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DIATOMS IN LAKES AND LAKE SEDIMENTS AS AN INDEX TO ENVIRONMENT

Final Report, Part 2

A STUDY OF PHYTOPLANKTON DISTRIBUTION, LAKE CLASSIFICATION, AND TROPHIC INDICATORS IN MINNESOTA LAKES

Stephen J. Tarapchak

University of Minnesota
Minneapolis, Minnesota

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DISCLAIMER

ABSTRACT

This study was designed to 1) investigate patterns of phytoplankton distribution, to 2) contrast schemes of lake classification based on chemical and biologic criteria, and to 3) evaluate properties of net phytoplankton, whole-water communities, and diatom assemblages as indicators of trophic state.

The number of net taxa, desmids, and the compound quotient is correlated with the trophic gradient, but diatom ratios and the diversity of these assemblages are not so correlated. Conversely, the standing crop of phytoplankton and species diversity in whole-water samples exhibit statistically significant correlations with regional gradient parameters. Typological studies reveal that lake groupings based on different sets of variables are dissimilar in size, composition, and location, especially those that involve biologic variables. Algal properties that exhibit distinct trophic preferences are the numbers of net taxa and desmids, standing crop, and species number of whole-water communities. Desmids, chrysophytes, diatoms, and blue-green algae contain taxa that are indicators of oligotrophy and mesotrophy.

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The Study Region

Minnesota and eastern North Dakota and South Dakota is a region of diverse topography and many lakes. Continental glaciers have been largely responsible for shaping the present-day landscape. A variety of glacial deposits, ranging in thickness from a negligible amount in northeastern Minnesota to as much as 500 feet in west-central Minnesota, covers most of the region (cf. Fig. 1).

Much of the area is heavily forested (Fig. 2). A mixed coniferous-deciduous forest occupies most of northern Minnesota. A narrow band of deciduous forest extends diagonally from northwestern through central to southeastern Minnesota. In the west and southwest the major vegetation is prairie, consisting of grasses, herbs, and shrubs, with small stands of deciduous woodland around the margins of some lakes.

Most of the lakes in the region have been formed in one way or another by Pleistocene glaciation (Zumberge 1952). The majority of lakes in northeastern Minnesota originated in ice-scoured basins in bedrock. Throughout central Minnesota, where the drift is much thicker, many lakes have resulted from the formation of ice-block basins or from moraine-dammed basins. Throughout the prairie the lakes are relatively shallow.

The chemistry and biological productivity of the surface waters in the region are determined by many factors, including

the mineral composition of the bedrock, the nature of the glacial drift, surficial deposits and soils, and by general climatic conditions and basin morphometry. The following discussion has been taken from Bright (1968), Arneman (1963), Eddy (1963), and Winter (1973).

In northeastern and parts of northern Minnesota, a thin cap of red glacial drift that is low in calcium, potassium, sulfur, and magnesium covers most of the region. Outcrops of igneous bedrock occur extensively throughout the area. Thinly to coarsely textured soils of gray-brown, brown podzolic, gray wooded, and brown forest types occur throughout the region. The lakes generally are low in nutrients and have active outlets.

Throughout central Minnesota, crystalline igneous and metamorphic rocks underlie relatively thick surficial deposits of calcareous glacial outwash and calcareous and noncalcareous glacial tills. The soils are chernozems, podzolic, and medium to finely textured prairie types. The complex of bedrock, glacial till and outwash, and soils is much higher in calcium, magnesium, and sodium than are the tills and soils of northeastern Minnesota. Most of the lakes are deep and have active outlets.

In southwestern and portions of western Minnesota, the bedrock consists of crystalline rocks that are overlain by patches of Cretaceous shale. The surficial deposits consist

primarily of calcareous glacial tills in the southwest, and calcareous clay and silts and sand in the extreme western portion of the region. Soil types in the prairie are variable but consist primarily of chernozem and medium to finely textured prairie soils and organic soils of glacial lake plains in the extreme western and northwestern region of the state. The complex of bedrock, soil types, and surficial deposits in southwestern Minnesota generally is high in calcium, potassium, and magnesium. The region of surficial Cretaceous shale in extreme western Minnesota is relatively lower in magnesium and calcium and is higher in sulfur. The lakes generally are shallow, and many lack active outlets.

Selection of Lakes

The study lakes were selected primarily on the basis of geographic location. Efforts were made to include lakes in each of the major vegetation zones in Minnesota (Fig. 2). Within these regions, specific lakes were chosen on the basis of their chemical characteristics (Bright 1968, Gorham 1971). In order to include a range of conditions within each province, typical as well as atypical lakes were selected.

The lakes were arranged in alphabetical order and numbered 1 - 68 (Fig. 3). Lake numbers are used consistently throughout the text, Tables, and Figures. The precise location of each lake is given by State, County, and identification number in Table 1.

CHAPTER II

METHODS, MATERIALS, AND OBSERVATIONS

Field Procedures

Most of the phytoplankton samples were collected on three major field excursions. Two trips were conducted during September and October 1970; a third was undertaken in September 1971. Collections from several lakes were obtained on minor excursions during fall 1970 and 1971 (Table 12). Sampling during both years was restricted to the fall season. This scheme permits algal properties or lakes to be compared on the basis of samples that represent the same seasonal community. In addition, the difficulties of obtaining a representative sample from a lake are minimized. At this time of year, the entire water column or the largest part of it generally is isothermal or nearly isothermal and well-mixed. Such homogeneity greatly reduces the bias that can be associated with attempts to obtain samples from lakes that might normally exhibit vertical stratification or "patchiness" in the distribution of phytoplankton populations (cf. Richard et al. 1970).

Samples were collected from the euphotic zone from a 10-foot aluminum pram or from a two-man rubber boat. In order to minimize the contamination of samples by populations of littoral and benthic algae, collections were made in the deepest

part of each lake, and as far removed from shore as possible. Sampling in each lake generally was limited to a single station.

Net phytoplankton samples were obtained by using a six-inch-diameter net of No. 20 mesh silk bolting cloth. The net was lowered to a depth of 2x secchi-disc transparency and then pulled slowly to the surface. Although secchi-disc transparency can be regarded as the lower limit of the euphotic zone (Hutchinson 1957), the distance was doubled in order to capture algal populations that may be carried by currents just below the euphotic zone, or that may sink temporarily out of the zone during periods of calm weather (cf. Hutchinson 1967). As a general practice, hauls were made on a diagonal, thus minimizing sampling bias that could occur as a result of temporary horizontal and vertical variations in the distribution of plankton. Concentrates were transferred to vials and preserved with three to six drops of Lugol's acetic acid solution (10 gm I_2, 20 gm KI, 200 ml distilled water, and 20 gm glacial acetic acid). The net was rinsed in lake water immediately after use, and again in the next lake before obtaining a haul.

The above procedure was abandoned in most prairie lakes. Many lakes are only three to six feet deep and have secchi-disc transparencies < 2.0 feet. Net hauls in these lakes consisted of surface water only.

Quantitative algal samples were collected by following a procedure recommended by Lund and Talling (1957). A five-eighths inch garden hose was lowered vertically to a depth of approximately 2x secchi-disc transparency. This "water column" sample was transferred immediately to a polyethylene container, shaken, and poured into amber glass bottles of 220 or 280 ml capacity. Each sample was preserved with five drops of Lugol's solution. In the shallow prairie lakes, water was obtained by allowing the sample bottle to fill at a depth of two feet.

At each lake a temperature profile was taken and specific conductance was measured. Temperature readings were obtained with a submersible battery-operated thermistor thermometer. Specific conductance was measured with a Model RA-2A conductivity meter (Industrial Instruments, Inc., N. J.). Measurements were made on "integrated" whole-water samples or on the surface water of shallow prairie lakes. For 35 of the lakes, 500 mls of unfiltered surface water was collected in polyethylene bottles and was used for measurements on the concentration of major cations and anions. These samples were refrigerated at approximately 10 C in the field.

Laboratory Procedures

The algal samples were processed by dividing each sample. One-half of the concentrate was preserved permanently with Transeau's solution (60 mls water; 30 mls 95% alcohol; 10 mls

formalin). The other half was readjusted with Lugol's solution and stored at 5 C.

The quantitative samples were readjusted with Lugol's solution, sealed with parafilm, and stored at approximately 5 C in the dark. This procedure allows a shelf-life of approximately one year. The amount of preservative added to the quantitative samples was recorded, and was incorporated as a factor into the conversion of raw counts to absolute numbers.

Identification of Algae

The following standard references were consulted routinely: Prescott (1962), Smith (1920), and Huber-Pestalozzi (1938, 1941, 1950). Identification of the Cyanophyta was facilitated with the works of Geitler (1932) and Tilden (1910). The taxonomic treatments by Skuja (1948, 1956, 1964) were indispensible in the identification of cryptomonads, flagellated chrysophytes, and other monads. Two additional works on chrysophytes, Bourrelly (1957) and Matbichko (1965), were necessary for accurate identification of many taxa.

Two groups of algae, the desmids and the diatoms, required specialized literature. For the desmids, I used Smith (1924), Irénée Maire (1939), and West et al. (1904, 1905, 1908, 1912). In special cases, I followed Krieger's (1965, 1969) treatment of the genus Cosmarium and Krieger's (1937) monograph on the

genus Closterium. Teiling's (1967) monograph on the genus Staurodesmus was used exclusively. The criteria established by Brook (1959a) for the Staurastrum anatinum-group of desmids were followed in all cases.

Diatoms were identified primarily with the aid of Patrick and Reimer (1966), Hustedt (1930), and Cleve-Euler (1951).

Net Plankton Analysis

The objective of the analysis of net plankton was to compile a list of all species in the tows. Wet-mount slides were prepared, ringed with fingernail polish and examined with a Leitz compound microscope. Preparations from each sample were examined until a "new" slide did not yield a previously unencountered species.

The net plankton analysis was carried out in two phases. Samples preserved in Lugol's solution were examined first for colonial and delicate forms that tend to dissociate within a few weeks of collection. Generally, five to seven slides from each of the samples were examined. The second phase involved an examination of 12 to 18 wet-mount slides from the samples that had been preserved in Transeau's solution. This preservative frequently causes protoplasts to recede from the cell wall, which is advantageous in identifying desmids and dinoflagellates. For most of these samples, at least 15 to 20 preparations were examined.

Accurate identification of some chrysophytes (e.g., Mallomonas spp. and Synura spp.) requires that the dimensions, shape, and scale architecture be viewed in detail. Samples containing these species were examined with a Leitz Ortholux microscope that was equipped with phase-contrast optics. Wet-mount slides were allowed to dry, and observations were made with the aid of a 90x oil immersion objective.

Two special taxonomic studies were undertaken. Desmid populations in approximately 35 samples were reexamined to insure that the separation of closely related species in the Staurastrum anatinum-group was internally consistent. Diatom preparations from 40 lakes were reexamined to confirm the identity of Synedra spp., Cyclotella spp., Fragilaria spp., Nitzschia spp., Stephanodiscus spp., and Melosira spp.

Since very little information exists on the precision of estimates on species numbers, samples from six lakes were examined in duplicate (Vermilion, Burntside, Moose, Mille Lacs, Big Kandiyohi, and Clear). The counting procedures are outlined above. Species number estimates range between $\pm$0.9 and $\pm$14.5 per cent of the mean, with a mean value of 7.6 per cent. This bias is judged as insignificant.

Calculation of the compound quotient

The value of the compound phytoplankton quotient (Nygaard 1949) is highly dependent upon the species that are used in its calculation. The quotient is calculated by summing the

number of species of Centrales, Chlorococcales, Myxophyceae, and Euglenineae and dividing by the number of desmid taxa in a sample. It is recommended that only planktonic taxa should be included in the computation (Brook 1959b, 1964, 1965). In this study, quotients were computed exclusively on the basis of the planktonic flora of net samples. Varieties were weighted equally with species following Brook (personal communication).

The taxa that were used to compute the quotient are listed in Table 57. These species are considered to be planktonic, primarily on the basis of habitat preference as cited in Prescott (1962), Smith (1920), Smith (1924), Nygaard (1949), and Brook (1971). The desmid taxa utilized by Brook (1959b, 1964, 1965, 1971) were used to compute quotients in this study. Several additional species of desmids, however, were included in these computations. These taxa are indicated in Table 58. They were used because they occur with moderate frequency in Minnesota lakes or because I have observed them in plankton samples from Michigan, Ohio, and North Carolina. Samples with a zero term in the denominator were assigned a value of one desmid occurrence (following Brook, personal communication).

Since very little information exists on the precision of quotient estimation, samples from six lakes were examined in duplicate (Vermilion, Burntside, Moose, Mille Lacs, Big Kandiyohi, and Clear). Quotients range between $\pm$0.5 and

±13 per cent of the mean, with a mean value of 6.4 per cent. These errors are judged as insignificant.

Diatom Analysis

Diatom preparation

Diatom preparations were made exclusively from the net plankton hauls. Portions of the samples were transferred to centrifuge tubes and treated with Chromerge (Manostat Corporation, N. Y.). After a 24-hour period, the tubes were centrifuged three times, washing with distilled water after each centrifugation.

The diatom material was resuspended in one to five mls of distilled water and shaken thoroughly, and small volumes were removed with a clean pipette and placed on 20 x 50 mm coverslips. Each coverslip was spotted three times, each "spot" consisting of a different number of drops of the suspension. This practice allows for the selection of a "spot" that is neither over- nor under-dispersed with regard to the distribution of frustules. The coverslips were permitted to dry at approximately 100 F, and subsequently were heated at 300 to 350 F for a period of at least one-half hour. Permanent slides were made by inverting the coverslip onto a glass slide that had received two drops of Hyrax mounting medium (refractive index 1.65).

Diatom sample size and species numbers

The first consideration in diatom analysis was to select a suitable sample size. An examination of numerous published

studies reveals that a "standard" sample size has not been established. For example, Patrick (1968) counted over 14,000 specimens per sample, Patrick (1963), Hohn and Hellerman (1963), and Patrick et al. (1954) examined 7,000 to 8,000 individuals per sample. A count of 300 cells per sample is used routinely by Williams (1964), and Stockner (1971) and Stockner and Benson (1967) examined 100 to 150 cells.

In the present investigation, I have selected a minimum count of 500 whole cells. The rationale for this decision is based on several considerations. 1) This study is designed to utilize dominant and common species with no emphasis on rare species. 2) The investigations of Bright (1968, and unpublished) and Bradbury and Megard (1972, and unpublished) are based on an examination of 400 to 600 whole-specimens per sample. Thus, the results of the present investigation are compatible with previous and current studies in this region. 3) An attempt to include rare species would necessitate counts of perhaps 5,000 to 10,000 specimens per sample. Such a procedure would be inordinately time-consuming and is not within the logistical bounds of the present investigation.

A slide from each lake was examined by the transect method. In general, specimens tend to be distributed randomly on the preparation; however, in many instances there is a marked "edge effect". Large cells, e.g., Stephanodiscus niagarae, Fragilaria crotonensis, F. capucina, and Asterionella formosa

tend to accumulate around the periphery of the preparation. Therefore, to reduce over-representation of such specimens, a transect across the preparation was always completed. Whole cells were tallied as 1.0; separated valves were recorded as 0.5. The exact sample size for each lake is given in Table 22, and summarized statistically in Table 24.

The number of species encountered in a sample is dependent upon sample size (cf. Hohn 1959). Because the decision to use a count of 500 whole-cells per sample is arbitrary, an attempt was made to investigate the numerical contribution of less abundant species to the community.

