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Multivariate analysis of the Lake Michigan phytoplankton community at Chicago¹

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BAYBUTT, R. I. and J. C. MAKAREWICZ (Dept. Biol. Sci., SUNY Brockport, Brockport, NY 14420). Multivariate analysis of the Lake Michigan phytoplankton community at Chicago. Bull. Torrey Bot. Club 108: 255-267. 1981.—Ordination techniques were used to analyze phytoplankton and water chemistry data collected between 1927 and 1978 from Lake Michigan at Chicago. Ordination analysis summarized the phytoplankton data and illustrated the progression from oligotrophy to eutrophy and the subsequent reversal of cultural eutrophication after 1970 in the nearshore waters of Lake Michigan at Chicago. The analysis highlighted a significant correlation between blue-green algal biomass and Na⁺ concentration. The increase in mean annual Na⁺ concentration in Lake Michigan at Chicago and the experimental evidence implying a Na⁺ requirement for blue-green algae suggested that the increase in blue-greens, although influenced by P enrichment and by other factors, such as CO_2 availability, allelopathic effects and N:P ratios, may also be linked with increases in Na⁺ concentration.

Key words: Lake Michigan, phytoplankton, sodium, multivariate analysis

Classical, non-ordination techniques relating alterations in phytoplankton composition and abundance to changes in essential nutrients in experimental or descriptive studies have been informative in assessing the trophic state of many lakes. In Lake Michigan, changes in flora indicative of the progression from an oligotrophic to a more productive state (Stoermer 1967) were attributed to variations in the abiotic environment. With increased phosphorus (P) loading (Tarapchak and Stoermer, 1976), silica depletion by diatoms in Lake Michigan would be expected to eventually cause their own reduction. Blue-green (Cyanophyta) and green (Chlorophyta) algae, which are not dependent on silica, were expected to become major components of the phytoplankton community (Schelske and Stoermer 1972). In the nearshore zone of the Chicago area of Lake Michigan, this alteration in the community did indeed occur, with an increase in the blue-green

algal populations and a decrease in diatom populations between 1970 and 1974 (Makarewicz and Baybutt 1981).

In their review of Lake Michigan phytoplankton research, Tarapchak and Stoermer (1976) examined indicator species to determine the trophic status of the lake. Generally, algal species indicative of eutrophic conditions were more abundant in the nearshore zone of Lake Michigan, especially in the Southern Basin. The generic composition and high algal biomass of the inshore waters of Lake Michigan near Chicago indicated that the inshore area was eutrophic by 1960 (Powers and Ayers 1967; Makarewicz and Baybutt 1981).

Makarewicz and Baybutt (1981) reviewed the long-term data (1927-1978) of the inshore region of Lake Michigan at Chicago available from the City of Chicago Water Filtration Plant and demonstrated the progression from oligotrophy to eutrophy and suggested a return of the inshore region near Chicago to a mesotrophic state by 1977. However, the reversal of cultural eutrophication suggested is confused by a dramatic increase in blue-green algae in recent years, which may be related to alterations in chemistry other than P of Lake Michigan.

Although changes in composition and biomass are informative in assessing the trophic state of Lake Michigan, a holistic

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approach (viz., ordination) examining the community as a unit may provide further information by summarizing data in a concise manner and allowing statistical comparisons between abiotic and biotic variables and environmental relations within a lake not possible by traditional techniques. In this study we analyze the phytoplankton community of the nearshore waters of Lake Michigan at Chicago in relation to available water chemistry data by polar ordination and reciprocal averaging, review hypotheses explaining blue-green algal abundance in regards to the Lake Michigan phytoplankton and water chemistry data and suggest a hypothesis for the recent increase in abundance of blue-green algae in the nearshore waters of Lake Michigan.

Methods. We define community trajectory as the displacement of scores (i.e., similarity coefficients) calculated to summarize the total interactions of the genera within the community at a given time. Instead of examining each genus and its biomass, community trajectory reduces the dimensionality of the data and allows the general patterns of the total community to be established. One method of selecting community trajectory scores is multivariate analysis.

