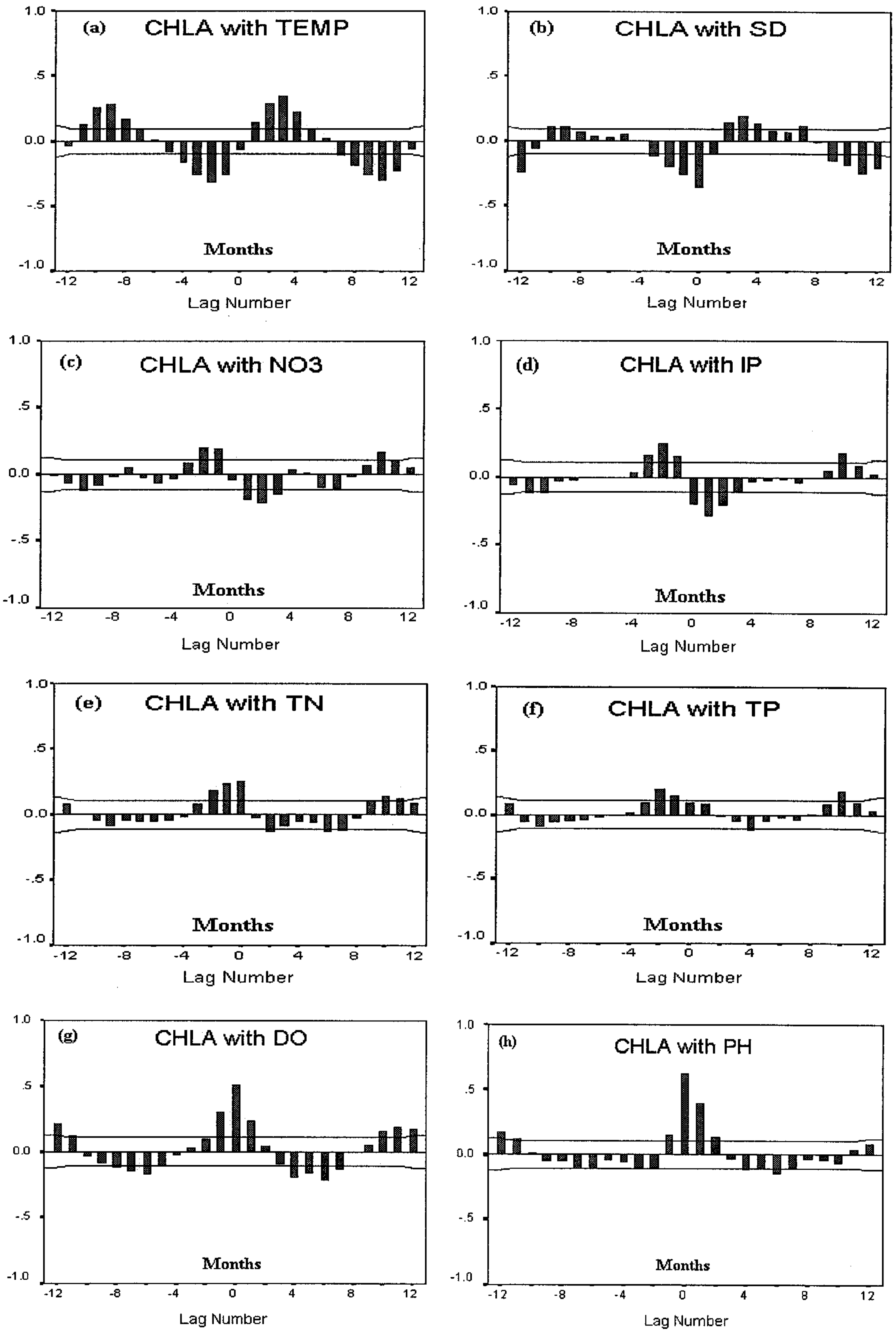

Figure 5. Cross correlograms of chlorophyll *a* versus (**a**) water temperature, (**b**) Secchi transparency, (**c**) nitrate, (**d**) inorganic phosphorus, (**e**) total nitrogen, (**f**) total phosphorus, (**g**) dissolved oxygen and (**h**) pH.