A slide from each of nine lakes was prepared by the techniques outlined above. Sufficient diatom material was used so that 2-6 complete transects through one "spot" would yield about 1000 individuals. Specimens were identified, scored according to species on data sheets, and tallied to a level of 100 $\pm$ 2 individuals. The procedure was repeated until 1000 $\pm$ 2 cells had been enumerated.

A representative plot is shown in Fig. 4. As expected, the number of species encountered increases with sample size. The form of the curves, however, varies in different lakes. For example, in Lakes Trout, Shagawa, Elk, and Salt the accumulation of species tends to be linear with increasing count size. In Lakes Burntside, Itasca, Sallie, and Spiritwood, the species/individual curves appear to "plateau" near 800

individuals. The sample size used in this study certainly does not reveal all of the species that are actually present in a sample; in fact, if the sample size is increased to 4,000-5,000 individuals, the number of taxa recorded could easily double (cf. Patrick et al. 1954).

The numerical importance of the dominant and common species and the minor contribution of the less abundant species, however, can be demonstrated in these analyses. The percentage value of newly encountered species for an increment can be read on the right-hand ordinate of Fig. 4. An examination of percentage values indicates that, after 600 individuals are enumerated, the contribution of newly encountered species is generally < 2.0 per cent. It is reasonable to conclude that for the sample size utilized in the present study, the dominant and common species are adequately represented.

Effects of sample size on ratio estimates

Intuitively, an estimate of a diatom ratio would be expected to be dependent upon sample size. No information on this phenomenon, however, appears to be available. The three ratios utilized in this study (i.e. A/C_s Stockner and Benson 1967, C/P Nygaard 1949, and a modified A/C_t expression) were examined.

The data generated in the above analyses were used for these purposes. Estimates of each ratio were computed at cumulative increments of 100 individuals, to a terminal level of 1000 ± 2 individuals. In addition, two slides from each of

the nine lakes were examined in cumulative increments of 100 ± 2 individuals, to a terminal level of 500 ± 3 individuals. The presentation of the results is limited to three representative analyses.

The A/C_s ratio, a measure of the abundance of Araphidineae divided by the abundance of Centrales, generally shows significant variations in value, especially from 100 to 400 individuals (Fig. 5). In several lakes, i.e. Pickerel, Salt, and Elk, the value of the ratio does not "plateau" with increasing sample size, even in the range of 500 to 1000 individuals. Stockner and Benson (1967) and Stockner (1971) routinely examine 100-125 cells in two preparations from a sample. Moreover, they attempt to detect "small" differences in ratio value, i.e. 0 - 1.0 (oligotrophic), 1.0 - 2.0 (mesotrophic), and 2.0 (eutrophic) lakes.

These observations demonstrate that the A/C_s ratio is highly dependent upon sample size, and that an examination of 100 to 300 individuals is probably inadequate. A count of 500 - 600 individuals per sample, however, appears to give a reasonable estimate of the ratio.

The results of the duplicate counts are given in Fig. 6. Except for Lakes Spiritwood and Itasca, A/C_s estimates show moderate to strong dependence on sample size. In all of the lakes except Trout, duplicate estimates are in better agreement with one another at 500N than at lower levels. Six of the lakes

show reasonably good agreement between duplicate estimates at 500N; however, Lakes Salt, Elk, and Trout show highly significant differences in value at this level.

The effects of sample size on estimates of Nygaard's ratio are presented in Fig. 7. The ratio is derived by dividing the number of centric species by the number of pennate species. In five of the lakes (Burntside, Salt, Spiritwood, Sallie, and Itasca) the ratio is relatively stable over a count size of 1000 individuals. In the other lakes, however, there is considerable variation in the value of the estimate.

An examination of duplicate counts also reveals a marked dependency on sample-size, and varying degrees of agreement between estimates at the same levels (Fig. 8). Only Lakes Salt, Spiritwood, and Sallie yield increment values that appear to be independent of sample size. C/P values in Lakes Trout, Shagawa, Pickerel, Elk, and Itasca, however, are highly dependent on the number of specimens examined and, in addition, show significant differences in duplicate values at most levels.

Nygaard does not state explicitly the range of C/P values for trophic types. On the basis of his examination of 15 lakes and 20 ponds in Denmark, it appears that he uses the following limits: 0 - 0.3 (oligotrophy), 0.1 - 0.75 (mesotrophy), and 0.6 - 6.0 (eutrophy). The dependence of this ratio on count size indicates that lakes could be assigned to extreme trophic categories simply on the basis of the number of specimens that are examined.

The A/C_t ratio was derived empirically during the present study. The number of species in the two diatom groups, instead of the abundance of individuals, is used to compute a ratio.

The influence of sample size on A/C_t estimates is similar to that already demonstrated for the A/C_s and C/P ratios. Except for Shagawa Lake, estimates show considerable variation in the range of 100 to 400 individuals (Fig. 9). In five lakes (Itasca, Sallie, Burntside, Pickerel, and Spiritwood), the ratio appears to be independent of sample size, but in the other lakes estimates are moderately to highly variable, even from 500 to 1000 individuals.

Duplicate estimates showed that only one lake, Pickerel, appeared to be insensitive to count size (Fig. 10). Ratio values from the other eight lakes exhibit varying degrees of sensitivity to sample size. Agreement between duplicate estimates at the level of 500 individuals was not necessarily better than at 100, 200, or 300 individuals. An estimate of this ratio, therefore, is highly sensitive to sample size.

Evaluation and precision of ratio estimates

The data generated in the above investigations can be used to compare the relative dependence of each ratio on the size of the count. A mean square error (MSE) statistic was calculated over each cumulative increment of 100 individuals. As the "best estimate" of the true value of each ratio, the estimate at 1000 individuals was used. The design of the test can be

stated as follows.

Let H_o,i = the best estimate of the ratio R for lake i,

H_1,i = estimate of R for the 100 individuals N for lake i,

H_2,i = estimate of R for 200 N for lake i,

..

..

H_9,i = estimate of R for 900 N for lake i;

for lake i, $h_1,i = H_1,i - H_o,i$

$h_2,i = H_2,i - H_o,i$

..

..

$h_9,i - H_9,i - H_o,i$;

where h_{1-9},i is equivalent to the error in an estimation of R. The MSE statistic for each level for all nine lakes is

$$\text{MSE } (H_1) = \sum_{i=1}^{9} h_1^2, \; i/n-1$$

$$\text{MSE } (H_2) = \sum_{i=1}^{9} h_2^2, \; i/n-1$$

..

..

$$\text{MSE } (H_o) = \sum_{i=1}^{9} h_9^2, \; i/n-1$$

where H_1, H_2, ... H_9 are the MSE estimates for each level and n is the number of observations (here n - 1 = 8).

One would predict that, as sample size increases, MSE should decrease, an indication that R is approaching the "true" value. Furthermore, the rate of decrease in slope indicates the rate at which the error of estimation is undergoing reduction. The ideal situation would be one in which there was a relatively low initial (100-individual level) MSE value, followed at subsequent intervals by rapidly decreasing MSE estimates.

Interval MSE values are shown in Figs. 11, 12, and 13. In all three cases, there is erratic variation from 100 - 400 individuals. MSE values for the C/P ratio show a relatively linear decrease beyond 400 individuals. The same trend is evidenced for the A/C_t ratio, but beginning at 500 individuals. Highly erratic MSE values throughout the range of 100 - 900 individuals are observed for the A/C_s ratio.

The relative magnitude of MSE interval estimates provides an objective basis for ranking the ratios. At the level of 800 - 900 individuals, the error in estimation is greatest for A/C_s, lower for A/C_t, and least for C/P.

Because of the paucity of information on the precision of ratio estimation, especially in samples from different environments, replicated counts for each ratio were evaluated statistically. Three independent measurements from each of the nine study lakes were used to calculate two expressions for dispersion, the standard deviations and the coefficient of variation C. V. (Tables 2, 3, and 4). Two of the estimates

for each ratio were taken from the duplicate (sample size) analyses (the 500 $\pm$ 2 individual level); a third was obtained from the routine analysis of the 68 lakes. Sample sizes for the latter estimates can be found in Table 22.

The range in C. V. and average value ($\bar{x}$ for nine lakes) of each ratio can be summarized as follows:

A/C_s, 0.76 to 72.76, $\bar{x}$ = 31.83 per cent

A/C_t, 11.67 to 92.7, $\bar{x}$ = 41.56 per cent

C/P, 2.37 to 77.39, $\bar{x}$ = 31.47 per cent

The precision of ratio estimates can be judged as good, in a few cases, to poor in other instances. A C. V. > 30 to 35 per cent indicates relatively poor precision, especially if an attempt is made to impose the criteria of trophic placement proposed by Stockner and Nygaard.

The factors responsible for moderate to poor precision were not investigated systematically. In the present study, it is likely that 1) the "edge effect", 2) the clustering of individuals, 3) the retention of the filamentous or colonial state in some species, e.g. Melosira spp., Fragilaria spp., and Asterionella sp., and 4) the variation in the distribution of specimens on the preparation, all contribute to this bias. Improvements in precision undoubtedly could be achieved by increasing the sample size or by replicating the counts, or both.

The foregoing investigations on diatom ratios have led to the following conclusions: 1) Ratio estimates are highly sensitive to sample size, especially in the range of 100-400

individuals. 2) Replicate determinations indicate that the precision of estimation infrequently is good (C. V. < 10 per cent), more often moderately acceptable (C. V. 15-30 per cent), and in about one-half of the samples poor (C. V. > 40 per cent). 3) The MSE statistic ranks the ratios according to their dependence on sample-size, in order of greatest to least, A/C_s, A/C_t, C/P.

Quantitative Analysis

The quantitative analysis of whole-water samples was based on the methods proposed by Utermöhl (1958) and Lund et al. (1958). The inverted microscope technique, which utilizes natural settling as a method of concentrating phytoplankton, minimizes damage and loss of organisms and substantially reduces counting errors. A Wild inverted microscope (M40-82741) was used for all observations.

The quantitative samples were shaken thoroughly, poured into five or 10 ml settling chambers, and allowed to settle on a flat surface. Previous experience has shown that pipette-transfer of sample aliquots can result in fragmentation of delicate algal colonies. Settling times of at least 24 hours (5.0 ml chambers) or at least 48 hours (10 ml chambers) were used. Algae were identified at magnifications of 100, 200, 500, and 1000X. Counts were made by the transect method (Utermöhl 1958, Lund et al. 1958) and at a magnification of 500X.

Previous statistical studies (Lund et al. 1958) have shown that counts of 400 individuals per sample generally result in counting errors that are $< \pm 20$ per cent. In the present study, generally one sample aliquot per lake was examined, and 450-700 individuals were tallied. In lakes with small crops, two or three aliquots were examined. These procedures are consistent with those recommended by the International Biological Programme (Margalef 1969) and by the Biological Methods Panel on Oceanography (Wood et al. 1969).

There is disagreement regarding the most meaningful units for expressing quantitative data, i.e. "abundance" may be expressed as organisms (= individuals), cells, cell or individual volumes, or biomass (cf. Margalef 1969, and Wood et al. 1969). I have recorded "abundance" as physical units, i.e. unicellular organisms, filaments, and colonies were assigned a value of one. This procedure is commonplace and entirely consistent with the aims of the present investigation. Initially, an attempt had been made to compute volume estimates of individual taxa. Species in different lakes, however, vary in their size. Reasonably accurate estimates of algal volume would require measurements to be made on tens of thousands of individuals. Such a procedure is beyond the logistical bounds of the present study.

Phytoplankters were partitioned into "net" and "nannoplankton" during quantitative analysis. Organisms $> 60u$ were tallied as net plankters; those of smaller dimension were recorded as

nannoplankters. The 60 u limit is arbitrary, but it is in close agreement with the values used by many other investigators (cf. Kristiansen 1971). All of the standing crop estimates are reported as organisms/ml. Each one of them represents an average estimate of the number of organisms in 1.0 ml of water from the "euphotic" zone. They do not represent areal estimates of standing crop.

The precision of quantitative estimates was evaluated by counting duplicate samples from eight lakes. These results are given in Table 5. Counts varied from $\pm$0.6 to $\pm$12.8 per cent about the mean, with a mean of $\pm$5.1. The corresponding values for C. V. ranged from 0.8 to 18.1 per cent, with a mean value of 7.2 per cent. These results indicate that precision in the present study is significantly higher than in many other studies.

Selection of diversity indices

Several indices have been used to express diversity in algal communities. In the present investigation, two of the most commonly used expressions, D (Margalef 1958) and H (Shannon-Weaver Information index, 1963), were selected. This permits the greatest degree of flexibility in comparing the results with other investigations.

The index

$$D = S - 1/\log_e N, \qquad (1)$$

where S is the number of species and N the number of individuals,

was proposed originally by Gleason (1922). The index is independent of a theoretical statistical distribution. It is based on the presumed linear relationship between the number of species and the logarithm of the area or the logarithm of the number of individuals in a habitat. D is calculated by summing the taxa in a sample, less one, and dividing by $\log_e N$.

In Information theory, a measure of the total diversity of a system is given by the expression

$$D_N = \frac{1}{N_s} \log_2 \frac{N_s!}{N_1!\ N_2!\ \cdots\ N_m!} \qquad (2)$$

where there are m species and N_s total individuals (Margalef 1958, Shannon-Weaver 1963). In samples that contain large numbers of species and individuals, as in plankton investigations, the expression is usually abandoned, because it is cumbersome and time-consuming to calculate. The application of D_N to plankton studies, however, is not legitimate (Pielou 1966). The index is intended for use in systems in which all m and N_s are known. Generally, it is impossible to record all species in a plankton collection.

As an approximation of D_n, Shannon's (1963) index of diversity is used routinely:

$$H' = -\sum_{i=1}^{n} pi \log pi \qquad (3)$$

where pi is the probability of occurrence of the ith species

and n is the number of species. In samples, pi is estimated from n_i/N_s, i.e. the number of individuals in the ith species divided by the total number of individuals. This index combines the number of species with the apportionment of individuals among species (evenness) into an estimate of diversity. The choice of logarithms is arbitrary. In the present study, diversity is reported as bits/cell for diatoms, and as bits/individual for quantitative samples. Logarithms to base 2 have been used exclusively. The mathematical derivation of H has been presented by Branson (1953) and Brillouin (1956).

The evenness component of H diversity, J, was computed and used as a community property (Pielou 1969). J is calculated by dividing H by the theoretical maximum diversity ($\log_2$ of the number of species).

Properties of the indices

Measurements of diversity that are based on different mathematical or statistical expressions would be expected to be dissimilar in value. An examination of equations (1) and (3) indicates that both indices are equal to zero in monospecific populations, and that the value of each index is maximal when every individual in a sample belongs to a different species. D and H, however, are intrinsically different measures of community structure.

The index D does not discriminate between dominant, common, and rare species, i.e. all taxa are weighted equally. This

can be demonstrated for communities of 500 individuals, each containing a different number of species.

No. Species	D
10	1.45
15	2.25
20	3.06
25	3.86

As demonstrated earlier (See diatom sample size), the number of species encountered in analysis is, in part, a function of sample size. Thus, D would be expected to be highly dependent upon the size of the count (See also Effects of sample size on diversity estimates below).

Estimates of species diversity derived by Shannon's equation (3) are regarded as having two components: the number of species; and the relative abundance of individuals among species. The effect of species number and relative abundance on values of H is not as apparent as in the case of D. To evaluate the effect of species number of estimates of H, data from the diatom analysis of nine lakes were considered. For each lake, a sequential incorporation of ranked species was performed, i.e. the species are ranked in abundance, from highest to lowest, with H being calculated after each successive species incorporation. These results are shown in Fig. 14. The value of H increases rapidly as the most abundant species are added. After the 10-15 most abundant taxa have been incorporated, the value of H tends to become asymptotic. The addition of "rare"

species, therefore, has little effect on the value of H. These observations are in agreement with those reported by Sager and Hasler (1969).