Multivariate techniques have been used successfully in terrestrial phytosociology (Bray and Curtis 1957; Grieg-Smith 1964; Orloci 1966; Hill 1973; Whittaker 1978). An effective technique in summarizing ecological data is ordination analysis, either direct (Whittaker 1967) or indirect (Bray and Curtis 1957; Orloci 1966; Hill 1973). Multivariate approaches to the analysis of algal data are less common but have been used to examine communities along specific environmental and seasonal gradients (Allen 1971; Levandowsky 1972; Allen and Koonce 1973; Holland and Claflin 1975; Baybutt 1978).

Using multivariate techniques, we analyzed data on phytoplankton and water chemistry from Lake Michigan collected at the South District Filtration Plant of the City of Chicago for over 50 yr. The sample site, data descriptions and a brief review of the phytoplankton community can be found in Makarewicz and Baybutt (1981). Data from the algal groups analyzed was expressed in biomass. The City of Chicago Water Treatment Plant has measured and calculated the volume of algal cells and colonies from their samples. We used these volumes or volumes calculated from the formulas of similar geometric solids, using mean dimensions of specific phytoplankton obtained from the literature (Patrick and Reimer 1966; Huber-Pestallozzi 1975; Prescott 1962). Species used for the volume calculation were selected on the basis of relative abundance determined from the work of Stoermer and Ladewski (1976), Stoermer and Yang (1970) and Briggs (1872). Volumes of the unidentified bluegreens, Chlorophyceae and diatoms are averages based on direct measurements of several genera not routinely identified but which are on the species list compiled by the Chicago Water Filtration Plant (apparently "rare" organisms are not routinely identified but are counted and recorded in their respective class). We converted algal volume to carbon by using Strickland's conversion (1960).

Water chemistry data were averaged on a yearly basis from seasonal surveys. The abiotic factors (dissolved Ca2+, Cl-, Mg2+, Na+, K⁺, sulfate, nitrite-N, nitrate-N, NH₄⁺, soluble reactive silica, total phosphate, orthophosphate, pH, alkalinity and hardness) were measured throughout the study by Standard Methods for Water Analysis (A.P.H.A. 1925, 1933, 1936, 1946, 1955, 1960, 1965, 1971, 1976). Sodium, K⁺ and Ca²⁺ were determined by flame spectrophotometry starting in 1949. The amino naphthol sulfonic acid method (A.P.H.A. 1960) was employed for phosphate analysis from 1949 into probably the early 1970's (Vaughn,³ pers. comm. to K. E. Damann,⁴ 1962). Phosphorus was not measured prior to 1949.

Programs for Polar Ordination and Re-

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⁴K. E. Damann, late Prof. Biol. Sci., S.U.C. at Brockport, N.Y.

ciprocal Averaging from the Cornell Ecology Program Series (Gauch 1977) were used to ordinate the data. A third technique, principle components analysis, did not yield any useful information because of extreme displacement of score values and is not reported. The automatic axis selection technique used relied on the first axis end points being selected by the reciprocal averaging procedure, which scales the axes relative to the square roots of the eigenvalues. The second axis was selected by the Bray-Curtis method for the selection of higher axes, using an orthogonal pair with the greatest separation. To partially define complex community gradients, which were represented by the ordination axes, regression analysis was used to establish relationships between the axes and the abiotic variables.

Results. THE 1927-1977 PERIOD. Ordination analysis of the 1927-1977 data was not immediately informative because of 'outliers' (Hill 1973). Outliers are species or samples which, due to their low similarities with other species or samples, compress the ordination scores for the other samples, thus distorting the axes and making interpretation difficult. Moore et al. (1970) and Hill (1973) have suggested successive refinement techniques to diminish the effects of outliers. The refinement procedure involves using the ordination to determine outliers, modifying or removing outliers and repeating the ordination analysis on refined data.