Table 3. Multivariate analysis of variance (Model II) for testing and quantifying the role of spatial and temporal variability in Lake Washington

	Time		Space		Space × Time	
Variable	Mean square DF (11,121)	Proportion of total variability (%)	Mean square DF (11,121)	Proportion of total variability (%)	Mean square DF (121,506)	Proportion of total variability (%)
Secchi transparency	16.4488*	20.95	9.5989*	12.22	0.6771	9.48
Nitrate	0.2355*	41.53	0.0447*	9.65	0.0080*	15.57
Inorganic phosphorus	0.0003*	27.91	0.0001*	10.69	0.0001*	10.81
Total Nitrogen	0.2469*	45.45	0.0286*	5.26	0.0088*	17.81
total Phosphorus	0.0009*	14.35	0.0001	1.75	0.0000	13.07
dissolved oxygen	85.7871*	68.67	9.1459*	7.32	1.0156*	8.94
pH	3.8589*	39.52	1.9271*	19.73	0.1184*	13.34
Chlorophyll *a*	382.5683*	49.67	37.1163*	4.81	4.8737	6.96

Wilks' lambda: Time: 0.0009* Space: 0.0486* Time × Space: 0.1491*.

Roy's Maximum Root: Time: 20.1247* Space: 5.9403* Time × Space: 1.2965*.

*Significant value at the 5% level.

Analysis based on the mean monthly values of Secchi transparency, nitrate, inorganic phosphorus, total nitrogen, total phosphorus, dissolved oxygen, pH and chlorophyll *a*, for each station during the study period 1995-2000.

month lag phases. It seems that except for the spring phytoplankton bloom, when a notable increase in pH (7.4–8.2) occurs within a period of 2 months, the bicarbonate system provides an effective buffer in the lake, minimizing the effects of autotrophic activity on lake pH.

The partitioning of the total variability observed in Lake Washington and the assessment of the contribution of its spatial and temporal components were obtained by executing a Two-Factorial Multivariate Analysis of Variance. Table 3 shows that both the MANOVA statistics used (i.e., Wilks' lambda and Roy's Maximum Root) showed the statistically significant main effects for space, time and their interaction in the total heterogeneity of the system. The apportionment of these effects among the various water quality parameters indicated that dissolved oxygen's pattern was mostly dominated by the temporal variability, accounting for more than 68% of variability, followed by chlorophyll *a*, nitrate, total nitrogen and pH (≥40%). Moreover, the limited variability in Secchi depth and total phosphorus over the annual cycle was reflected in the relatively low proportions (≤20%) of overall variability attributable to the temporal component; whereas inorganic phosphorus had intermediate levels (≈28%) of variability attributable to the temporal component. Spatial variability for these parameters was rather low, accounting for less than 12% overall for all of the parameters; pH was the only exception, with differences among the stations explaining about 20% of its variability. Furthermore, the results indicated that the interactions of space with time described a significant proportion of the total variability, in some cases exceeding 10%. This suggests that there are some periods during the annual cycle when some sections of the lake have statistically different trends for nitrate, total nitrogen, inorganic phosphorus and pH. Chlorophyll *a* and dissolved oxygen had significant and time consistent homogeneity over the lake. The remaining variability was attributed to interannual differences in the timing of the onset and collapse of the spring bloom. A preliminary statistical analysis of the data showed that none of the water quality parameters assessed had a statistically significant trend during the 6 years of the study, but the $n = 6$ is low and so is the statistical power, therefore we cannot extract inferences for trends in the interannual variability.

To address the validity of extrapolating results from specific portions of the lake to predict dynamics over the entire system, the quantification of the distribution of the spatial variability in Lake Washington, was obtained by the Hierarchical Multivariate Analysis of Variance (Table 4). This analysis used a dummy factor called "space" that discriminated between offshore and inshore stations. The two levels of this factor were defined by the formula:

$$\text{space} = \begin{cases} \text{I for stations [0804], [0807], [0814],} \\ \quad \text{[0817], [0829], [0832] and [0834]} \\ \text{O for stations [0826], [0831], [0840],} \\ \quad \text{[0852] and [0890]} \end{cases}$$