Equivalence of indices

Phytoplankton communities have been compared on the basis of diversity values derived from different indices (cf. Margalef 1964 and 1968). It is pertinent here to investigate the numerical equivalence of the index values generated by H and D.

Three paired data sets of H and D were used for these comparisons. 1. A hypothetical population in which $H = H_{max}$ (theoretical maximum diversity) was constructed (Fig. 15). D and H values were calculated at each species level, to a total of 70 species. 2. The diatom diversity values that were generated in the present study (Fig. 16). 3. The diversity values of the whole-water samples that were generated in the present study (Fig. 17).

Correlation coefficients between H and D and paired t-test computations (Lewis 1966) for these contrasts are set out in Table 6. In each case, both indices are highly correlated, but the mean values are highly dissimilar. These observations indicate the indices do not yield values that are numerically equivalent. D and H should not be used interchangeably in comparing the diversity of algal communities.

Effects of sample size on diversity estimates

In any study that deals with species diversity of algal communities, one of the major objectives should be to obtain estimates that are independent of sample size. An examination of the literature demonstrates that investigators have used widely differing count sizes and appear to have avoided or ignored the bias that may be introduced by sample size. Biased estimates impose serious limitations on the extent to which valid comparisons can be made internally in a study, and, ultimately, hamper an objective evaluation of data reported by independent investigators.

In the present study, an attempt was made to evaluate the effects of sample size on estimates of D and H in diatom and in whole-water communities. Samples from nine lakes, representing the spectrum of chemical conditions encountered in the study region, were selected for study.

The data generated previously in the studies on diatom ratios were used in these analyses. Quantitative samples were adjusted so that three to four complete transects across the chamber were necessary to enumerate 1000 specimens. Individuals were tallied to a level of 100 $\pm$ 2 individuals, the data sheets scored according to species, and the procedure continued in cumulative increments of 100 $\pm$ 2 individuals until 1000 $\pm$ 2 specimens had been counted. In addition, duplicate counts from the same sample were made in increments

of 100 ± 2 individuals, to a terminal level of 500 ± 2 individuals. The presentation of results is limited to three plots that are representative of the nine analyses.

Diatoms

The effects of sample size on estimates of D and H in diatom communities are shown in Fig. 18 and Fig. 19, respectively. In Lakes Elk, Spiritwood, Trout, and Burntside, D is markedly sensitive to count size, especially in the range of 100 to 500 individuals. In the other lakes, the effects are less dramatic.

Comparatively, estimates of H are relatively stable throughout the range of 500 to 1000 individuals. Significant variations are noted in some lakes, but these occur between 100 and 300 individuals.

The results of duplicate counts for D and H are presented in Fig. 20 and Fig. 21, respectively. In most samples, D shows a marked dependence on sample size. Paired values in the range of 100 to 300 individuals, however, can vary significantly. Generally, duplicate values of D at a level of 500 individuals are in relatively good agreement with one another. Lakes Itasca and Burntside, however, show relatively large discrepancies between paired values even at the level of 500 individuals.

Conversely, estimates of H at and above the level of 200 individuals are less affected by count size.

Whole-water communities

The effects of sample size on estimates of D and H in whole-water samples are shown in Fig. 22 and Fig. 23, respectively. An estimate of D generally is markedly dependent on count size. In Lakes Itasca, Minnetonka, Vermilion, Loon, Elk, and Pickerel, D shows a highly dramatic dependence in the range of 100 to 500 individuals. In most of the lakes, D tends to increase with increasing sample size, and then to "plateau" at larger sample sizes. In three lakes (Shagawa, Vermilion, and Loon), however, D continues to increase even at larger sample sizes. Over the range of 100 to 1000 individuals, estimates of H tend to be remarkably consistent. Variations are confined primarily to the interval of 100-200 individuals.

Duplicated estimates of D and H are shown in Fig. 24 and Fig. 25, respectively. D tends to increase with increasing sample size. Estimates at the level of 400 to 500 individuals generally are in better agreement with one another than at lower levels. Lakes Minnetonka and Elk, however, exhibit a divergence of paired D values as the sample size is increased.

Paired H estimates, conversely, are in good agreement with one another, especially above the level of 200 individuals. There is no evidence of the degree of variability exhibited by D.

These observations demonstrate that, in diatom and whole-water communities, estimates of D can be highly dependent upon sample size. The explanation for this phenomenon is that the

index does not discriminate between the relative abundances of the species in a sample. A species that contributes a fraction of a per cent to a community (cf. Fig. 4) is weighted equally with a species that is a dominant member of the community. If the accumulation of species in a sample is rapid relative to the increase in total individuals (e.g. in communities with high diversity), the value of D generally tends to increase. Conversely, communities with relatively low diversity may show values of D that decrease as the size of the sample is increased.

From these observations it can be concluded that, in diatom communities, an estimate of D in the range of 100 to 400 individuals is biased. Counts of diatoms in which 500 to 600 individuals per sample are enumerated, as in the present study, provide estimates that are moderately sensitive to sample size.

Estimates of D in samples of whole-water, likewise, are sensitive to variations in sample size. In the present study, counts normally range between 450 to 750 individuals per sample. Index values are probably slightly to moderately biased by sample size.

A measure of H diversity in both types of samples is a highly conservative estimate of community structure. An enumeration of 300 cells in diatom communities or 300 individuals in quantitative samples, provides estimates that are virtually independent of sample size. The sample sizes used in this study are large enough to eliminate the bias.

The pronounced effects of sample size on D estimation is a highly significant observation. Margalef (1964) has suggested a trophic scale that is based on phytoplankton diversity values. Lakes with a value of 3.5 to 4.0 are classified as oligotrophic; those with values of 1.0 to 2.5 are considered eutrophic. Although Margalef does not give precise values for "mesotrophic" lakes, diversity estimates in the range of 2.5 to 3.0 are implied.

An examination of the effects of sample size on D in whole samples demonstrates that Lakes Elk and Nokay (Fig. 22) could be assigned to different trophic categories, depending entirely upon the size of the count. For diatom communities, Lakes Spiritwood and Burntside, likewise, could be placed in different trophic categories.

Evaluation and precision of diversity estimates

The comparative dependence of H and D on sample size can be ascertained with the use of the mean square error statistic (MSE). The rationale for the application of this statistic was given previously. As the best estimate of the true value of diversity, the estimate at 1000 individuals was used.

The results of these analyses are shown graphically for diatoms (Fig. 26) and for whole-water samples (Fig. 27). In both cases, H exhibits a very low initial MSE statistic, indicating that even at small sample sizes, the error in estimation is much lower for H than for D. In addition, H becomes asymptotic more

rapidly and at lower MSE levels than D. These data indicate that H is essentially independent of sample size between 300 and 400 individuals. Estimates of D, however, tend toward independence between 700 and 800 individuals.

Extremely few data have been published on the precision of diversity estimation. To assess the degree of variability that is inherent in counting techniques, replicate estimates of D and H in diatom and whole-water samples were evaluated statistically. Each data set consists of the nine samples. The three estimates of H and D diversity for each lake are independent measurements from the same sample.

The results of these calculations for the diatom samples are summarized in Table 7 and 8, respectively. The C. V. for D ranges from 1.49 to 27.17 per cent, with a mean of 10.70 per cent. H estimates are more precise. The C. V. ranges between 0.65 and 14.55 per cent, with a mean of 5.94 per cent.

The precision of D and H estimation in the quantitative samples is summarized in Table 9 and 10, respectively. Each estimate is based on a count of 500 $\pm$ 5 individuals. The C. V. for D ranges between 1.26 and 19.19 per cent, with a mean of 9.37 per cent. Replicate values of H generally are more precise than D. The C. V. for H ranges between 0.03 and 4.21 per cent, with a mean C. V. of 1.92 per cent.

These observations demonstrate that the precision of H estimation can be judged as good to excellent. A greater degree of precision was detected in whole-water samples than in diatom

samples. This probably is due to the combined effects of a reduced "edge-effect" and to a lesser degree of clumping in the samples.

In general, replicate estimates of D are less precise than H. The values of D reported in this study can be judged as acceptable to moderately acceptable. They can be used to evaluate regional trends or to compare groups of lakes by using average diversity values. A considerable degree of caution, however, should be exercised in comparing lakes on the basis of estimates that differ by < 20 per cent.

Chemical Measurements

The chemical analyses of major cations and anions were performed by Dr. M. Mantuani. The methods are essentially those outlined in Standard Methods (1965). The methods used by Bright (1968) are detailed in his report. Chemical analyses provided by E. Gorham are based primarily on the procedures given in Mackereth (1963).

Data Computation

Many of the statistical analyses were performed with a Control Data Corporation 3600 computer located at the University of Minnesota. Extensive use was made of several programs (University of Minnesota Statistical Programs Manual, Anderson and Frisch 1971): UMST 500; UMST 530; UMST 600; UMST 610.

Two programs for computing standing crop, several diversity indices, and related statistics were developed specifically for use in this study (Tarapchak and Buben 1973).

CHAPTER III

PHYSICAL-CHEMICAL CONDITIONS

In this investigation, temperature profiles were taken in each lake, and measurements were made on transparency, specific conductance, and the concentration of major anions and cations. The regional trends displayed by each of the latter three measurements are discussed in detail.

Temperature

The temperature of the surface waters of the lakes ranged between 5.0 and 17.5C (Table 11). These values are well below temperatures that normally occur at this latitude in July or August. The results of depth profiles of temperature indicate that most lakes were isothermal. Thermal stratification at depths below normal mid-summer levels, however, was encountered in several relatively deep, wind-protected lakes (Table 12).

Transparency

Secchi-disc transparency of the surface waters exhibits an 80-fold difference between the lowest (0.5) and highest (40.0 feet) measurements (Table 11). On the average, transparency is high in the lakes of northeastern Minnesota, and intermediate in lakes of the central region of the state. The prairie lakes, especially those in North Dakota and South Dakota, have transparencies that generally are < 3.0 feet, and often < 1.0 foot when visible algal blooms are present (Table 12).

Reciprocal secchi disc values are highly correlated with individual solutes, specific conductance, and the standing crop of algae (Table 13), an indication that transparency decreases with general chemical enrichment.

It is of interest to compare the transparency measurements made in this study with two previous investigations. Peterson (1971) sampled 1,451 lakes in Minnesota, and reported a median of 7.8 feet. His computations reveal that 818 lakes in northern Minnesota have a median transparency of 8.5 feet. Lakes in the central and in the southern area of the state have lower secchi disc values (5.5 feet for 411 lakes). The median value detected here is roughly comparable to Peterson's results, especially if the highly turbid lakes in South Dakota and North Dakota are eliminated in the computation.

The transparency measurements made by Bright (1968) can be compared directly with those of the present study. Eighteen lakes sampled by Bright also were included in the present study. For these lakes, the mean secchi disc value detected by Bright was 10.17 ($s = 11.5$); that of the present study was 9.51 ($s = 10.5$). A t-test utilizing a pooled estimate of variance indicates that the values are not significant at $P = 0.01$. Although transparency varies seasonally in the same lake, it seems to be reasonably stable over a broad region.

Specific Conductance

The salinity of the lake waters, expressed as specific conductance (umhos cm^{-1} at 25C), exhibits over a 2,000-fold difference in value (Table 11). The measurements range from 14 (Dogfish No. 17) to 31,783 (Eckelson No. 18), with a mean of 2,036 and median of 293. The disparity of an order of magnitude between the latter two values is due to the extremely high levels of salinity that were encountered in several prairie lakes.

Specific conductance may be used as an expression for salinity because of the degree of correlation between the two measurements (Hutchinson 1957). In this study, the mean level of salinity was 52.7 meq/l. A correlation between specific conductance in umho cm^{-1} at 25C and salinity in meq/l for 63 lakes yields a coefficient of 0.922. The predicting equation is $y = 36.5$ (salinity) + 163.

On a geographic basis, regional differences in salinity are reasonably well delineated. The general pattern consists of low (< 75) levels in lakes of northeastern Minnesota, intermediate values (150 to 500) in the majority of lakes located in central Minnesota, and high levels (> 1,000) in most of the prairie lakes (Table 12). These trends are comparable to those already reported by Bright (1968) and by Gorham (1971 and unpublished).

Specific conductance is a relatively conservative parameter in the majority of north-temperate dimictic lakes of moderate size. In small lakes with large drainage basins and in shallow prairie lakes, however, variations of over 100 per cent can occur seasonally or from year to year. Because of the importance of specific conductance in the ensuing analyses, the measurements that were made in the present study were compared with previous estimates (Bright 1968, Gorham unpublished).

These estimates are summarized in Table 14. A cursory examination of the data indicates that, except for a number of prairie lakes (No's. 8, 28, 48, 53, 58, 62) and several Shield lakes (No's. 33, 55, 64), replicated measurements for the same lake are in reasonably good agreement with one another.

In order to determine if this set of salinity measurements (1) is statistically similar to previous measurements (2), paired data sets for 52 lakes were compared (Table 14). The previous measurements were computed as a mean, and then all available estimates for each of the lakes were averaged. The results of these computations were:

		$\bar{x}$	s	r
1.	Present	1,202	3,054	1-2 = .759
2.	Previous	1,133	2,389	1-3 = .952
3.	Combined	1,175	2,569	2-3 = .922

A t-test utilizing a pooled variance estimate indicates that none of these contrasts is significantly different at $P = 0.05$. Because of the observation that differences in

salinity do occur seasonally, and can be expected to change dramatically in many of the shallow prairie lakes, I have elected to use the average value (3) in all subsequent calculations and analyses.

Specific conductance is significantly correlated with each of the major solutes, and exhibits a positive correlation with standing crop and an inverse correlation with secchi disc measurements (Table 13).

Major Solutes

The concentration of major cations and anions for 63 study lakes are presented in Table 15. These measurements were compiled from three sources: 1) the analyses performed in the present study; 2) the unpublished data of Gorham; and 3) the analyses reported by Bright (1968). Except for a number of prairie lakes, independent analyses of the major solutes in northeastern and central lakes are in extremely good agreement with one another. The procedure in selecting a representative suite of major solutes for these lakes was to utilize the determinations made in the present study. For lakes that were not analyzed chemically in the study, the data of Bright (1968) or Gorham (unpublished) are utilized.

A comparison of independent analyses of major solutes from several prairie lakes reveals that the concentration of individual ions varies by as much as 50 to 100 per cent. In an effort to select representative concentrations, two or more sets of data are averaged for some of the lakes.

The concentration of cations and anions in freshwater lakes should equal one another (Hutchinson 1957). For the ion suites given in Table 15, the concentration of cations and anions is 31.9 and 20.8 (meq/l), respectively (ratio = 1.18). This is a poor balance. If seven lakes are omitted (No's. 2, 3, 18, 23, 30, 38, 46), the mean cation and anion concentrations for 56 lakes are 12.5 and 12.2 meq/l, respectively (ratio = 1.02).

Summary statistics for the major solutes are set out in Table 11. Each ion exhibits a large range in value, especially chloride, sodium, and sulfate. Most ions are positively and significantly correlated with one another (Table 13).

The chemical characteristics of the surface waters exhibit marked regional differences. Lakes in northeastern Minnesota are dilute bicarbonate waters. Those distributed throughout central Minnesota are moderately to highly buffered bicarbonate waters. The prairie lakes are bicarbonate or sulfate waters, with relatively high concentrations of magnesium and sodium. A more detailed discussion of regional differences in solute concentration is presented in Chapter V.