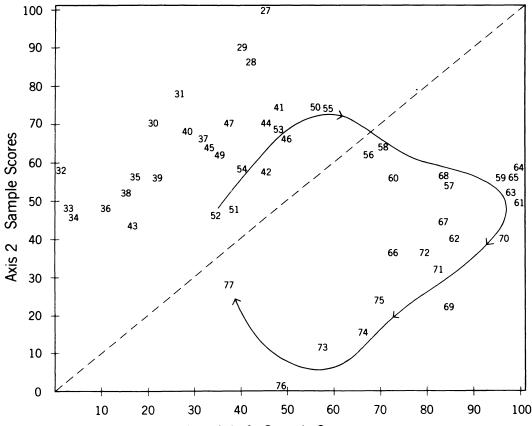
We used the refinement process to combine three diatom groups (all the Stephanodiscus species) and the four blue-green algal groups (Oscillatoria, Anabaena, Gomphosphaeria and the unidentified genera of blue-greens) into two single groups, Stephanodiscus and blue-greens, respectively. The necessity of grouping the Stephanodiscus species may be related to the apparent taxonomic confusion that existed in identifying species of this genus at the Chicago Water Filtration Plant (Ginsburg,⁵ pers. comm., 1978). The extremely low biomass of individual blue-green algal genera for the major part of the 50-yr period is a possible reason for the necessity of combining this particular group.

Because of the low biomass (<1% for 50 yr) and the absence of *Nitzschia* and the Chrysophyceae in some years, extremely low similarity measures were evident for these two groups producing a distorted ordination. A vast difference in scores, such as the one between Nitzschia and the Chrysophyceae and the rest of the data, will produce clustering of the ordination scores into uninterpretable packets, which must be separated either by removal of the major cause or by splitting data into smaller groups (Gauch 1977). The inability to split the two assemblages into smaller taxonomic groups necessitated the removal of Nitzschia and the Chrysophyceae from the ordination entirely.

After completing the successive refinement process, we used reciprocal averaging (RA) and polar ordination (PO) to ordinate the data. RA, which is a more objective technique than PO and produces a more ecologically meaningful first axis than other techniques (Gauch 1977), was used to select the first axis end points of both RA and PO. However, RA was affected by curvilinear distortion (Gauch, Whittaker and Wentworth 1977) in the second and higher axes. A second axis was obtained by using PO, which is not as susceptible to curvilinear distortion.

Comparison of axis 1 scores with total biomass revealed a biomass gradient beginning in 1934, when biomass was lowest for the 1927-1977 period, and ending in 1961, when maximum biomass was observed (Makarewicz and Baybutt 1981). The relatively close graphic positioning of 1952 and 1977 on the ordination diagram (Fig. 1) and the large shift in the scores from 1950-1951 indicated the beginning of a cyclic pattern in the community trajectory. Because of the separation of the two time periods and the apparent cyclic nature of the trajectory, the data were split into two groups, 1927-1955 and 1952-1977, for further ordination analysis. The ordination analysis of the 1927-1955 period did not

⁵W. Ginsburg, Chief Water Bacteriologist, Water Purification Laboratory, Chicago, IL.



Axis 1 Sample Scores

Fig. 1. Polar ordination of genera (mg C/m³) from Lake Michigan at Chicago for 1927-1977. Ordination scores scaled from 0 to 100.

reveal any interpretable trends or patterns in the phytoplankton community.

THE 1952-1977 PERIOD. For the 1952-1977 period (Fig. 2), one outlier beyond the original *Nitzschia* and Chrysophyta was found, the green algae. The green algae had low biomass and accounted for less than 1.1% of the total 1952-1977 community biomass. Because the green algae population was low, the similarity measures with the rest of the community also were low. The low similarity of this group with the rest of the community and the actual low biomass produced a distorted ordination and necessitated removal of this group to produce a meaningful ordination.