It was found that the previously mentioned spatial heterogeneity of pH is mostly derived from the differences between the deep and shallow sections of the lake, since the bicarbonate system is less effective at

Table 4. Hierarchical multivariate analysis of variance for testing and quantifying distribution of spatial variability in Lake Washington

Variable	Space: Mean Square DF (1,638)	Space: Proportion of Total Variability (%)	Station: Mean Square DF (10,638)	Station: Proportion of Total Variability (%)
Secchi transparency	59.6728*	9.12	6.8601	5.79
Nitrate	0.2056*	6.46	0.0206	2.80
Ammonium	0.0001	0.18	0.0001	0.90
Inorganic phosphorus	0.0004*	5.07	0.0000	4.11
Total Nitrogen	0.0578*	0.00	0.0588	6.78
total Phosphorus	0.0000	0.00	0.0001	0.26
dissolved oxygen	97.3883*	7.62	6.4580	1.90
pH	25.5672*	28.43	0.3402	1.26
Chlorophyll *a*	128.5200*	1.40	35.7989	1.80

*Significant value at the 5% level.

"Space" is a dummy factor denoting the differences between the offshore and inshore stations.

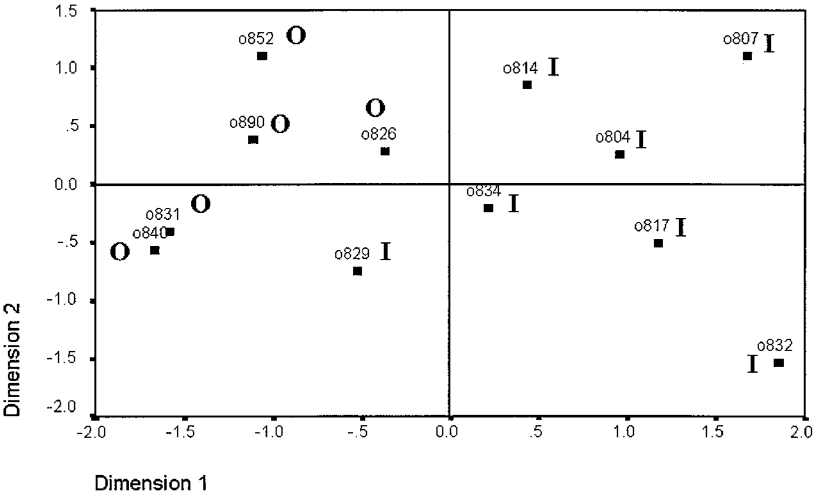

Figure 6. Application of multidimensional scaling for grouping the stations based on their monthly mean values of water temperature, Secchi transparency, ammonium, nitrate, inorganic phosphorus, total nitrogen, total phosphorus, dissolved oxygen, pH and chlorophyll *a*.

buffering pH fluctuations in shallower and smaller water masses. This inference is further sustained by the similar spatial trends of dissolved oxygen, though the phytoplankton biomass was remarkably uniform over the lake. The heterogeneity of nitrate was more dependent on the differences between the central and the near shore parts of the lake (6.5%) than the differences within these spatial compartments (2.8%), whereas inorganic phosphorus was more equivalently distributed between these two factors (5.1% and 4.1%, respectively). The concentrations of these nutrients are mostly regulated by the balance between the exogenous discharges and the phytoplankton uptake, leading to transitory accumulations or depletions in various parts of the lake and driving certain periods of the annual cycle. The effects of these processes on the spatial patterns of the system were further clarified by the application of non-parametric multivariate methods and visual representation of the results.

The configuration of the stations in space based on multidimensional scaling is illustrated in Figure 6. The positive part of the horizontal axis (dimension 1) is mostly associated with high values of chlorophyll a, dissolved oxygen and pH, and low values for nitrate and inorganic phosphorus. Scores on the vertical axis (dimension 2) increased with nitrate, inorganic phosphorus, total nitrogen and total phosphorus concentrations. It can be seen that the discrimination between offshore and inshore stations was the most clear result of this analysis. Moreover, the group of the deeper sampling sites was further subdivided into a new bipolar pattern: the group of the stations [0831], [840] located at the southern part of the lake and stations [826], [0852], [890] at the central and northern parts of the