CHAPTER IV

REGIONAL PATTERNS IN PHYTOPLANKTON DISTRIBUTION

One of the major objectives of the present study is to investigate patterns in the distribution of phytoplankton in Minnesota lakes. The existence of a broad spectrum of trophic conditions in the region provides a framework within which to evaluate numerous properties of diatom and phytoplankton communities as indicators of trophic conditions. The analyses undertaken here will focus primarily on net phytoplankton expressions, diatom ratios, standing crop of algae, and species diversity in communities of diatoms and whole-water phytoplankton.

Each of these expressions has been used or hypothesized as an indicator of trophic conditions in north-temperate lakes. The results of the present observations can be used to test these hypotheses generally, and to determine the degree to which the expressions apply to Minnesota lakes. Ultimately, these results will form a basis for selecting phytoplankton variables that can be used in investigating classification schemes of Minnesota lakes.

The Gradient Parameters

The concentrations of major anions and cations, secchi-disc transparency, and specific conductance indicate that the surface waters in Minnesota lakes exhibit marked trends along a diagonal that is oriented roughly northeast to southwest in the state. The lakes in northeastern Minnesota are chemically dilute

waters of high transparency. Prairie lakes in Minnesota and especially those in North Dakota and South Dakota are highly saline waters of relatively low transparency. Between these extremes in central Minnesota, lakes tend to increase in salinity from north to south, and in a westerly direction as well. The salinity levels and transparency of these waters are intermediate between the extremes.

The lakes in this region can be regarded as differing substantially in their nutrient levels and productivity. Moyle (1954) has shown that concentrations of total phosphorus and nitrogen increase from northeast to southwest. Mean levels of total phosphorus, for example, are 0.025 ppm in the northeast, 0.030 to 0.050 ppm in central Minnesota, and 0.100 ppm in the prairie. Total alkalinity (= $CaCO_3$ ppm) also increases from northeast to southwest. The mean alkalinity levels given by Moyle for these geographic provinces are similar to those detected in the present study.

The regional trends described above can be regarded as a trophic gradient (cf. Moyle 1954). On a volumetric basis, the northeastern lakes are lower in nutrients and less productive on the average than the lakes in central Minnesota. The prairie lakes in turn have higher nutrient levels and are more productive than those in the central region of the state. It should be emphasized, however, that "productivity" as used here and by Moyle is based on volumetric considerations. Most of the lakes

in the prairie are shallow, with euphotic zones that frequently are less than 1.0 m in depth (cf. Table 12). On an areal basis, however, the euphotic zones of the deeper lakes in central Minnesota may be more productive than those of the prairie.

The parameters that were selected to characterize the gradient are specific conductance, total alkalinity ($CaCO_3$), calcium plus magnesium ($\sum$ Ca + Mg), and secchi disc (SD). Each parameter exhibits a relatively large range between its extreme values (Table 11). The first three are low in the northeastern lakes and are high in the saline prairie lakes. Secchi disc is inversely correlated with these parameters, being high in the northeast and low in the prairie lakes. The standing crop of phytoplankton was used as a sole biological gradient parameter. Although it is a community property under investigation, it is used here as a rough measure of the level of plankton productivity (cf. Vollenweider 1971). The justification for its use is that it is significantly correlated with each of the other gradient parameters (Table 13). These five parameters that are used to define the gradient meet the requirements of trophic-state indicators. A further discussion and a rationale for their use as trophic-state variables in lake classification is presented in Chapter V (Trophic State And Selection Of Indicators).

All of these parameters are significantly correlated with one another (Table 13). Multiple correlation analyses, using each parameter alternatively as the dependent variable, indicate that the coefficients are highly significant (Table 16). These parameters, used singly or in combination, are regarded as representing a quasi "continuum". Collectively, they define the range of trophic conditions existing in the region. The symbols that are used throughout the remainder of the text and Tables are given in Table 17.

Methods Of Analysis

A variety of methods is available for the analysis of gradients. The techniques generally are either direct or indirect (cf. Whittaker 1967). Direct analysis will be used here. Simple and multiple correlation analyses were selected for this investigation (Steele and Torrie 1960). Simple correlation coefficients are given as r, multiple correlation coefficients as R. The significance of partial correlations for individual GP is indicated in the multiple correlation analyses.

The assumptions that underlie simple and multiple correlation analyses are similar. Both methods require that the dependent and the independent variable(s) are distributed independently and normally. In the case of some variables, the assumption is warranted; in others it is not. The theoretical distribution of the variables can be approximated by examining the mean to variance ratio. The fact that many distributions are not random

can be tolerated statistically, because the sample size is reasonably large and many of the variables and parameters have been transformed.

In order to insure that significant correlations are not masked by the choice of units (e.g. arithmetic values), phytoplankton variables and GP in many instances were transformed to $\log_{10}$ or reciprocal values. It should be emphasized that significant correlations between individual GP or combinations of GP and phytoplankton variables do not imply a direct "cause" and "effect" relationship. The distribution of algal variables is undoubtedly controlled or regulated by more than a single environmental parameter (cf. discussion in Hutchinson 1967). For example, it is unlikely that COND, ALK, $\sum$CA + Mg, or SD individually or in combination regulate the regional distributional patterns of the algal variables that are considered in this study. Such speculation could lead to spurious conclusions. The primary emphasis of the analyses undertaken here does not represent an attempt to establish direct cause and effect relationships; rather, it is intended to investigate and to document trends in algal distribution over a trophic spectrum. Partial correlation coefficients between algal variables and GP and their statistical significance are given along with the results of multiple correlation analysis. They are presented as baseline information, and are not intended to represent parameters that have a primary effect on the distribution of diatom and phytoplankton variables.

Net Phytoplankton Analyses

The results presented in this section deal with the taxa that were observed in the analysis of samples of net phytoplankton. Approximately 700 species, varieties, and forms, exclusive of diatoms, were identified in the study. This listing was edited to 272 species by eliminating those taxa that do not exhibit planktonic affinity (Chapter II, p. 12). These species are listed in Table 57. The diatoms considered to be planktonic forms were added to this listing (Table 57). These species are regarded as planktonic organisms primarily on the basis of habitat preference as cited in Stockner (1971), Hustedt (1930), and Cleve-Euler (1951). All of the analyses presented here are based solely on the planktonic algal flora.

The net phytoplankton expressions evaluated here are the total number of taxa, the compound phytoplankton quotient, and the diversity of planktonic desmids.

Species Number

The number of net plankton taxa (S) is believed to decrease with increasing nutrient content of lake waters (cf. Brook 1965, Vollenweider 1971). In this region S would be expected to be high in the northeastern lakes and to decrease along the gradient.

For the 68 study lakes, S exhibits a 20-fold range in value and a mean of nearly 40 taxa per sample (Table 18). Generally, S is high in the northeastern lakes (> 50 S), intermediate in

the lakes of central Minnesota (30 - 50 S), and relatively low in the prairie lakes (cf. Table 19 for S in each lake).

Regional correlations between S and most GP, especially COND and 1/SD, are inverse and are highly significant (Table 20). Similarly, multiple correlation coefficients between S and selected combinations of GP are usually > 0.60, indicating a distributional pattern that is well-developed in the region (Table 21).

It is of interest to compare these results with a previous investigation that was conducted by Brook (1971, unpublished). He sampled 55 lakes in Minnesota during summer 1965-1967 that range between COND of 24 and 1,456 ($\bar{x}$ = 280). Species totals for the lakes range between 11 and 53 ($\bar{x}$ = 27.7) and exhibit correlation coefficients with COND and COND of -0.358 and -0.378, respectively. These values are significant at P = 0.01, but they are lower than those of the present study.

It is possible that the narrower salinity range sampled by Brook might be responsible for the lower correlations, or there may, in fact, be seasonal differences in the distribution of S over the gradient. One way of attempting to resolve the problem is to perform a correlation analyses between paired sets of S estimates, and then to test the means for significant difference. Thirty-four lakes are common to both investigations.

Paired S estimates yield a correlation coefficient of 0.573, indicating moderately high agreement. The mean value

of Brook's estimates and those of the present study are 28.1 ($s = 10.3$) and 50.1 ($s = 17$). A t-test utilizing a pooled estimate of variance results in a significant difference at $P = 0.05$. These observations suggest that seasonal variation in the distribution of S must occur over the gradient.

Despite the internal discrepancy between the two data sets, S exhibits a marked trend of decreases in number over the gradient. These results are in accord with the concept that phytoplankton communities are more diverse in environments that are low in nutrients and less diverse in lakes of high nutrient status.

Compound Phytoplankton Quotient

The compound phytoplankton quotient (CPQ), a measure of the ratio of the number of taxa of four planktonic groups (Chlorococcales, Centrales, bluegreens, euglenoids) to desmids in a sample, is believed to be low in oligotrophic lakes (< 1.0) and high in enriched (> 2.5) waters (Nygaard 1949, Brook 1965). In this region, CPQ should be low in the northeastern lakes and should increase in value over the gradient.

CPQ computations are set out in Table 19. The quotient exhibits a 15-fold difference between extreme values and a mean of 5.01 (Table 18). Quotients generally are relatively low in the northeastern lakes (< 3.0), intermediate in the lakes of central Minnesota (3.0 - 6.0), and high in the prairie lakes (> 6.0).

Correlations between CPQ and all GP are significant (Table 20) and indicate increasing values over the gradient. A representative plot is shown in Fig. 28. Similarly, multiple correlation coefficients between CPQ and combinations of GP are highly significant (Table 21). It is highly probable that the quotient would yield even better coefficients if zero terms in the denominator had not been given a value of 1.0. This effects an underestimation of the true value at higher salinity levels, thereby reducing the degree of correlation.

These results may be compared with those of a previous investigation on the distribution of CPQ values in the region (Brook 1971, unpublished). The number of lakes and the salinity spectrum were defined previously. Brook's observations indicate that CPQ ranges between 0.6 and 18.0 ($\bar{x}$ = 5.5). Correlation coefficients between CPQ and COND and <u>COND</u> are 0.529 and 0.552, respectively.

The range and mean value detected by Brook are similar to those observed in this study. The correlations with specific conductance, however, appear to be higher. This could be due to a salinity difference, or it could represent seasonal variability.

The two sets of CPQ values were compared by computing correlation coefficients and by testing the mean values for statistical difference (34N). The correlation coefficient is 0.354, indicating a significant (P = 0.01) but moderate

correlation between the data sets. The mean CPQ value calculated by Brook is 6.48 (s = 4.64); that of the present study 4.10 (s = 2.96).

A paired t-test utilizing a pooled variance estimate reveals that a significant difference P = 0.10 does exist between the two data sets. This observation suggests that seasonal variations in the distribution of CPQ can occur over the gradient. Even though the quotient may not be stable, it does exhibit a distinct regional trend. In principle, these observations support the contention that CPQ is sensitive to trophic conditions.

Desmids

The number of planktonic desmids (DESMID S) is believed to decrease with nutrient enrichment of lake waters (Brook 1959b and 1965, Nygaard 1949). In this region, the diversity of the flora should be high in the northeastern lakes and should decrease over the gradient.

The number of taxa in Minnesota lakes exhibits a 25-fold range in value and a mean of 7.4 (Table 18). Generally, numbers are high in the northeastern lakes (>15), intermediate in the lakes of central Minnesota (8 - 15), and low in the prairie lakes (Table 19).

Regional correlations between desmid richness and most GP, especially COND, are all highly significant (Table 20). This marked inverse trend of decreasing numbers over the transect

is also reflected by multiple correlation coefficients that are generally > 0.60 (Table 21).

These results were compared with the desmid distribution studies of Brook (1971, unpublished). His observations reveal that DESMID S ranges between 0 and 19 ($\bar{x}$ = 5.1) and exhibits marked inverse correlations with COND (r = -0.442) and COND (r = 0.650). The range of Brook's values is smaller than that detected in the present study, whereas the mean values appear to be comparable.

The results of the present study were compared directly with Brook's observations by performing correlation analysis and by testing the paired data sets statistically. A correlation between paired data sets for 34 lakes yields a coefficient of 0.747, indicating a high degree of similarity in regional distribution. The mean values, however, are noticeably different. Brook's observations produce a mean of 5.3 (s = 4.53); those of the present study yield a value of 10.0 (s = 6.4). A t-test with a pooled estimate of variance indicates that a significant difference exists at P = 0.10, an indication that the diversity of desmids varies seasonally over the gradient.

Despite these differences, the concurrent decrease in DESMID S with increasing nutrient content of the waters is highly pronounced in the region. These observations support the general hypothesis that the diversity of desmids is sensitive to trophic conditions.

Diatom Ratio Analysis

The analysis of diatoms in net phytoplankton samples yields approximately 350 taxa. The flora is represented by an assemblage of Araphidineae, Centrales, monoraphs, and biraphs. The most abundant species in each of the study lakes, expressed as a per cent of the total count (N), are set out in Table 22. The most abundant taxa in many of the lakes are planktonic members of the Araphidineae and Centrales (cf. Table 22). All of the analyses presented here are based on computations utilizing the "complete" diatom flora in each of the samples.

The diatom ratios evaluated here consist of two expressions that have been formally proposed as trophic indicators. The distribution of the components of these ratios are also evaluated, and an attempt is made to evaluate alternative diatom ratios.

Stockner's Ratio (A/C_s)

The ratio of the abundance of planktonic Araphidineae to Centrales in deepwater sediment has been proposed as an empirical index of lake eutrophication (Stockner et al. 1967, Stockner 1971). The ratio is based on the observation that in unproductive lakes, the collective abundance of the Centrales (Cyclotella, Melosira, and Stephanodiscus) is greater than the combined abundance of the Araphidineae (Fragilaria, Synedra, and Asterionella). Generally, major shifts that are marked by

an increase in the relative abundance of the Araphidineae characterize lakes that are affected by cultural eutrophication. Although the ratio has been applied most frequently in stratigraphic analyses, Stockner reports estimates from plankton counts that are comparable in value to those reported for sediments. In the present study, one would predict that A/C_s values should be low in the northeastern lakes and increase along the gradient.

Computed A/C_s ratios for Minnesota lakes are shown in Table 23. Samples with zero abundance in either component were adjusted by assigning a ratio value of 100 or 0.01. For the 68 lakes, A/C_s estimates range from slightly greater than zero to over 100 (Table 24).

The distribution of A/C_s over the gradient appears to be highly irregular. High and low values occur together in lakes of the northeast, the central, and the prairie (see Table 23). A representative plot is shown in Fig. 29. Correlations between A/C_s and GP are all insignificant (Table 25). Similarly, this ratio fails to exhibit significant coefficients when it is correlated with selected combinations of GP (Table 26).

The above analyses are based on arithmetic values of the ratio. It is possible that regional trends may exist, but they could be obscured because of the form of data expression. In order to investigate this possibility, A/C_s estimates were transformed to $\log_{10}$ values and were then correlated with GP. The ratio exhibits a significant, negative correlation ($P = 0.01$)

with COND ($r = -.355$). These observations indicate that A/C_s is correlated with the gradient, and that the trend is a reversal of that proposed by Stockner.

It is instructive to examine the distribution of the components of the A/C_s ratio. Summary statistics for the Araphidineae (A_s) and the Centrales (C_s) are given in Table 27, and correlations with individual GP are given in Table 28. The range in abundance and mean values of both groups are comparable. A_s exhibits a significant, negative correlation with the gradient, but C_s does not. These results suggest that A_s exhibits an ecological preference for maximum development in the northeastern lakes (cf. No's. 6, 9, 13, 33, 34, 39, 42, 55, 64). Conversely, the maximum development of C_s tends to occur in the prairie lakes (cf. No's. 1, 2, 3, 5, 7, 8, 15, 18, 38, 41, 48, 53, 56, 58).