The refined axis 1 scores were found to be correlated with the total community biomass (r = 0.94) and significantly related to the concentrations of nitrate-N and total phosphate (Table 1). Total biomass, however, when compared to the nitrate-N and total phosphate concentrations, revealed a significant correlation only with nitrate-N (P < 0.01). The great amount of scatter between total biomass and nitrate-N concentrations (Fig. 3) suggests that other factors besides nitrate-N are affecting community structure. The interaction of nitrate-N with the total community is not readily apparent and may be coincidental.

The second PO axis scores were correlated with the logarithm of the blue-green algal biomass (r = 0.81). As blue-green algal biomass increased (Fig. 4), axis 2 scores moved higher on the axis (Fig. 2). Regression analysis of the PO scores and the abiotic variables revealed a single relationship with Na⁺ (Table 1) and with no other nutrient including Cl⁻. Further analysis re-

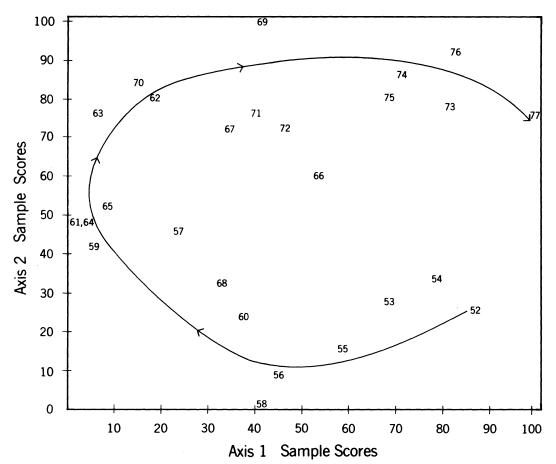


Fig. 2. Polar ordination of genera (mg C/m³) from Lake Michigan at Chicago for 1952-1977. Ordination scores scaled from 0 to 100.

vealed a significant regression relationship between the blue-green algal biomass and Na⁺ concentration (Table 2).

Discussion. In a traditional approach to the analysis of phytoplankton data for the Chicago water intakes (Makarewicz and Baybutt 1981), the progression from an oligotrophic to a eutrophic state in the inshore area at Chicago is illustrated. The emergence of the eutrophic indicator species (Tarapchak and Stoermer 1976) Stephanodiscus tenuis Hust. and S. binderanus (Kütz.) Krieg in 1956 and 1961, respectively, plus the increase in blue-green algae and the general decrease observed in the relative abundance of the oligotrophic-mesotrophic algal forms of Asterionella, probably A. formosa (Stoermer and Yang 1970), and Rhizosolenia, probably R. eriensis (Stoermer and Yang 1970), components of the phytoplankton community in the 1930's and 1940's, were all indicative of the progression to a eutrophic state. The accelerated eutrophication observed also produced a significant shift in the seasonal periodicity and in the apparent temperature optima of the phytoplankton community with spring peaks occurring in March (optimum temperature = $0-4^{\circ}$ C) from 1957 to 1976 instead of in May-June (optimum temperature = 10° C) as in the 1937-1956 period (Makarewicz, Baybutt and Damann 1979).

More recently (1970-1978), there has been a consistent general decrease in community phytoplankton biomass, especially of the eutrophic species *Stephanodiscus* spp. (19% in 1970 to 3% in 1977). The current trend in the phytoplankton community appears to illustrate a reversal of the

Axis	T-value	df	F-ratio	R ²	
Regression	3.57**	22	7.42**	43.5%	
Log Nitrogen	2.52**				
Log Phosphate	2.35**				
Axis 2					
Regression	-2.58**	24	22.2***	46.0%	
Sodium	4.72***				
** significant at P <	< 0.01				
*** significant at P <					

Table 1. Regression analysis of polar ordination scores for 1952-1977.

eutrophication process (Makarewicz and Baybutt 1981).