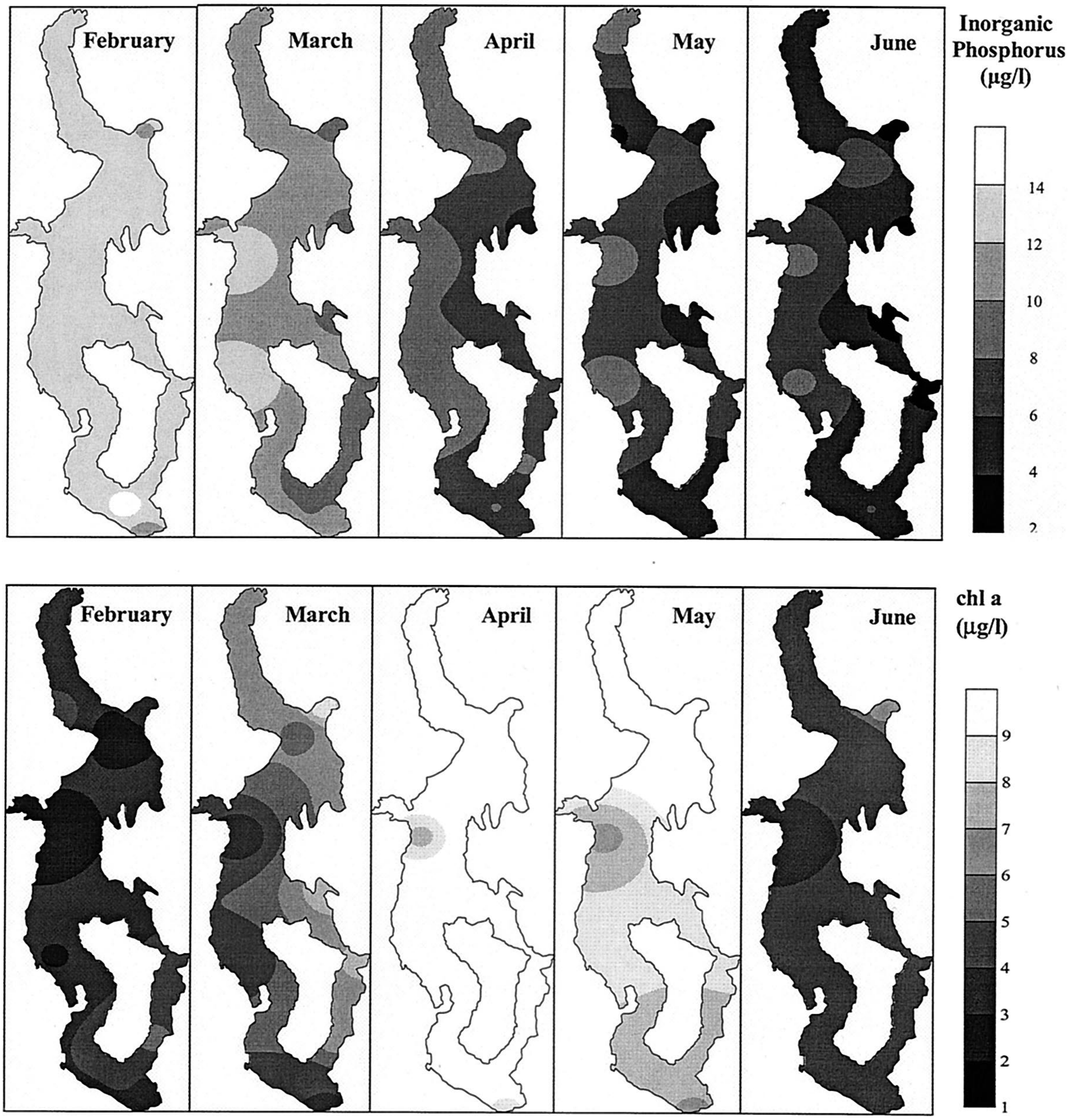

Figure 7. Spatial heterogeneity of inorganic phosphorus and chlorophyll *a* in Lake Washington during the period of the spring phytoplanktonic bloom.

lake. A possible reason for this pattern may be the lower nutrient levels in the southern end of the lake, which may in turn be due to Cedar River inflows. The low Cedar River total phosphorus concentration (which was the lowest among the streams in the watershed) enhanced by the hydrodynamic regime of this area may have diluted nutrient concentrations in the southern end of Lake Washington. On the other hand, the shallow stations were totally dispersed in the plot, not allowing for any kind of hypothesis generation about their groupings. These stations may be more directly influenced by shoreline activities and more tightly related to the quality and quantity of the respective inflowing stream waters.