Collectively, the observations on A/C_s and its components demonstrate that the ratio as used by Stockner does not reflect trophic conditions in Minnesota lakes. The failure of the estimates to increase in value over the gradient is due to the fact that A_s is inversely related to the gradient and C_s does not exhibit a significant trend. This interaction of the components therefore produces ratio estimates that do not relate to the gradient.

This study has produced preliminary evidence to support the view that A_s, and to a lesser degree C_s, exhibits an

ecologic preference that is exactly the opposite of that proposed by Stockner. An attempt to rationalize these discrepancies would be purely speculative and will not be purused here.

The observation that transformed values of A/C_s are inversely related to the gradient was unexpected. This discovery suggests that the ratio may respond in an exponential manner to trophic conditions in the region. This evidence, coupled with the inverse trend exhibited by A_s, suggests that an A/C ratio that is based on logarithmic estimates may reflect trophic conditions in Minnesota lakes.

Nygaard's Ratio (C/P)

The ratio of the number of taxa of Centrales relative to the number of pennate species in plankton samples is an empirical expression that supposedly reflects trophic state (Nygaard 1949). This assumption is based on the premise that members of the Centrales (C) are numerically greater in enriched waters, whereas pennate (P) species are numerically predominant in low-nutrient environments. In this region, C/P values should be low in the northeastern lakes and should exhibit an increase in value over the gradient.

Estimates of the C/P ratio in Minnesota lakes are given in Table 23, and summary statistics in Table 24. Samples with a zero value for either component are adjusted by assigning a value of one to the missing term. For the region, C/P

estimates range between values that are slightly greater than zero to estimates that are slightly over 2.0.

C/P estimates do not, however, exhibit distinct regional trends over the gradient. High and low values occur together in the same region, but there is a tendency for estimates to be lower in the prairie. A representative plot is shown in Fig. 30. C/P values are not well-correlated with GP. The only significant correlation is with COND (Table 25). Similarly, multiple correlation coefficients between C/P and combination of GP are all non-significant (Table 26).

These analyses are based on arithmetic estimates. In order to determine if significant correlations could be generated between transformed C/P and GP, the estimates were computed as $\log_{10}$ values and then were correlated with specific conductance. C/P exhibits inverse correlations with COND ($r = -0.385$) and COND ($r = -0.372$) that are significant at $P = 0.01$. These analyses indicate that C/P does exhibit a trend over the gradient, but it is inversely rather than positively related to increasing nutrient level. The trend is a reversal of that proposed by Nygaard, i.e. C/P tends to be higher in the northeastern lakes and lower in the saline lakes of the prairie.

It is instructive to examine the regional distribution of the components of the C/P ratio. Summary statistics for C and P are presented in Table 27, and correlation coefficients between the components and individual GP in Table 28.

There is a 10-fold range in the value of C and a 30-fold range in the estimates of P. C exhibits significant inverse correlations with specific conductance and secchi disc, whereas P fails to exhibit a correlation with GP. In Minnesota lakes, the diversity of C is higher in the unproductive northeastern lakes than in the enriched prairie lakes. The diversity of Pennales, conversely, appears unrelated to trophic conditions in the region.

The observations on C/P and its components demonstrate that the ratio, as proposed by Nygaard, does not reflect trophic conditions in Minnesota lakes. The failure of the estimates to increase in value over the gradient is due to the fact that the diversity of C decreases over the gradient, and P is distributed randomly. This interaction of components produces ratio estimates that do not relate to the gradient.

This study provides evidence that C exhibits a greater diversity in lakes of low nutrient status than in eutrophic waters. These observations are not in accord with Nygaard's predictions. An attempt to rationalize these discrepancies would be purely speculative and will not be pursued here.

The finding that the transformed C/P estimates results in a significant correlation with the gradient was unexpected. The ratio may, in fact, respond inversely and in an exponential manner to increases in trophic status. Further observations are necessary to verify the present findings.

Modified Ratio

Early in the analyses of diatom ratios, it was observed that the ratio of the number of taxa, instead of abundance, in the Araphidineae (A_t) and the Centrales (C_t), result in a range of values that is similar to the one proposed by Stockner (Table 24). This ratio is computed for each of the study lakes (Table 23), and is then investigated to determine if it exhibits regional trends in the study area.

The results of the correlation analyses are set out in Table 25. Arithmetic values of this ratio do not exhibit correlations with individual GP, nor does logarithmic transformation of the estimates result in significant correlations. A representative plot is shown in Fig. 31.

The components of the ratio, however, do exhibit regional trends (Table 28). The diversity of both diatom groups tends to be higher in the northeastern lakes than in the other regions. The failure of the ratio to exhibit regional correlations is due largely to the fact that the range and mean values of both groups are comparable, and to concurrent decreases in the diversity of both groups over the length of the gradient. This ratio appears to be unrelated to trophic conditions in Minnesota lakes.

Alternative Ratios

The analysis on species numbers and relative abundances of the major diatom groups in Minnesota lakes provides data

that can be used to investigate alternative ratios. A series of empirical analyses was undertaken to determine if a "ratio" could be produced that would respond to the trophic gradient. The diatom components (A_s, C_s, A_t, C_t, P) set out in Table 23 were used as numerator and denominator alternatively and in all possible combinations. Each ratio was then correlated with individual GP.

The results of these analyses indicate that none of the trials produced a "ratio" that exhibits more than one significant correlation ($P = 0.05$) with an individual GP. These observations suggest that the major groups of diatoms, expressed as species numbers or as relative abundance, do not yield ratios that reflect trophic conditions in Minnesota lakes.

Quantitative Analyses

The analysis of samples of whole water yielded about 750 taxa, approximately one half of which were not detected during the examination of samples of net phytoplankton and diatoms. The flora is represented by an extremely large assemblage of all groups of algae. The most abundant taxa in each of the study lakes, expressed as a per cent of the total, are set out in Table 29.

The most striking feature of these studies is that the majority of lakes in northeastern Minnesota and many of the lakes in central Minnesota and in the prairie as well support relatively large populations of small cryptomonads, chrysophytes,

and diatoms. The underlined percentage values in Table 29 indicate that the populations are nannoplanktonic (< 60u). Even in lakes with large populations of bluegreens, diatoms, and chlorophytes, some of which are in a "bloom" state, these small organisms contribute substantially to the size of the total community.

The primary objectives of the analyses undertaken here are to investigate trends in the distribution of the standing crop of total, net-, and nannoplankton over the gradient, and to investigate the relative apportionment of net- and nannoplankton as a function of the total standing crop of phytoplankton.

Standing Crop

The standing crop of phytoplankton generally is much higher in eutrophic waters than in oligotrophic lakes (cf. Rawson 1956, Rodhe 1969, and Vollenweider 1971). In this region, SC should be low in the northeastern lakes and increase in size over the gradient, reaching maximum abundance in the enriched prairie lakes.

In Minnesota lakes, SC exhibits a difference of nearly four orders of magnitude between extreme levels, with a mean of 20,105 organisms/ml (Table 30). Lake Spiritwood (No. 58), with a bloom of the zooplankter Daphnia, had the lowest SC (89 organisms/ml). The largest SC (403,893 organisms/ml)

was detected in Lake Eckelson (No. 18), which supported a bloom of the brackish-water diatom Chaetoceros muelleri (Table 29).

Although there are local variations in the same geographic region, SC exhibits a pattern of increase over the gradient (Fig. 31). Lakes in northeastern Minnesota generally support crops of 1000 to 6000 organisms/ml. SC in the central region of the state normally ranges between 1000 and 30,000 organisms/ml. Most of the prairie lakes support crops that range between 5,000 and 70,000 organisms/ml.

SC exhibits a distinct pattern of distribution over the gradient. It is significantly correlated either arithmetically or logarithmically with most individual GP (Table 31), and it exhibits moderately high multiple correlation coefficients with selected combinations of GP (Table 32). Although this trend was anticipated, it is surprising to detect correlations that are so pronounced. Estimates of SC were based on individuals in this study. It is highly probable that the correlations would be even better if measurements were based on volumetric or biomass estimates. Precise numerical comparisons between these results and the observations of other workers is difficult, because of the differences in measurement. The spectrum of SC values detected in Minnesota lakes is comparable to that observed by other authors (cf. Nygaard 1949, 1955; Willen 1969; Kristiansen 1964, 1971; and Schindler and Holmgren 1971; and Kalff 1972).

Net/Nannoplankton Standing Crop

The use of the inverted microscope technique has resulted in the observation that nannoplankton (< 60u) often contributes substantially to SC in many lakes. There is a general belief that nannoplankton can constitute the major fraction of the biomass of phytoplankton in oligotrophic lakes, whereas net phytoplankton is numerically or volumetrically greater in eutrophic waters (cf. Kalff 1972, Pavoni 1963, Schindler and Holmgren 1971, and Kristiansen 1971). It is not known, however, just how the absolute size and the relative apportionment of the two fractions vary together over a spectrum of trophic conditions.

In this study an attempt was made to investigate these relationships. For the purposes of analysis NET SC and NANNO SC are expressed in absolute numbers and as percentage values of total SC.

NET SC in Minnesota lakes exhibits a range of over five orders of magnitude and a mean of nearly 12,000 organisms/ml (Table 30). Although there is local variation among lakes in the same geographic region, NET SC tends to be low in the lakes of the northeast, intermediate in the lakes of central Minnesota, and relatively high in many prairie lakes. This regional pattern is reflected by significant, positive correlations with individual GP (Table 31), and by significant correlations with most combinations of GP (Table 32).

NANNO SC in the study lakes ranges over three orders of magnitude between extreme values, with a mean of over 8,000 organisms/ml (Table 30). There are local variations in NANNO SC among lakes in some regions, but it exhibits a general tendency to increase over the gradient. The pattern is not so distinct as the one detected for NET SC. Correlations between NANNO SC and individual GP are lower (Table 31), and multiple correlation coefficients with some combinations of GP are not significant (Table 32).

The relative apportionment of NET SC and NANNO SC in the lakes can be investigated by expressing each fraction as a percent of the total SC. These results are summarized in Table 30. The range for both fractions is similar; however, the mean percentage value for NANNO SC is nearly twice that of NET SC. On a regional basis in Minnesota lakes, the percentages of the NET and NANNO fractions are inversely related (Table 31). NET exhibits positive and NANNO negative correlations with COND, SD, and SC (Figs. 33 and 34).

The above observations indicate that the absolute size of NET SC and NANNO SC increases with increasing nutrient levels. The two expressions are, in fact, correlated ($r = 0.590$). It appears that higher nutrient levels are conducive to concurrent increases in the size of both fractions. The indirect relationship between NET and NANNO reveals, however, that the fractions vary inversely over the gradient.

Collectively, the observations on SC and NET SC in Minnesota lakes are in accord with the general assumption that both quantities increase with nutrient enrichment. Each expression may serve as an indicator in lakes of this region. The trend displayed by NANNO SC, however, does not conform to the hypothesis that the proportion of nannoplankton decreases with increases in nutrient level.

Community Structure Analyses

Indices of diversity are expressions of structure in communities. A rationale for their application in ecologic studies has been given by Patten (1962), Margalef (1958, 1968), and Hutchinson (1967). In general, assemblages with large numbers of species, relative to the total numbers of individuals, yield high index values. Conversely, communities that are characterized by a numerical dominance of one or a few taxa result in relatively low values.

Studies on species diversity in communities of phytoplankton are few in number. On the basis of limited data, it is believed that phytoplankton responds to increases in nutrient level by exhibiting decreases in its diversity. This generally occurs by a decrease in the number of species in the community and by a lower degree of apportionment of individuals among the species (evenness). These trends have been observed in the marine environment (cf. Carpenter 1971, Hulburt 1963, and Margalef 1967) and in freshwater lakes (Margalef 1964 and Goldman 1970).

Margalef (1958, 1968) gives the following ranges (in bits/individual) for trophic states of north-temperate lakes: oligotrophic (>3.5), mesotrophic ($2.5 - 3.5$), eutrophic (<2.5). Index values below 1.0 can occur in bloom situations and values as high as 6.0 or more can occur in highly diverse communities, i.e. ultraoligotrophic conditions in lakes or in the marine environment.

The structure of communities of diatoms and whole-water phytoplankton in Minnesota lakes was investigated by utilizing D (eq. 1) and H (eq. 2) as indices of diversity (Chapter II, p. 25). In addition, the number of species S and evenness J were utilized as related community properties. S and J can be used in an objective manner here, because of the consistency in sample size. J ranges between zero and 1.0.

Diatom Diversity

Estimates of species diversity in communities of diatoms in Minnesota lakes yield index values of H and J that are within the expected ranges (Table 34).

The distribution of these four properties over the gradient is highly irregular. Representative plots for D and H are shown in Figs. 35 and 36. Both low and high values occur together in lakes of the same geographic region. Correlations of the four properties with individual GP are all insignificant (Table 35), as are coefficients between each property and selected combinations of GP (Table 36).

In order to determine if the use of arithmetic values obscures significant regional trends, each index and related statistic was computed as $\log_{10}$ and reciprocal expressions. The results of a correlation analysis between transformed index values and individual GP, however, did not produce a correlation coefficient > $\pm$1.10.

The failure of species diversity to exhibit significant regional trends prompted a further analysis of the data. It is possible that the use of the "complete" flora, which includes non-planktonic populations, may mask regional patterns in species diversity of the planktonic communities. The listing of species in each lake was edited by eliminating all non-planktonic populations, and the indices and related statistics were recomputed. The results of a correlation analysis with individual GP, however, are similar to those given in Table 35. No coefficient exceeds $\pm$0.210, a non-significant value.

These observations suggest that species diversity in diatom communities does not respond to the trophic spectra of Minnesota lakes. Seasonal studies would be necessary to confirm or reject the present observations.

Phytoplankton Diversity

The structure of whole-water phytoplankton communities was investigated by examining the distribution of the "total" assemblage and also by examining species diversity in the net- and nannoplankton fractions.

Estimates of species diversity in communities of total phytoplankton in Minnesota lakes yield index values of H and J that are within the ranges proposed by Margalef. The maximum value of D, however, is twice as large as that expected on the basis of Margalef's predictions. Three lakes, for example, have index values > 10.0: Big No. 6 (10.40), Ball Club No. 4 (12.38), and Elk (10.12). No explanation can be offered for this phenomenon.

On a regional basis, each index does exhibit variations among lakes of same region. The value of each index, however, tends to be higher in the northeastern lakes, intermediate in the lakes of central Minnesota, and low in the prairie lakes. Representative plots for D and H are depicted in Figs. 37 and 38, and in Figs. 39 and 40, respectively.

The distributional pattern of each index over the gradient is inversely related to individual GP. D, H, and S exhibit highly significant correlations with most parameters (Table 38), especially COND and 1/SD. These marked trends are reflected by multiple correlation coefficients that are generally in the range of 0.50 to 6.0 (Table 39 and 40). J, however, does not exhibit a regional trend that is as pronounced as those of the other indices. Evenness is correlated better with 1/SD and SC than with other GP. Multiple correlation coefficients generally are < 0.50, and many combinations produce results that are non-significant.

The above results indicate that the indices D and H and S respond to trophic conditions by exhibiting progressive decreases in value. These observations on community structure are in accord with the general hypothesis that species diversity is sensitive to trophic conditions.

Species diversity in communities of net- and nannoplankton have never been investigated quantitatively. In Minnesota lakes, H and S are estimated individually in each of the two fractions. The indices D and J are not computed because of the high degree of bias that is introduced by small sample sizes.