Ordination analysis also reflected the observed changes in the trophic state of the nearshore area off Chicago. Separation of data by the ordination analysis into two distinct time periods (Fig. 1) reflected changes in community composition produced by the eutrophication process. Also, the biomass gradient along the first axis illustrates the stages of eutrophication with those years with high phytoplankton biomass (>300 mg C/m³) (Likens 1975), indicative of a eutrophic state near the upper end of the axis, while those with low biomass (<100 mg C/m³) indicative of oligotrophy are at the lower end of the axis.

Changes in the phytoplankton community during the time period 1952-1977 (Fig. 2) illustrated the process of cultural eutrophication through 1970 and its subsequent reversal. The ordination scatter dia-

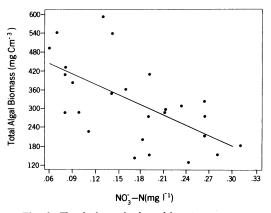


Fig. 3. Total phytoplankton biomass versus mean annual nitrate-nitrogen concentration (1952-1977).

gram illustrates the progression from a low algal biomass in 1952 to a high algal biomass in 1961. Those years with a biomass indicative of eutrophy (>300 mg C/m³) are below 50 and those with biomass indicative of mesotrophy (100-300 mg C/m³) are above 50 on axis 1. The total community biomass was correlated with the axis 1 scores and the increase in diatoms through 1961 and the decline after 1964 is clearly projected along this axis.

The decrease in algal biomass, the decrease in abundance of eutrophic indicator species, the apparent increase in silica concentrations (Makarewicz and Baybutt 1981) and the results of the multivariate analysis suggested a reversal of cultural eutrophication of Lake Michigan near Chicago. Only the increase in abundance of the blue-green algae (Fig. 5) to $\sim 22\%$ of the total biomass in 1977, due mostly to Oscillatoria and Gomphosphaeria, argues for accelerated eutrophication. This shift in the community to blue-green algae is generally characteristic of north-temperate lakes undergoing accelerated eutrophication (Hutchinson 1967; Tarapchak and Stoermer 1976).

The increase in percent composition of blue-green (Fig. 7) species and decrease in diatom species may be the response to accelerated eutrophication predicted by Schelske and Stoermer (1972). With decreasing silica levels due to diatoms responding to increased levels of P, species, such as bluegreens and greens with a minimal requirement for silica, may replace diatoms. However, the decrease in net algal biomass, the small increase in *Asterionella* and *Fragilaria*, the decrease in ambient phosphate

Regression	-3.74**	24	26.50***	50.5%
Sodium	5.15***			

Table 2. Regression analysis for blue-green algae versus Na⁺ (1952-1977).

concentrations, the decrease in P loading, and the apparent increase in silica concentrations in nearshore waters of Lake Michigan at Chicago in recent years (Makarewicz and Baybutt 1981) suggest that this might not be the case. Furthermore, blue-greens failed to respond to P enrichments (in fact, they decreased in percent composition) in bioassay experiments when silica concentrations were maintained at ambient levels of Grand Traverse Bay of Lake Michigan (Stoermer et al. 1978). However, the result of the above experiment is compromised somewhat by the initiation of these experiments during the fall cooling period when blue-green populations were declining in numbers in the bay.

A response to decreased P loading (Fig. 6) to the nearshore region of Lake Michigan appears to be a decrease in community phytoplankton biomass. The increase in abundance of blue-green algae since the 1940's (Figs. 4 and 5) is possibly a response to some factor other than P (e.g., other nutrients, allelopathic effects). Although alkalinity (annual range = $98-126 \text{ mg/l CaCO}_3$) and pH (annual range = 7.6-8.6) are high (also, see Fig. 5), indicating a low CO_2 availability, CO_2 levels do not appear to be low enough to favor blue-green algae growth. For the alkalinity range observed at Chicago, a pH value of greater than 8.75 would be required before free CO₂ levels would favor blue-green algae growth (King