Phytoplankton has a prominent role in Lake Washington and significantly influences the patterns of the other water quality parameters, especially during the spring bloom. The chronological sequence of maps in Figures 7 and 8 present the spatial and temporal evolution of the four main water quality parameters (inor-

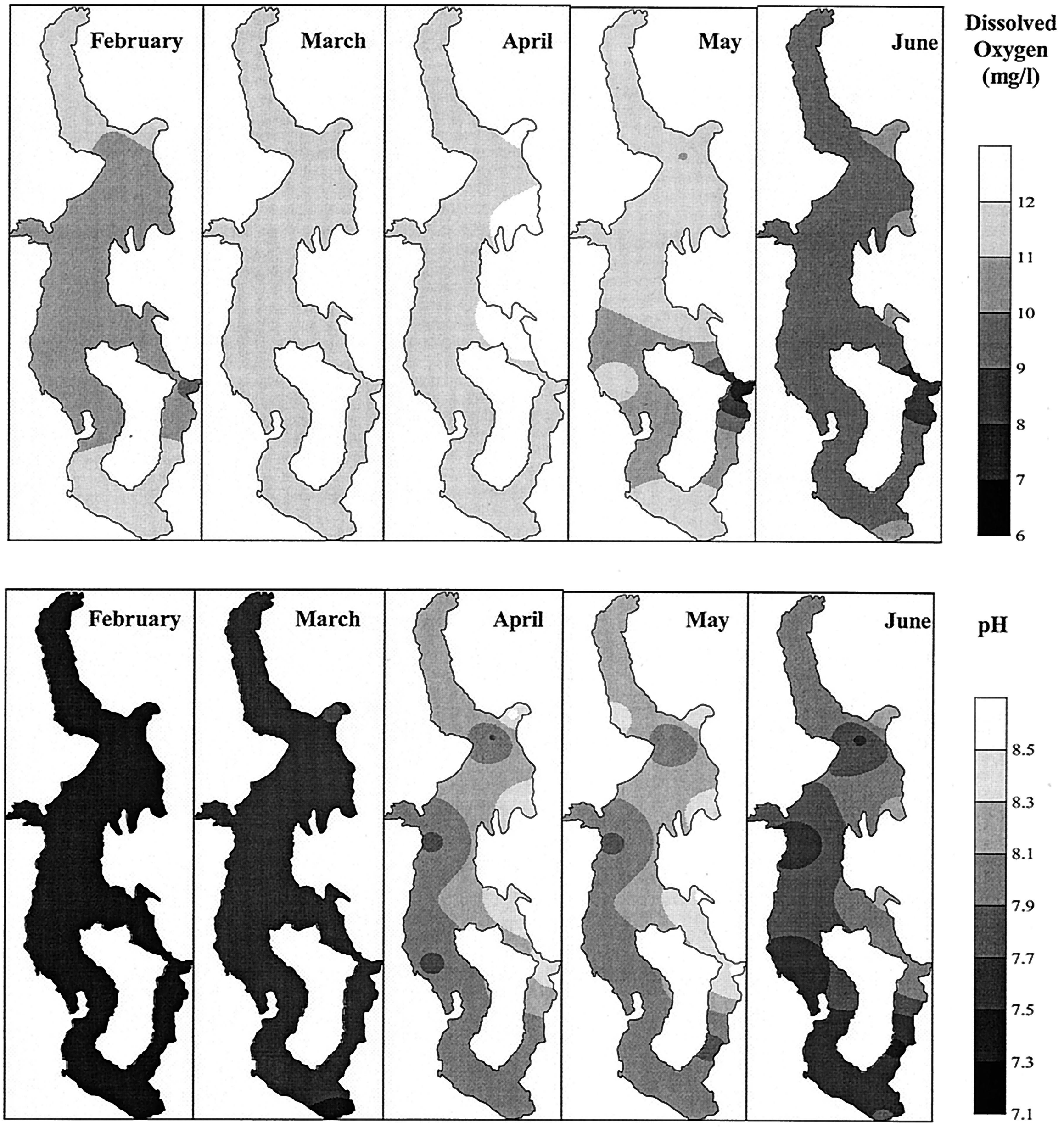

Figure 8. Spatial heterogeneity of pH and dissolved oxygen in Lake Washington during the period of the spring phytoplanktonic bloom.