The range and mean values for NET H and NANNO H and the number of taxa in each fraction are summarized in Table 37. Both fractions yield diversity statistics that are similar in their range and mean values. The minimum and maximum estimates of H are within the range of diversity values that are to be expected in north-temperate lakes (Margalef 1967).

The distribution of NET H and NANNO H and S in each of the fractions exhibits an inverse relationship with increasing nutrient levels (Table 38). NET H and NET S are significantly correlated with almost all individual GP, especially COND and 1/S. Multiple correlations between NET H and combinations of GP yield coefficients that are highly significant and generally range between 0.50 and 0.60 (Table 41).

The correlation of NANNO H with GP is not as pronounced as that detected for NET H. NANNO H exhibits a highly significant correlation only with COND. Multiple correlation coefficients, likewise, are lower and yield non-significant results with certain combinations of GP (Table 41). NANNO S, conversely, is highly correlated with most individual GP, especially COND.

These observations indicate that species diversity in communities of net- and nannoplankton exhibits a pattern of distribution that is inversely related to increasing nutrient levels in Minnesota lakes.

CHAPTER V

LAKE CLASSIFICATION IN MINNESOTA

Lakes can be classified by using any number of physical, chemical, or biological criteria. The traditional approach to lake typology has been to utilize a single "indicator" to identify lake groups. This procedure, accompanied by a subjective evaluation of similarity among lake groupings, has been judged as unsatisfactory (cf. Brezonik 1969, Shannon 1969). Lakes are more amenable to rational classification if they are considered as multi-dimensional entities, i.e. they are best described by a number of variables. The multiplicity of potential "indicators", however, poses the problem of identifying the most suitable classificatory variables.

Since there exists no ideal set of indicators, rational classifications of lakes are best investigated by utilizing logical sets of variables. The chemical and biological data generated in the present study provide an opportunity to explore the nature of the lake groupings that can be established by using logical but dissimilar sets of variables. The primary objectives of the analyses undertaken here are in turn: 1) to delineate lake groupings based on major solute chemistry, and to compare them with previous studies; 2) to select variables that meet the requirements of trophic-state indicators, and to use them to explore the nature of lake groupings; 3) to delineate lake groupings that are based on sets of phytoplankton

taxa; and 4) to compare these classification schemes with one another.

Cluster Analysis

In order to minimize subjectivity in classification, cluster analysis was selected as a method for identifying logical groups of lakes. Generally, this multivariate technique is used to establish clusters of objects in a p-dimensional hyperspace that are described by the p-data attributes of the objects. Cluster analyses are of two types: Q-type, the grouping of N objects on the basis of p variables, and R-type, the grouping of the p variables that are measured on N objects. The former is used exclusively in the present analysis. This technique has the advantage over other procedures because it is objective, it provides a means of sorting data rapidly and in a reproducible fashion, and, most importantly, it does not require that the optimum number of groups be determined prior to analysis.

The basic elements of most clustering routines are:

1. a measure of the similarity among objects (or distance measure)
2. the clustering criterion
3. the computational procedure

Theoretical and statistical aspects of cluster analyses can be found in Morrison (1967), Sokal and Sneath (1963), and Lee (1971). A rationale for the application of the technique to the problematics of lake typology can be found in Brezonik

and Shannon (1971), Sheldon (1969), Brezonik (1969).

I have chosen an agglomeration analysis devised by Orloci (1967) and modified by E. J. Cushing. The technique amounts to identifying clusters of points (lakes) in p-dimensional hyperspace, where specified variables have been measured on each lake. Similarity among objects can be calculated by using either of two mutually exclusive measures: absolute or standard distance.

Absolute distance is defined as the shortest distance between pairs of points; it is calculated on the basis of standardized or non-standardized variable scores. Standard distance is defined as the length of the chord that connects two points on the surface of a sphere of unit radius. Further details on these similarity measures are given by Orloci.

The clustering criterion imposed on the analysis is the within-group sum of squares. In the computation, all possible fusions in twos of the entities $k(k-1)/2$ are formed and tested (note: k is the number of objects to be classified). A union of two entities is accepted if the increase of the within-group sum of squares by it is less than it would be by fusing either of the two with another entity in the samples. Clustering proceeds in successive cycles, gradually uniting lakes into larger and larger groups until all of the lakes are fused into a single entity. The results are interpreted by examining the number of major stems that are present in the hierarchical arrangement, and by evaluating the values of average within-group

dispersion (Q/k values). The distance between each object is optional output and permits the objects to be arranged in a linear array. Low values of within-group dispersion, i.e. dense clusters of lakes, imply good within-group similarity and good between-group dissimilarity.

Despite the objectivity afforded by cluster analyses, a number of difficulties can arise with their use. Different distance (or similarity) measures, sorting strategies, and forms of data expression can alter variance computations and, thus, yield dissimilar results (Sheldon 1969). Because of the desire to establish lake groupings that are as free as possible from these ambiguities, a series of "test" analyses was undertaken as an integral part of the investigation of chemical lake types in the region.

Specifically, Orloci's agglomeration analysis was performed alternatively with different distance measures and forms of data expression. A cluster analysis routine, devised by W. Johnson, that uses a shape measure (coefficient of variation) was used to test the results of the agglomeration analyses.

Chemical Lake Types

Previous Classification Schemes

Several classification schemes that are based on the chemistry of surface waters in Minnesota have been proposed. It is instructive to examine them prior to the analysis undertaken here.

Moyle (1954) delineated four generalized lake types by evaluating regional trends in the levels of alkalinity, pH, sulfate, salinity, and total nitrogen and phosphorus. The types correspond to three geographic provinces within the state: 1) soft-water lakes of low salinity that lie primarily in granitic bedrock basins in northeastern Minnesota; 2) enriched, hardwater lakes in north-central and central Minnesota whose basins are in gray glacial tills; 3) productive, saline lakes with high sulfate concentrations that are located in the prairie regions of southwestern and western Minnesota. A fourth type consists of those prairie lakes in western Minnesota and the Dakotas that are highly saline and have high concentrations of sodium, sulfate, and chloride.

Three lake types were established by Bright (1968) on the basis of salinity and equivalent proportions of major ions of 40 lakes. Each lake group corresponds to a major vegetation zone (see Fig. 2): 1) the coniferous-deciduous forest of northern Minnesota; 2) the narrow band of deciduous forest; and 3) the prairie of southern and western Minnesota.

The groups proposed by Gorham are based on measurements of conductivity and concentrations of major ions in over 200 lakes. He classifies the lakes into four geographically distinct groups: 1) dilute bicarbonate waters in non-calcareous glacial drift in northeastern Minnesota; 2) bicarbonate waters of intermediate concentration in calcareous drift that extends

from north to south in central Minnesota; 3) concentrated sulfate-bicarbonate waters in western Minnesota; and 4) sodium sulfate waters of high salinity in western Minnesota near the Dakotas.

It is apparent that the lake groupings established by these authors differ significantly from one another. The scheme proposed by Gorham, unlike that of Bright, does not match boundaries between forest or soil types. Although Moyle's groupings appear to be similar to Gorham's types, the groupings are so generalized that the correspondence is superficial.

Chemical Types

The study lakes were classified by cluster analyses on the suite of seven major anions and cations (Table 15). Solute concentrations were used first as raw data (meq/l) and then in standardized form. The standardization procedure consists of subtracting the mean from each of the observed values and then dividing the difference by the standard deviation (Sokal and Sneath 1963). All variables are weighted equally in the analyses. Both measures of between object similarity (i.e. absolute and standard distance) were used individually with each data set. The results of these analyses are set out in Table 42. A dendrogram based on Run 3 (standardized solute values, absolute distance) is depicted in Fig. 41.

If it is assumed that the study lakes represent a reasonable cross-section of lakes in this region, three relatively

well-defined lake groups can be identified in each run. The groups are designated here as Type 1 (the lakes in northeastern Minnesota), Type 2 (lakes in central Minnesota), and Type 3 (lakes in the prairie of Minnesota, North Dakota, and South Dakota). Several highly saline prairie lakes form a residual cluster that is considered here as a provisional group, Type 4. In one analysis (Run 2, standard distance, meq/l), a group of seven lakes forms a cluster that is transitional between Type 2 and Type 3. This group is designated tentatively as Type 2/3. R_1 and R_N are single and multiple residuals, respectively. A single residual is a lake that fuses into a major lake cluster at high Q/k levels. The fusion generally occurs after the cluster is completely formed. A multiple residual is a small number of lakes that fuse together because they differ more from the character of the major clusters than they do from each other. They can enter a major cluster at high Q/k values after it is formed (cf. Sheldon 1969). Although three major lake types were identified in each run, the size and composition of the groups does vary as a function of data expression and distance measure. Type 1 (16 and 17N) and Type 2 (22 to 25N) are relatively consistent in the number of lakes assigned to each group, but Type 3 (9 - 16N) and Type 4 (5 - 9N) exhibit considerable variability in size.

The fact that different combinations of distance measure and data expression result in lake clusters of dissimilar

composition poses an immediate problem of selecting the analysis that provides the most objective series of lake groupings. A formal procedure for such an appraisal does not appear to be available. This can be accomplished, however, by a subjective evaluation of each of the clusters formed in the runs, and by comparing different combinations of distance measure and data expression with respect to the number of differences in lake placement. The analyses presented in Table 42 can be summarized as follows:

Data Expression	Distance Measure (Orloci)	No. Differences
meq/l	Absolute/Standard	22
Standardized Variables	Absolute/Standard	12
meq/l/Standardized Variables	Absolute	3
meq/l/Standardized Variables	Standard	28

The greatest number of differences in lake placement in a particular cluster is generated with the use of standard distance. Lakes are more frequently detected as members of the same cluster when the absolute distance measure is used with raw data or with standardized variables.

An examination of individual dendrograms (Runs 1 - 4) indicates that standard distance, whether used with raw or standardized data, yields fusions that are anomalous. For example, in Run 2 (raw data) Lake Meander (No. 42), otherwise a Type 1 lake, is incorporated at high sum of squares into the Type 2 cluster; Mud (No. 48) and Thief (No. 46), lakes generally

sorting out as Type 3 or Type 4 members, and Mitchell (No. 46), normally recognized as a Type 2 lake, become incorporated at relatively low Q/k into Type 1. Lamb (No. 34), Superior (No. 60), and Dogfish (No. 17), normally recognized as Type 1 lakes, fuse at low Q/k into the Type 2 cluster.

When standard distance is used with standardized variables (Run 4), similar anomalies are detected. Lakes Alkaline (No. 3) and George (No. 23), both of which are highly saline prairie lakes, fuse with one another, and become incorporated at high Q/k into the Type 1 cluster. Lake Eckelson (No. 18), normally recognized as a Type 4 member, becomes incorporated as a residual into Type 1.

These fusions involving standard distance are judged as aberrant. They occur either as a result of a pre-empted linkage (a nonsense-linkage) in the clustering routine, or as a direct function of the standardized distance measure. Orloci (1967) has demonstrated the standard distance minimizes the distance among lakes and lake clusters. This can cause a larger number of residuals to be detected, and can result in intermediate or transitional lake groupings. The results of these studies bear out this phenomenon (Table 42). Run 2 (meq/l and standard distance) gives rise to a transitional cluster, and Run 4 (standardized variables and standard distance) yields the largest number of residuals. Cluster analyses involving standard distance result in some fusions that are judged as having little value in establishing logical groupings of lakes.

Such anomalies, however, are not encountered when absolute distance is used as the similarity measure. In combination with standardized variables (Run 3), Lakes Alkaline (No. 3) and George (No. 23) fuse with one another and Lakes Alkali (No. 2) and Salt (No. 52), together with Eckelson (No. 18), form a highly heterogeneous group (Type 4). The combination of absolute distance and raw data results in an identical sorting of lakes, except for a two-member residual, Mineral (No. 44) and Waubay (No. 67), that fuses at high Q/k into the Type 3 cluster. On the basis of these observations, absolute distance is judged as the most appropriate distance measure.

Because of the fact that different cluster analysis routines and the form of the data can result in variations in the size and composition of lake groups (Sheldon 1969), cluster analyses were performed on data that was expressed in the form of mg/l. In addition, an independent cluster analysis routine was used to check the results presented above.

A series of clustering runs was performed by using Orloci's absolute and standard distance measure with data expressed in raw form (mg/l) and in the form of standardized variables. The results of these analyses are similar to those presented in Table 42. Three major lake groups were identified, comparable in size and composition to those detected previously. Standard distance resulted in anomalous fusions. The absolute distance measure in combination with raw and standardized variables,

however, yield lake clusters that are nearly identical to those detected in the previous analyses.

The independent clustering routine (W. Johnson) was performed with data expressed in raw form (meq/l) and as standardized variables. The size and composition of the lake groups are virtually identical to those detected with Orloci's agglomeration analyses (Runs 1 and 3).

Characterization of Types

The groups detected in Run 3 (Fig. 41) were accepted as yielding a classification that is satisfactory for the purpose of delimiting major groups in the region. The only minor exception was that Lake Big Kandiyohi (No. 7) was placed in Type 3, because an additional set of data indicates that the cation-anion values used may have been too low. Summary statistics for the major solutes in each type are set out in Table 43. Except for calcium and alkalinity, the mean concentration of each ion is observably different ($P = 0.05$) among the groups. The major types can be delimited and characterized as follows (range and mean values of specific conductance in umho cm^{-1} at 25C are given in parentheses).

Type 1. This group is composed of all of the lakes in northeastern Minnesota and includes Lakes Deming (No. 16) and Josephine (No. 32) in northern Minnesota. The high degree of within-group similarity is reflected by the low Q/k levels. The waters are of low salinity

(range 15–89, $\bar{x}$ = 42), with HCO_3^- and calcium being the major anion and cation, respectively.

Type 2. This group is composed of most of the lakes that are located in central Minnesota. The prairie lakes Big Kandiyohi (No. 7), Fish (No. 21), Heron (No. 28), Mitchell (No. 46), and Pickerel (No. 50) are peripheral members of the cluster. This group also reflects a high degree of within-group similarity. The waters are of moderate salinity (range 156–705, $\bar{x}$ = 303). Concentrations of calcium and magnesium are nearly equivalent, and HCO_3^- is the major anion.

Type 3. Lakes in this group are located in the prairie or are situated in the deciduous forest near the prairie. The degree of within-group similarity is low (high Q/k values), indicating a relatively high degree of variability in the concentration of major ions. Salinity levels are high and exhibit a large range (707 – 9,180, $\bar{x}$ = 2,044). Sulfate and magnesium are the most important ions.

Type 4. This group is residual in its composition. It is composed of five prairie lakes (Alkali No. 2, Alkaline No. 4, Eckelson No. 18, George No. 23, and Salt No. 52) that are dissimilar in chemical composition. Salinity levels are high (7,976 – 31,783, $\bar{x}$ = 17,768), and sodium and sulfate are the major ions.

Summary statistics for specific conductance are set out in Table 46 and are depicted graphically in Fig. 42. The mean salinity levels are significantly different among all of the types, indicating a high degree of dissimilarity. The clusters formed by the use of major anions and cations are judged as lake groupings that exhibit marked differences in their ionic proportions.

Comparisons with Previous Classifications

Several comparisons between the classification developed in this study and previous schemes merit mention. The composition of the major lake groups is nearly identical with the one proposed by Gorham (1971, and unpublished). The only differences involve several highly saline lakes in western Minnesota. A number of these prairie lakes are listed by Gorham as Type 3 lakes, or as lakes that are transitional between Type 3 and 4 (e.g. Mineral No. 44, and Alkali No. 2, Mud No. 48, and Thief No. 62). The results of this study indicate that all of these lakes, except Alkali, sort out as members of Type 3. An examination of Fig. 41, however, indicates that Type 3 is highly heterogeneous in composition, and Type 4 is fundamentally a residual group. The most appropriate placement of these lakes can be resolved only by identifying the limits of Type 3 and 4 more precisely.