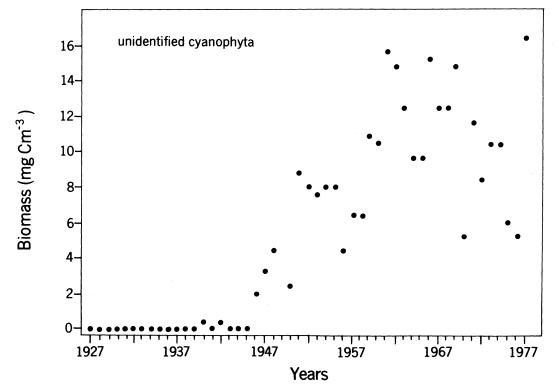


Fig. 4. Unidentified blue-green algae biomass from Lake Michigan at Chicago (1927-1977).

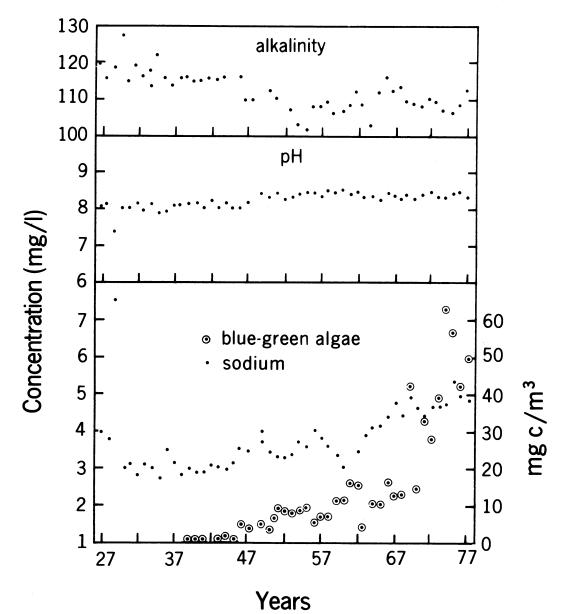


Fig. 5. Mean annual alkalinity, pH, sodium and blue-green algae biomass in Lake Michigan at Chicago (1927-1977).

1972). Schindler (1977) and Fee (1979) have suggested that low N:P ratios are conducive to growth of N-fixing blue-green algae. However, N:P ratios (Table 3) have been relatively high since the increase in abundance of blue-greens began in \sim 1970 (Fig. 5). Some other factor apparently controls the recent increase in blue-green algae.

The inverse relationship between blue-

green algae and diatoms suggests a possible allelopathic effect (Fig. 7). Various species of the emerging dominant blue-green algae Oscillatoria are known to release metabolites inhibiting population growth of diatoms (Keating 1977, 1978). Once a critical effective concentration is reached, allelopathy provides a mechanism by which blue-green algae may eventually predomi-

Table 3. The N:P ratios for 1970-1978 from Lake Michigan at Chicago. Ratios are by weight of NO_3^- - N to filtrable $PO_4^3^-$ - P.

Year	N:P ratio
1970	13
1971	14
1972	9
1973	17
1974	12
1975	25
1976	25
1977	25
1978	57

nate in a lake. Since a critical effective concentration has to be reached before dilution effects are overcome, it is unlikely that allelopathy is a mechanism affecting their occurrence initially or at low densities.

The regressions of Ca²⁺, Mg²⁺, K⁺, sulfate, nitrite-N, nitrate-N, NH4⁺, Cl⁻, soluble reactive silica, total phosphate, pH, alkalinity and hardness on axis 2 ordination scores or selective groups of phytoplankton were not statistically significant. On axis 2 of the ordination diagram (Fig. 2), the increase in blue-green algae (i.e., Oscillatoria and Gomphosphaeria and the unidentified genera of blue greens) is reflected by higher axis 2 scores. The ordination selected Na⁺ as a regression-related variable to the second axis scores. The relationship between the blue-green algae, Na⁺ and the second PO axis is interesting because it suggests that the concentration of Na⁺ is affecting recent blue-green algae development in Lake Michigan.