ganic phosphorus, chlorophyll *a*, dissolved oxygen and pH). These maps were based on the monthly mean values for each station averaged during the study period of 1995–2000. The interpolation was based on the Inverse-Distance Weighting Method. Moreover, it should be noted that these plots only depict trends in the epilimnion of Lake Washington and do not take into account the effects of the vertical mixing processes. Inorganic phosphorus concentrations approached their highest annual values ($\geq$12 μg/l) in February, with well-defined maxima in the shallower areas and the northern part of the lake, which had significant inflows from the Sammamish River. Meanwhile, phytoplankton biomass (2.5 μg/l) and pH (7.2–7.4) remain totally unaffected, since the physical conditions (light, temperature) are limiting the phytoplanktonic growth. Dissolved oxygen (DO) concentrations had a uniform distribution over the lake, with concentrations generally around 10 mg/l. The limiting effects of the physical forcing are partially reduced in March and therefore the first signs of the primary producer-driven responses are observed mostly around the northeastern shoreline, accompanied by a decrease in inorganic phosphorus in the respective portions of the lake. pH is stable (7.2–7.4), whereas dissolved oxygen increases to greater than 11 mg/l throughout the lake. This marked increase in DO can only be partly explained by increased photosynthetic activity. Another partial explanation for this change could be the influence of the inflowing stream water, characterized by similar DO values which have their annual maxima during this specific period (KCWQR 2000).

The dynamics of the lake during the following 2 months (April and May) are mostly dominated by the spring phytoplankton bloom, resulting in a spatially uniform increase in chlorophyll *a* ($\geq$9 μg/l) and dissolved oxygen ($\geq$11.5 mg/l), whereas inorganic phosphorus is reduced to one-half of its previous concentrations and approaches 6 μg/l, particularly in the northeastern parts of the lake. Meanwhile, the shallow sections of the lake were characterized by an increase in pH ($\approx$8.4), indicating the ability of autotrophic activity to impact the bicarbonate system. The high pH values persisted in shallow water until June, whereas chlorophyll *a* and DO were significantly lower (3 μg/l and 8.5–9 mg/l, respectively) by this time. Inorganic phosphorus had its minimum values over the annual cycle (4 μg/l) during June.

Another interesting aspect of this system's behavior was the lag in the responses and the narrower ranges of the water quality parameters fluctuations in the central western area around Mont Lake Cut. This section is the deepest part of the lake and therefore vertical mass-transport influences epilimnion dynamics, which, however, is not taken into account by the present study since the hypolimnetic data were excluded prior to the analyses.

Discussion

We assessed temporal, spatial patterns and cause-effects relationships for phytoplankton dynamics in Lake Washington, a moderately large, mesotrophic and temperate lake. This was done to elucidate the most important mechanisms that govern this lake's behavior and to determine possible deviations from classical conceptual models of phytoplankton community seasonal dynamics (Sommer and others 1986, Lampert and others 1986, Marshall and Peters 1989). This analysis was based on a database that provides a high spatial resolution for the study of the phytoplankton community and its interactions with the physical and chemical environment (light, temperature, nutrients) over the annual cycle. Our approach to this system follows the "traditional" concept of a physically controlled phytoplankton community, where its seasonality is driven from seasonal changes in temperature, light, nutrients or from mechanisms such as the balance between sinking due to gravity and resuspension by turbulence (Hutchinson 1967). The rationale of this approach for describing Lake Washington dynamics and the information that is lost when not considering biological interactions of the system (such as resource depletion followed by competition, grazing and predation), will also be discussed.