The classification of Minnesota lakes by Bright (1968) does not compare favorably with the present scheme. Bright's

coniferous forest group includes all of the Type 1 and many of the Type 2 lakes of the present study. In addition, Lakes Fish (No. 21) and Pickerel (No. 50), regarded by Bright as prairie lakes, sort out here as Type 2 members.

The lakes in the deciduous forest, recognized by Bright as a distinct group, includes members of Types 1, 2, and 3. The group of lakes detected as a transitional cluster (2/3, Run 2) does include a number of the deciduous forest lakes. This was not, however, verified in the other runs (Table 42). On the basis of the present analysis, the lakes in the deciduous forest do not appear to constitute a lake type that is intermediate between coniferous forest and prairie.

Trophic-State Lake Types

Trophic State and Selection of Indicators

It is generally agreed that the "trophic state" of a lake is both a consequence and a reflection of its nutrient level (cf. Hasler 1947, Vollenweider 1971). A lake generally responds to increased rates of nutrient supply by exhibiting certain changes in its physical, chemical, and biological properties. Most commonly, the standing crop of the primary and secondary producers increases, transparency of the surface water decreases, the oxygen content of the hypolimnion decreases, and the composition of the biota shifts in character and quantity. In addition, the productivity of the littoral zone generally increases, and the character of the sediments changes.

Unfortunately, trophic status cannot be expressed by any simple statement or by any single measurement (Brezonik 1969). The modern concept of trophy is that it is both multidimensional and hybrid, i.e. trophic state is best described by a combination of physical, chemical, and biological parameters, rather than by a single indicator (Margalef 1958, Brezonik 1969, and Shannon 1969). The selection of the most appropriate parameters for use in trophic classifications, however, is largely an empirical procedure.

In the present study, the criteria proposed by Brezonik and Shannon (1971) are used initially as a guideline in the selection of indicators. Their criteria may be stated as follows:

1. An indicator should be measureable and relatively simple to estimate.
2. An indicator should have basic significance in terms of trophic state i.e. it should be a measure of trophic state and exhibit sensitivity to general levels of trophy.
3. An indicator should be quantifiable and permit differentiation among lakes of differing trophic state.
4. An indicator should be unique, i.e. it should not be a direct or indirect measure of the same indicator or property.

Note: Brezonik and Shannon propose criterion 4 as a requirement that an indicator should not be a redundant expression. As an example, they claim that the use of specific conductance and salinity or the use of either of these two parameters with dissolved solids constitutes a redundant pair of indicators.

In Minnesota lakes there are numerous physical, chemical, and biological parameters that have potential value as indicators of trophic state. Extensive reviews of trophic indicators and their application to typology have been presented by Brezonik and Shannon (1971), Hooper (1969), Brezonik (1969), and Vallentyne (1969). They include such physical parameters as transparency, mean or maximum depth, the ratio of mean depth to surface area, and per cent littoral area. Frequently, the following chemical variables have been used as indicators: alkalinity, specific conductance, dissolved oxygen concentrations and profiles, chlorophyll, and particularly the nutrients nitrogen and phosphorus. Numerous biological parameters have been considered as trophic indicators, including primary production, the quality and quantity of littoral vegetation, the composition and biomass of bottom fauna and fish populations, and numerous phytoplankton expressions. The latter class of indicators consists of standing crop, species diversity, and various types of qualitative and quantitative algal quotients.

In the present study, it was virtually impossible to 1) measure many of the parameters outlined above and to

2) determine if they are satisfactory indices of trophic state. Initially, an attempt had been made to investigate two morphometric parameters as potential indicators of trophy: maximum and average depth. Morphometric data in the form of bathymetric maps, however, are not available for many of the study lakes (Department of Conservation, St. Paul, Minnesota). Maximum depth measurements are available for many but not all of the lakes (cf. Department of Conservation, St. Paul, and Megard 1967). It was not used as a potential indicator for the following reasons: 1) the lakes of central Minnesota on the average tend to be deeper than the northeastern lakes, and the prairie lakes tend to be very shallow relative to the northeastern lakes. This trend will violate the criterion that is used to select indicators (see below). 2) On the basis of available data, there appears to be considerable variation in the maximum depth of many northeastern lakes (Superior 900 feet, Clearwater 130 feet, and Lamb, Meander, Dogfish are less than 30 feet) and in many of the lakes in central Minnesota (Nokay, Spectacle, Frances, and Sallie are less than 50 feet; Ball Club, Elk, Long, and Christmas are greater than 80 feet; and Mille Lacs is less than 30 feet).

An attempt also was made to utilize total phosphorus and total nitrogen as indicators. Measurements were made on several lakes in northeastern Minnesota and in the prairie of South Dakota and North Dakota. An exhaustive search of the chemical data available in the Department of Conservation (St. Paul,

Minnesota) failed to produce measurements for more than 19 lakes. These data are too few to incorporate them as classificatory variables.

The procedure used to select indicators in this study is similar to that employed by Brezonik and Shannon (1971). Quantitative trophic-state parameters tend to increase or to decrease progressively from "oligotrophy" through "mesotrophy" to "eutrophy". Indicators, therefore, should be positively or negatively correlated with one another. The above authors, for example, used primary production, chlorophyll, total organic nitrogen, total phosphorus, secchi-disc transparency, specific conductance, and Pearsall's ratio of monovalent to divalent cations in their attempts to classify lakes in Florida. Each parameter in their study is significantly correlated ($P = 0.01$) with each of the other parameters. Nearly all of the coefficients (r) between pairs of variables exceeds ± 0.5.

The parameters selected as trophic indicators of Minnesota lakes are enumerated and discussed below. They are judged as meeting the criteria of Brezonik and Shannon, and they are not considered to be redundant.

Physical-Chemical Indicators

1. Specific conductance (COND) is taken as a general measure of the concentration of dissolved solutes. COND tends to be higher in productive and lower in unproductive lakes (cf.

Brezonik and Shannon 1971). For Minnesota lakes, COND appears to be a good indicator of trophy (Table 13 and 16).

2. Transparency (SD) is generally accepted as a general index of productivity (cf. Vallentyne 1969, Vollenweider 1971). Although SD is affected by conditions that may be unrelated to trophy, e.g. silts or humic materials, it is generally high in unproductive waters and low in productive waters. In this region SD measurements appear to be a good indicator of trophy (Tables 13 and 16).

3. Alkalinity (ALK) is generally considered to be an index of productivity (cf. Vollenweider 1971). Highly buffered lakes tend to be more productive than lakes of low alkalinity. For Minnesota lakes, ALK appears to be a moderately good indicator (Tables 13 and 16).

4. A summation of the concentration of calcium and magnesium ($\sum$ Ca + Mg) was used as a trophic indicator. This index has not been employed extensively but it has been proposed by Zafar (1959) as a parameter that differentiates between states of trophy. It appears to be a moderately good indicator for Minnesota lakes (Tables 13 and 16).

Initially, an attempt had been made to utilize Pearsall's (1922) ratio of monovalent to divalent cations (NA + K/CA + Mg) as an indicator. In the English Lake District, Pearsall observed that lakes with a ratio < 1.5 and with high nitrate and silica produced algal blooms. Similarly, Brezonik and Shannon (1971)

have found that the ratio is an acceptable index for differentiating between trophic conditions in lakes of north-central Florida. If the ratio is applicable to Minnesota lakes, it should be inversely proportional to trophic state. A correlation analysis between the ratio and COND and COND yields coefficients of 0.701 and 0.563, respectively. The ratio is directly rather than inversely proportional to trophic state. The index was therefore judged as inapplicable in the study region.

Phytoplankton Indicators

5. The standing crop of phytoplankton (SC) is generally accepted as an index of trophic state (cf. Vollenweider 1971, Shannon 1969). Lakes with low SC tend to be less productive than eutrophic waters. SC is judged as a moderately good indicator for Minnesota lakes (Tables 13 and 32).

Although the standing crop of net and nannoplankton could be considered separately as indicators (Table 33), their incorporation along with SC would constitute a redundancy.

6. The compound phytoplankton quotient (CPQ) has been used successfully as an index of trophy for lakes in Great Britain (Brook 1965) and in Denmark (Nygaard 1949). CPQ values are low in unproductive lakes and high in eutrophic lakes. This index appears to be a moderately good indicator for Minnesota lakes (Tables 20 and 21).

7. The number of net phytoplankton taxa (S) is generally recognized as an indicator of trophy (cf. Brook 1971, Vollenweider 1971). S is low in eutrophic waters and high in unproductive lakes. S appears to be a good indicator in Minnesota lakes (Tables 20 and 21).

8. Species diversity of whole-water communities (H) is an index that has not been used extensively, but it has been proposed as a potentially sensitive indicator of trophy (Hooper 1969, Brezonik 1969). Values generally are high in unproductive lakes and low in eutrophic waters. H appears to be a moderately good index for Minnesota lakes (Tables 35 and 36).

These eight classificatory variables should not be regarded as the only indicators that apply to Minnesota lakes. They are used here as variables that meet the requirements of trophic-state indicators, and they can be used to investigate the nature of classification schemes. Further investigations on other physical, chemical, and biological parameters, a number of which were discussed above, may lead to the identification of variables that could complement the present set of indicators or that may, in fact, be better indicators of trophy.

Trophic-State Types

Classification schemes based on trophic-state indicators (TSI) were investigated empirically by performing cluster

analyses on selected suites of variables. Because of the fact that the indicators were measured in different units, it is necessary to standardize them. Specific conductance, alkalinity, $\sum$ Ca + Mg, and the standing crop of phytoplankton indicate eutrophy in a positive sense, i.e. an increase in the value of the indicator is associated with an increase in apparent trophic state. Each variable was standardized by subtracting the mean from each of the observed values and then dividing the difference by the standard deviation. Phytoplankton diversity, secchi disc values, and the number of net taxa, however, are inversely related to increasing trophic state. These values were computed first as reciprocals, and then standardized, as above, on the basis of the resulting statistics. All variables were weighted equally in analyses. Orloci's absolute distance measure, judged previously as the most satisfactory similarity measure, was used in all analyses.

A series of 16 clustering runs was performed by using selected combinations of the eight TSI. The results of eight analyses, which are representative of the 16 runs, are set out in Table 44. In each analysis, four major lake groups are detected. The groups are designated here as Type 1, 2, 3, and 4. Clusters consisting of fewer than five lakes that enter a major cluster at high Q/k values are designated as residuals. R denotes a single residual. R_n indicates a residual cluster, with n being equal to the number of lakes. In several analyses

(Runs 5, 6, 7), a group of lakes was found to be transitional between Type 2 and Type 3. Because it occurred in seven of the runs, it has been designated as Type 2/3.

The most obvious feature of these analyses is that the size and composition of the clusters vary, depending upon which combination of TSI was used. The number of differences is greatest between Runs 1 and 8 and between Runs 6 and 8. In both cases, nearly one-half (31N) of the lakes were detected as being members of different clusters. The number of differences was fewest between Runs 6 and 7 (1N) and between Runs 1 and 3 (6N).

It is instructive to examine these results by considering the maximum and minimum number of lakes that constitute each type, and to determine the extent to which a specific lake is consistently recognized as a member of the same cluster. The number of lakes assigned to each of the types can be summarized as follows (numbers in parentheses refer to the Run number in Table 44):

Type	Maximum No.	Minimum No.
1	24 (8)	15 (5)
2	30 (1)	20 (6)
2/3	6 (5, 6)	5 (7)
3	12 (3)	5 (4, 5)
4	10 (7)	5 (2)
R	6 (2, 4)	2 (3)

In all cases except Type 2/3, there is a large range in the number of lakes assigned to a specific type.

The number of lakes that are identified consistently, or in most runs, as members of the same major type can be observed in the following summarization:

Type	All 8 Runs	6 of 8 Runs
1	15	17
2	14	20
3	0	3
4	0	0
R	0	2

These findings indicate that many of the Type 1 and 2 lakes located in northern and central Minnesota are consistent members of each group. Lakes identified consistently as Type 3 and 4 members, however, are few in number. Most of these lakes sort out as Type 2, 2/3, 3, 4 or as residuals in alternative runs.

Collectively, the above observations reveal that the use of different sets of TSI can give rise to lake clusters that are markedly dissimilar in their size and composition. If a matrix of difference values, i.e. the numbers of differences in lake placement between any two runs is constructed for all 16 runs, a general trend emerges. The composition of the major clusters becomes more and more dissimilar with the addition of biological TSI. The maximum number of differences occurs between the set of four physical-chemical TSI (Run 1) and the

four biological TSI (Run 8).

Characterization of Types

For the purposes of the present study, it is impractical to characterize the types that have been identified in all of the runs. It is more instructive instead to delimit the lake groupings that were formed by three sets of TSI: 1) the four physical-chemical indicators (Run No. 1); 2) the biologic indicators (Run No. 8); and 3) the complete set of eight indicators (Run No. 7). Runs 1 and 8 produced the greatest number of compositional differences; whereas Run 7 yielded a classification scheme that was intermediate between these two extremes.

The most convenient procedure for delineating the lake groupings is to examine the mean values of the classificatory indicators (Table 45), and then to view the types against the salinity ranges that they occupy. Salinity ranges and mean values are depicted graphically in Fig. 42 and are summarized statistically in Table 46. Within this framework, it is then possible to discuss the composition of the types. A complete listing of the lakes in each type for all of the runs is given in Table 44.

Physical-chemical TSI (Run No. 1)

The four lake types detected in this analysis yield indicator values whose means are dissimilar. All of the TSI, except

secchi disc values, exhibit progressively higher mean values from Type 1 through Type 4. The relatively high mean value of SD in Type 4 is due largely to the incorporation of Lake Spiritwood (No. 58) into the cluster. SD in this lake is 13.0, whereas four of the other five lakes have SD values < 3.0 feet. The low mean SD estimate in Type 3 is due to SD levels in each of the eight lakes that do not exceed 2.5 feet. The salinity ranges of Type 1 and 2 lakes are well separated, but Types 3 and 4 overlap with each other and with Type 2 as well. The mean salinity levels of all groups except 3 and 4 are statistically dissimilar.

Type 1 is restricted in its composition to the northeastern lakes, except for Lakes Deming (No. 16) and Josephine (No. 32) in northern Minnesota. Type 2 encompasses most of the lakes in central Minnesota, and includes a number of moderately saline prairie lakes in western and southwestern Minnesota and in South Dakota. Type 3 is composed entirely of prairie lakes in southwestern Minnesota and North Dakota. The lakes representing Type 4 are located in the prairie of Minnesota, North Dakota, and South Dakota. The group does, however, include two saline lakes in northwestern Minnesota (Mud No. 48 and Thief No. 62).

Biologic Indicators (Run No. 8)

The four lake groups detected with this suite of TSI yield indicator values whose means are not all statistically

dissimilar. All of the TSI, except H diversity, exhibit progressively higher values from Type 1 through Type 4. The observation that the mean value of H is higher in Type 4 than in Type 3 is due to the fact that the lakes that constitute Type 4 (No's. 3, 5, 15, 18, 28, 37, and 46) have H estimates that range between 2.2 and 3.95. The lakes in Type 3 (No's. 27, 30, 38, 41, 53, 56, 63, and 67) exhibit diversity estimates that range between 0.805 and 2.162. Except for standing crop, the mean values of the indicators are not always large between adjacent types (cf. Type 3 and 4). The salinity ranges occupied by each group overlap; in fact, Type 3 is totally eclipsed by Types 2 and 4. The mean salinity levels between Types 2 - 3 and 3 - 4, however, are not statistically different.