The exact metabolic basis for a Na⁺ requirement is not known (O'Kelly 1968); however, Lund (1965) states that Na⁺ may be involved with respect to the balancing of ions. Phosphate is indeed a highly charged anion that tends to associate strongly with cations (Van Wazer 1958). The active Na^{+}/K^{+} pump regulates the distribution of ions across the membrane and has the ability to accumulate ions within the cell or expel other ions. The role of the pump may be important to cell growth in that Na^+ may stimulate K^+ uptake (K^+ is necessary for protein synthesis and osmoregulation) and that Na⁺ influx (passive) may be coupled to P influx during active growth (Raven 1975). Sodium may also stimulate P uptake, especially in the presence of light (O'Kelly 1968). In the green algal *Chlorella*, the monovalent cations K^+ , Na⁺, Li⁺ and Rb⁺ are essential for the formation of polyphosphate bodies within the cell and are necessary for the uptake of phosphate (Peverly, Adamec and Parthasarathy 1978). Mohleji and Verhoff (1980) demonstrated an increase in P uptake by *Selenastrum capricornutum* as Na⁺ increased from 0 to 4 mg/l.

Laboratory studies have indicated that Na⁺ will stimulate blue-green algae development. In an examination of culture media for blue-green algae, Kratz and Meyers (1955) observed that growth in Anabaena variabilis Kg. emend. Geith, Anacystis nidulans Drouet and Nostoc muscorum (Kütz.) ceased in the absence of Na⁺ but was reestablished upon its addition. Anabaena requires Na⁺ to maintain a steady high rate of photosynthesis in resting cells (Allen 1952). Similarly, Anabaena flos-aquae (Lynb.) Bréb. requires both Na⁺ and K⁺ for growth (Bostwick, Brown and Tischer 1968). Ward and Wetzel (1975) observed an increase in C fixation in Anabaena cylindrica with the addition of small amounts of Na⁺ (5 mg/l) but not with large amounts of Na⁺ (50-150 mg/l). Allen and

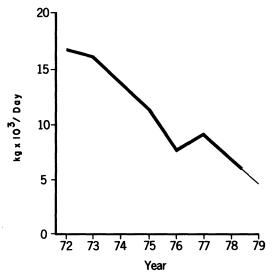


Fig. 6. Phosphorus loading from sewage treatment plants in Lake Michigan. Modified after Great Lakes Commission (1979).

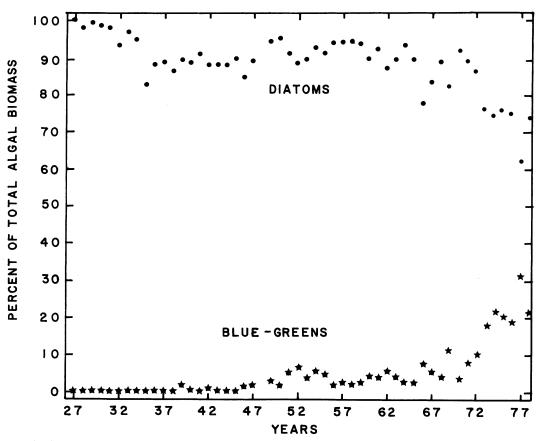


Fig. 7. Relative abundance of blue-green algae and diatoms in Lake Michigan at Chicago (1927-1977).

Arnon (1955) determined that 5 mg/l of Na⁺ is required for optimal growth of *Anabaena cylindrica* Lemm. while Kratz and Meyers (1955) noted that 4 mg/l of Na⁺ would not support maximum growth in three different blue-green species. A blue-green algal requirement for Na⁺, first shown by Emerson and Lewis (1942), is well established in the literature with an optimum growth rate at 5 mg/l (Fogg *et al.* 1973).