Based on the mean value of the atomic ratio TN:TP (mean 50) we infer that phosphorus is the limiting element for primary production in Lake Washington. Inorganic phosphorus and nitrate constitute 50% or more of the total phosphorus and nitrogen pools during most of the annual cycle. Autotrophic uptake, water column mixing and exogenous loading from tributaries primarily regulate the nutrient concentrations in the lake. During the winter, physical factors temperature and especially low light availability limit nutrient uptake by primary producers, resulting in high winter nutrient concentrations ($NO_3 \approx 300$ μg/l and IP $\approx$ 13 μg/l). The most common phytoplankton genera during this period were the diatoms *Aulacoseira, Stephanodiscus, Asterionella, Fragilaria,* the chlorophytes *Actinastrum, Ankistrodesmus* and the cryptophyte *Cryptomonas.*

As physical conditions become more favorable due to an increase of the day length and solar warming, a major phytoplankton bloom is stimulated in late February-early March. The transition phase from winter conditions to the spring algal bloom in Lake Washington is very abrupt and is characterized by a quadrupling of chlorophyll a concentrations (2.5–10 μg/l) and a substantial reduction in inorganic nutrient concentrations ($NO_3 \approx 200$ μg/l, IP $\approx$ 9 μg/l) during a period of less than 1 month. This well-differentiated spring bloom contradicts the concept of a moderate increase of phytoplankton biomass in oligotrophic lakes as described in the meta-analysis of 56 north-temperate lakes from Marshall and Peters (1989), where Lake Washington was classified as oligotrophic (Table 1 of the study). During the development of the bloom, the increased photosynthetic activity has a regulatory role in the carbon cycling processes (pH 8.4) and also causes the annual dissolved oxygen ($\geq$11.5) maxima. Low nutrient concentrations (6 μg/l)—especially for phosphorus—probably cause the major decrease in algal biomass after May, to a level of 2.5–3 μg/l during the summer-stratified period. This low-biomass phase persists throughout the summer, since thermal stratification minimizes vertical mixing in the lake and nutrient replenishment from the hypolimnion. The summer mixing depth varies from 8–10 m, whereas the vertical eddy diffusion rate based on heat flux measurements is estimated to be about 0.02 cm^2/sec (Quay 1986). Shifts in the phytoplankton community composition also occurs with diatoms being replaced by chlorophytes (*Oocystis*, *Sphaerocystis*) and cyanobacteria (*Anabaena*, *Anacystis*, *Microcystis*), which have lower growth rates but are also more resistant to sedimentation because of their buoyancy.

In its current recovered state, Lake Washington does not develop a significant autumn phytoplankton bloom and true succession biological events up to the period of the autumn erosion of the mixed layer are not observed, at least in ways usually reported in classical conceptual models (Sommers 1986, Marshall and Peters 1989). Similarly, the phytoplankton composition remains fairly constant with the most noticeable change being the reappearance of *Melosira* as a dominant genus after September. The duration of the thermally stratified period varies from 210–280 days and the lake usually becomes isothermal in December. During the time thermal stratification decays, epilimnetic nutrient concentrations increase markedly, mostly due to the release of the nutrients formerly in the hypolimnion. Reduced light availability, deep mixing and low temperatures result in low or negative net primary production, which causes a decline in phytoplankton biomass to the winter minimum (2–2.5 μg/l).

It can be claimed, however, that this conceptualization of the lake as being driven by physical factors contradicts somewhat the interpretation of many classical studies that emphasize the role of biological interactions on the temporal development of phytoplanktonic communities in idealized "standard" lakes (Sommer and others 1986). In other words, we are addressing the question: "Which is the role of zooplankton in the lake and how objectively can someone conceptualize Lake Washington without taking into account zooplankton dynamics?" Since zooplankton data were lacking from this monitoring program, we sought information from past (Edmondson and Litt 1982, Infante and Edmondson 1985, Edmondson 1994, 1997), and recent (Scheuerell and others 2002) studies of the lake. It appears that arguments for a dominant role of zooplankton and significant interactions with the phytoplankton community can be supported for only two periods of the annual cycle. The first period is associated with the spring phytoplankton maximum and the subsequent collapse of the spring bloom. It was observed that this maximum occurs very close to the time when *Diaptomus* populations—the dominant species of zooplankton at this time—climb above a point (25 ind/l) at which its density is sufficient to produce grazing rates that exceed phytoplankton growth rates. At the same time, the fraction of primary production respired by the zooplankton community was about 0.6, which was the highest value over the annual cycle (Devol 1979). However, at times phytoplankton biomass was observed to increase after this zooplankton density was reached and therefore it is not clear if grazing rates or nutrient limitation is the primary cause for the decline of phytoplankton biomass and the species composition shift at the end of the spring bloom.