Interestingly, populations of Oscillatoria and Gomphosphaeria appeared and readily grew after mean annual Na⁺ concentrations in Lake Michigan at Chicago reached ~4.5 mg/l (Fig. 5). Although our data are sketchy, the decrease in Na⁺ and concurrent increase in blue-green algal biomass suggest a possible interaction in Lake Michigan at Chicago (Table 4). Sodium levels have increased in Lake Michigan at Chicago (Fig. 5).

Besides enriching lakes with P, N and organic material, urbanization also enriches lakes with Na⁺ (Provasoli 1958) from such sources as industrial (Torrey 1976)

Table 4. Sodium concentration and blue-green algae biomass in selected months. Sodium was measured usually in March, June, September and December.

	1969		1970		1972		1973	
	April	June	March	June	March	June	March	June
Sodium (mg/l)	6.0	4.6	5.9	4.2	5.0	4.6	6.0	3.7
Blue-green algae (mg C/m ³)	5.6	100.0	11.2	16.6	14.1	61.7	3.8	112.2

and domestic (Weinberger et al. 1966) wastes and from winter salting of roads (O'Connor and Mueller 1970), which eventually reach the lake via storm and combined sewers (Torrey 1976). In Lake Washington, Provasoli (1958) suggested that the occurrence of blue-green algal blooms may be related to increased Na⁺ levels caused by urbanization of the lakeshore and by possible inputs of small amounts of sea water into the lake from a canal. Sharp (1971) suggests that the mounting problems of nuisance algae (i.e., blue-green algae) in the Twin City lakes may be attributed to a Na⁺ build-up from street salt. Benoit (1969) states that blue-green algae may be limited in their growth by low Na⁺. By comparing lakes, further circumstantial evidence for a relationship between Na⁺ concentration and blue-green algae is evident.

In Lakes Erie and Ontario, the Na⁺ concentration has been greater than 5 mg/l since the late 1800's (Weiler and Chawla 1969). Both lakes have a significant bluegreen algal population (Vollenweider, Munawar and Stadelman 1974; Munawar and Munawar 1975). In Lake Huron where the Na⁺ concentration in 1968 was 3.2 mg/l (Weiler and Chawla 1969), blue-green algae were not a significant part of the open water phytoplankton; in waters affected by Saginaw Bay effluents, blue-green algal populations were high.

Saginaw Bay is heavily polluted (Vollenweider, Munawar and Stadelman 1974) and taxa of the Cyanophyta are the major component of the phytoplankton community (Munawar and Munawar 1975). Although Na⁺ concentrations were not measured for Saginaw Bay, Weiler and Chawla (1969) and Schelske and Roth (1973) have indicated that the Cl⁻ concentration has been double that of any other area in the lake for some time. Assuming that most of the Cl⁻ enters the lake as a Na⁺ salt and that a ~1:1 relationship between Na⁺ and Cl⁻ exists, Na⁺ concentrations should also have increased.

Lake Superior has Na^+ concentrations well below the other lakes, and the Na^+ and K^+ concentrations actually decreased from 1930 to 1968 with the average concentration in 1968 being 1.3 mg/l (Weiler and Chawla 1969). Blue-green algae do not comprise an important part of the Lake Superior phytoplankton community (Munawar and Munawar 1975).

With the enactment of the phosphate controls in 1972, P loading has decreased (Fig. 6) with a resulting decrease in overall algal biomass. However, Na⁺ is not removed by sewage treatment plants, and it is likely that Na⁺ inputs from storm drainage and surface runoff have increased with the increased use of salts for melting snow and ice in the winter. The increase in mean annual Na⁺ concentrations in Lake Michigan at Chicago and the experimental evidence of a Na⁺ requirement for blue-green algae suggest to us that the increase in bluegreen algae, although influenced by the enrichment with P and other factors such as CO₂ availability, allelopathic effects and N:P ratios, may be linked with the increase in Na⁺ concentration.

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