The second period when zooplankton seems to have clear interactions with the phytoplankton is during the summer, when zooplankton nutrient recycling (mostly by *Daphnia pulicaria* and *Daphnia thorata*) provides 60–90% of the phosphorus input to the mixed layer (Richey 1979). During this time, the fraction of primary production respired by the zooplankton community was 0.25 and remained at this level from June to September (0.04 during the winter), indicative of an equilibrium between phytoplankton-zooplankton that sustains the algal biomass around a level of 3 μg chl *a*/l (Devol 1979). Additional evidence of a co-dependence and tight relationship between phytoplankton community and *Daphnia* is the decrease in *Daphnia* fecundity, from an average spring level of 3 to 1 egg per female during the summer period. Increased cyanobacteria concentrations and especially decreased algal biomass (chla concentrations) was shown to have the strongest correlation with fecundity (Scheuerell and others 2002). Ballantyne and others (2002) showed a variety of measures of phytoplankton biomass (i.e., chl *a*, particulate carbon, particulate nitrogen, particulate phosphorus, C:N and eicosipentaenoic acid) were good predictors ($r^2 = 0.61-0.74$) of daphnid growth when food was seston from Lake Washington. Phytoplankton-*Daphnia* dynamics seem to be a significant regulatory factor for the phytoplankton community properties (abundance and composition) from late spring until the end of September (Schindler unpublished data). During the remaining annual cycle the zooplankton dynamics seem to follow the interactions of phytoplankton with the physical driving forces of the system or alternatively to be the effect rather than the cause of phytoplankton patterns.

Another basic aim of this study was the partitioning of the total observed variance in the lake which indicated that patterns in Lake Washington are mostly dominated by temporal variability, whereas spatial heterogeneity is rather low. However, it was found that there are some periods during the annual cycle when some sections of the lake have different trends in terms of nitrate, inorganic phosphorus and pH. These spatial discontinuities in the case of pH were mostly attributed to the differences between the deep and shallow sections of the lake, since the bicarbonate system is less effective in buffering pH in the smaller water bodies, making them more susceptible to wider fluctuations (Harris 1986). Lags in the responses and narrower ranges with respect to nitrate and inorganic phosphorus characterized the deep central western area of Lake Washington and are mostly associated with mass exchanges due to vertical mixing between the upper and lower layers of the lake. Moreover, the lower nutrient levels in the southern end of the lake can be attributed to the dilution effects of discharges from the nutrient-poor Cedar River. The influence of this heterogeneity on primary producers and grazers of the system is questionable. For example, this study showed that the phytoplankton biomass increases more or less uniformly during the spring bloom. The horizontal distribution of *Daphnia* in Lake Washington was described as fairly patchy compared to *Diaptomus* populations, however, the observed patterns were neither consistent nor general and were associated most closely with wind (direction, velocity) than with phytoplankton distribution along the horizontal plane (Edmondson and Litt 1982).

The spatial and temporal variability of Lake Washington is dominated by phytoplankton dynamics, which in turn are mostly associated with the availability of physical and chemical resources (light, temperature, nutrients). In our study we found regular intra-annual patterns for the most important environmental variables, but the lack of clear biological interactions between the phytoplankton and higher trophic consumers in the lake during parts of the annual cycle and the dependence of the planktonic community upon the stochasticity of weather can result in unpredictability of the system. Past incidents have suggested that unusual meteorological conditions may have been the cause of significant and unexpected structural shifts in the phytoplanktonic community, i.e., the 1988 outburst of *Amphanizomenon* (Edmondson 1997). A compromise between space and time of the current monitoring program, with emphasis on greater temporal resolution, might be a beneficial step for further illuminating the dynamic properties of the system during the transient periods of the year, especially the periods before, during and immediately after the spring bloom.

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