The types are highly heterogeneous in their composition. Type 1 includes all of the lakes in northeastern Minnesota and a number of the moderately saline lakes in northwestern Minnesota as well. Lake Pickerel (No. 50) in South Dakota is also a member of this type. Type 2 is restricted primarily to the lakes of central Minnesota, but it does include several prairie lakes in western and southwestern Minnesota. Type 3 is restricted primarily to the prairie lakes of southwestern and western Minnesota and to South Dakota and North Dakota. Type 4, except for Long Lake (No. 37) in northern Minnesota, is composed of prairie lakes located in southwestern Minnesota and in North Dakota and South Dakota.

Chemical-Biological Indicators (Run No. 7)

Five major types were detected with the complete suite of eight TSI. All of the indicators show highly significant F-statistics; however, many of the indicators are not statistically different among each of the types. The lack of statistical dissimilarity between the mean values of several indicators in some of the types is brought about partially by the formation of the transitional Type 2/3. The five lakes that constitute this cluster (Elk No. 20, Minnewaska No. 45, Mud No. 48, Spiritwood No. 58, and Thief No. 62) exhibit levels of ALK, $\sum$Ca + Mg, and COND that are higher than the corresponding mean levels of Type 3. The lakes sort out as an intermediate group, however, because the mean values of SD, SC, H, S, and CPQ, approximate those of Type 2. The salinity range for Type 1 is unique, and that for Type 2 overlaps slightly with Type 3. Type 4 eclipses Type 3 partially and Type 2/3 entirely. Despite the degree of overlap in salinity range, all but three possible combinations are statistically significant (cf. Types 2 - 3, 2/3 - 3, 2/3 - 4).

The composition of the types is basically intermediate between Run 1 and 8. Type 1 lakes are restricted to the northeastern region, except for Josephine (No. 32) and Deming (No. 16). Type 2 includes many of the lakes in central Minnesota and the prairie lakes Fish (No. 21), and Pickerel (No. 50). The composition of Type 3 includes only prairie lakes, except for Lakes Halsted (No. 27) and Long (No. 37).

Type 4 is composed strictly of prairie lakes in western and southwestern Minnesota and in North Dakota and South Dakota. The transitional Type 2/3 is composed of 5 lakes, all on or near the prairie.

There are a number of generalizations that can be drawn from the results of the classification schemes based on TSI (Table 45 and Fig. 42). The use of the four physical-chemical TSI (Run No. 1) results in several lake types that are well-separated; however, the two groups of prairie lakes (Types 3 and 4) are relatively similar. This occurs partially because of the relatively high SD values in several of the highly saline prairie lakes, and because the mean levels of COND and $\sum$Ca + Mg in the two types do not differ substantially from one another.

The utilization of biological TSI (Run No. 7) results in some lake clusters whose mean salinity levels are dissimilar, but there is considerable overlap in the salinity ranges that they occupy. This occurs partially as a consequence of the relatively high H values in Type 4, and partially because the mean values of some indicators do not differ markedly between some of the adjacent types.

The "intermediate" nature of the types formed by the use of the eight TSI (Run No. 7) represents a "balancing" effect between the physical-chemical and the biological indicators. Collectively, these observations indicate that the biological

TSI, relative to the physical-chemical TSI, exhibit considerable variation in lakes of the same geographic region. This is especially true of the lakes in the prairie. In general, their use as classificatory variables produces lake groupings that are not as sharply delimited as those formed by the physical-chemical TSI.

Biospecies Lake Types

There have been no attempts to classify the lakes of Minnesota on the basis of the phytoplankton flora. Previous investigations on the distributional patterns of planktonic diatoms (Bright 1968, unpublished) and net phytoplankton (Brook 1971, unpublished) in the region have focused primarily on detecting species and species associations.

The composition of the algal flora, i.e. the occurrence and distribution of individual taxa, however, can be regarded as a set of variables and can be used for the purpose of classifying the lakes (cf. Brown 1969). Theoretically, this approach represents the antithesis of the one adopted by the above authors and by many other investigators (cf. Hutchinson 1967), because the species themselves are used to establish lake groupings. In practice, however, the approaches are complementary rather than mutually exclusive, since each provides related information. The net phytoplankton flora is used here as a means of investigating lake types in the region.

Initially, the lakes were arranged in order of increasing salinity and the species were plotted accordingly. When the data are viewed in this form, it is difficult to detect the optimum number of lake groups that are present in the data set, and it is equally difficult to visualize the degrees of similarity among many lakes. Many taxa either have distributions that are cosmopolitan or near-cosmopolitan or they occur sporadically. Some species do have distributions that are largely confined to a particular geographic region, e.g. the northeastern lakes, whereas other taxa have distributions that span at least two geographically distinct regions, e.g. the northeastern lakes and the lakes of central Minnesota.

The analyses undertaken here on biospecies classification schemes are exploratory and highly empirical. The use of cluster analysis, however, provides an objective means of delineating lake groupings and allows the types to be compared with one another. The algal groups Chlorococcales, dinoflagellates, and euglenoids were omitted from analysis. These algal suites either contain few species whose distributions are confined to specific geographic regions, or they contain a small number of taxa that occur so infrequently that an analysis would be strongly weighted by absence data (Table 57). The chrysophytes, although they contain numerous taxa whose occurrences are restricted to the northeastern lakes and to the lakes of central Minnesota, were not utilized in analysis. Species in this group occur so infrequently in the prairie that an

analysis would be strongly weighted by absence data.

Biospecies Types

Lake classification schemes were investigated by performing cluster analyses on four sets of phytoplankton data: diatoms (25N), desmids (39N), bluegreen (29N), and the entire net phytoplankton flora (167N). The species utilized in the clustering runs are set out in Table 57. Species of diatoms, desmids, and bluegreens with fewer than three occurrences were omitted from the analysis. Taxa that occur so infrequently cannot be regarded as exhibiting a preference for a particular community type (cf. Fager 1963). All of the analyses were conducted on the basis of presence/absence data (Table 57). This approach is more conservative than utilizing abundance data, because the relative abundances of the species would be expected to vary to a greater degree than presence/absence data.

Prior to the analysis, each species was coded and assigned a presence value of 1.0 if it occurred in a sample. The similarity between lakes and clusters of lakes is based directly on the number of taxa in common and indirectly on the number of taxa not in common. Lakes with an identical flora are most similar; those with no taxa in common are most dissimilar. Orloci (1967) has demonstrated that the absolute distance measure exaggerates differences among objects, whereas standard distance minimizes these differences. For each of the four data sets, separate clustering runs were performed by using

both absolute and standard distance. It was found on inspection that the size and composition of the groups were very similar; hence, the presentation of results is limited to those generated with absolute distance.

The results of the four analyses are set out in Table 47. Three major groups were detected in each of the runs. They have been designated here as Type 1, 2, and 3. It is apparent that the size and composition of the types vary depending upon which set of algal data is used. The results can be summarized initially by examining the number of lakes that constitute the types in each of the analyses:

Group	Type 1	2	3
Diatoms	31	27	10
Desmids	15	33	20
Bluegreens	13	17	38
Total phytoplankton	13	27	28

The dissimilarity among the composition of Types 1, 2, and 3 in the runs can be examined by constructing a matrix of difference values. The greatest degree of dissimilarity occurs between diatoms and bluegreens (37N), bluegreens and total phytoplankton (33N), and desmids and diatoms. The composition of the lake groupings is most similar between desmids and total net phytoplankton (only 14 differences) and between bluegreens and net phytoplankton (19 differences).

Despite the relatively high degree of dissimilarity among the lake groupings that is produced by the use of different suites of algal taxa, several lakes are recognized consistently as members of the same type.

Type 1: Big (No. 6), Burntside (No. 9), Clearwater (No. 13), Iron (No. 29), Kimball (No. 33), Lamb (No. 34), Trout (No. 64), Vermilion (No. 66), and Wilson (No. 68).

Type 2: Carman (No. 10), Clear (No. 12), Elk (No. 19), Fish (No. 21), Halsted (No. 27), Minnewaska (No. 45), Pickerel (No. 50), Sallie (No. 51), Tanager (No. 61), Upper Minnetonka (No. 65).

Type 3: Alkali (No. 2), Alkaline (No. 3), Eckelson (No. 18), George (No. 23), Isabel (No. 30), Salt (No. 52), Traverse (No. 63), Waubay (No. 67).

The lakes in Type 1 are all confined to the northeastern region. Those lakes in Type 2 are limited to central Minnesota or to low salinity lakes in the prairie. The composition of Type 3 is limited primarily to prairie lakes of high salinity.

Characterization of Types

The types produced by each suite of phytoplankton taxa can be characterized first by viewing the salinity range that each one occupies, and then by considering the specific composition of the groups. Salinity ranges and mean values for the types are plotted in Fig. 43. Summary statistics, including the results of significant difference computations, are given in Table 48.

Diatoms. This suite of species results in groupings that are heterogeneous in composition. The salinity range spanned by Type 1 completely eclipses that of Type 2 and partially overlaps Type 3. Types 1 and 3 are statistically dissimilar, as are Types 2 and 3, but Types 1 and 2 are not.

Type 1, the largest group, constitutes nearly half the study lakes. The group is composed of all but one of the lakes in northeastern Minnesota, and it includes many of the lakes in north-central Minnesota. Three lakes in the deciduous forest (Frances No. 22, Christmas No. 11, and Spectacle No. 57) and two prairie lakes (Spiritwood No. 58 and Minnewaska No. 45) are members as well.

Type 2 is composed of lakes within the deciduous forest belt and includes many of the prairie lakes in southwestern Minnesota and in South Dakota. Lakes Sanborn (No. 53) and Long (No. 38) in North Dakota and Lake Shagawa (No. 55) in northeastern Minnesota are also members of the group. Type 3, the smallest group, consists of only 10 lakes, all of which are located in the prairie.

Desmids. The lake groups formed by this suite of chlorophytes overlap considerably with one another. Type 3 totally eclipses the salinity range of Type 2, and it overlaps substantially with the range occupied by Type 1. Types 1 and 2 are statistically dissimilar as are Types 1 and 3; Types 2 and 3 are not, however.

Type 2, the largest group, is composed mostly of lakes that are located from north to south in central Minnesota. It includes many of the prairie lakes in southwestern and western Minnesota and in the Dakotas. It also includes two highly saline prairie lakes, Eckelson (No. 18) and Salt (No. 52). Type 1, the smallest group, consists of all of the lakes in northeastern Minnesota, except Lakes Shagawa (No. 55) and Superior (No. 60), and includes Moose (No. 47) and Goose (No. 25) in north-central Minnesota. Type 3 is composed entirely of prairie lakes in Minnesota and in the Dakotas, but it does include Lakes Superior (No. 60) and Shagawa (No. 55) in northeastern Minnesota and Lakes Long (No. 37) and Josephine (No. 32) in northern Minnesota.

Bluegreens. The cyanophyte flora results in groups that are highly heterogeneous in their geographic composition. The salinity range occupied by Type 1 eclipses that of Type 2, and both Type 1 and Type 2 are eclipsed totally by Type 3. Despite the degree of heterogeneity, however, each of the types is statistically dissimilar from all others.

Type 1 is composed of nine of the 16 lakes in northeastern Minnesota, several lakes in central Minnesota (Goose No. 25, Gladstone No. 24, and Spectacle No. 57), and Elk (No. 20) on the prairie. Type 2 includes approximately half of the lakes in central Minnesota. Crane (No. 14) in northeastern Minnesota and four of the prairie lakes (Big Kandiyohi No. 7, Fish No. 21, Minnewaska No. 45, and Pickerel No. 50) are also members of this

Type. Type 3 constitutes over half of the study lakes. The assemblage includes nearly all of the prairie lakes, many of the lakes in central Minnesota, and five of the lakes in northeastern Minnesota, Superior (No. 60), Vermilion (No. 66), Dogfish (No. 17), Meander (No. 42), and Loon (No. 39).

Total Net Phytoplankton. The entire suite of planktonic taxa results in groupings whose salinity ranges overlap, especially those of Type 2 and 3. All of the mean values, however, are statistically dissimilar.

Type 1 includes all of the lakes in northeastern Minnesota, except Shagawa (No. 55) and Superior (No. 6). Type 2 is limited almost exclusively to the central region of the state, but it does include four moderately saline prairie lakes (Pickerel No. 50, Minnewaska No. 45, Big Kandiyohi No. 7, and Fish No. 21). Type 3 is limited in its composition to the prairie of Minnesota, North Dakota, and South Dakota, but it does include Lakes Superior (No. 60) in northeastern Minnesota and Long (No. 37), Josephine (No. 37), and Deming (No. 16) in northern Minnesota.

The results of these analyses permit a number of generalizations to be made concerning schemes of lake classification based on suites of phytoplankton taxa (Table 50 and Fig. 43). The lake groupings formed in each of the four analyses tend to overlap substantially, as evidenced by the salinity ranges that are occupied by each of the types. The composition of the lake

groupings produced by the desmid and the diatom flora is markedly heterogeneous. The mean salinity levels of some types are not statistically dissimilar. The suite of bluegreens and the entire net phytoplankton flora also result in lake groupings whose salinity ranges overlap. The mean salinity level of each type, however, is statistically dissimilar.

Collectively, these observations provide evidence to support the view that suites of phytoplankton taxa do not produce lake clusters that are well-separated from one another. The explanation for the degree of overlap among the salinity ranges occupied by the types is that some species occur throughout the region, whereas others are distributed over at least two geographic provinces.

The only possible exception to this generalization is the scheme of lake types produced by the complete net phytoplankton flora. Although the salinity ranges of the types do overlap, the mean values are extremely well-separated from one another.

The fact that some types exhibit mean salinity levels that are statistically dissimilar, however, provides evidence that there are certain species that occur principally in specific lake types. Indicator species will be evaluated in Chapter 7.

Comparative Lake Classification Schemes

One of the major questions that arises in lake typology is: How similar are lake groupings that have been formed by

using different sets of criteria? The previous analyses, based on data sets consisting of major solutes, TSI, and phytoplankton species, provide an opportunity to investigate this problem in a manner that is reasonably objective.

The procedure adopted for these comparisons is the same as that employed in previous analyses. Contrasts are made on the basis of 1) the salinity range that is occupied by each type, and 2) the statistical significance of the mean values. Direct contrasts among major solute and TSI classifications and among biospecies groupings are possible because the number of groups formed in the analyses is similar.

Contrasts Between Chemical and TSI Schemes. Salinity ranges and mean values for the major solute and TSI classification schemes are depicted graphically in Fig. 42 and summarized statistically in Table 49.

The salinity range occupied by Type 1 in three of the analyses is identical. The biologic TSI, however, result in a group that spans a much larger range. Its mean value is statistically dissimilar from all other groupings.

Type 2 exhibits salinity ranges that are dissimilar, especially the one occupied by the biologic TSI. The mean values of the four groupings reflect observable differences; however, none of them is statistically dissimilar at $P = 0.05$. If the level of rejection is lowered to $P = 0.10$, the mean values between major solutes and biologic TSI and between

biologic TSI and chemical-biologic TSI are dissimilar.

Note: Type 2/3 was omitted from analyses.

Type 3 exhibits moderate differences in salinity range and mean values. These differences, however, are not significant, indicating a high degree of similarity in composition.

Type 4, except for the major solute grouping, occupies broad salinity ranges. None of the groupings, however, is statistically dissimilar.

These comparisons reveal that the types formed by major solutes and by TSI indicator sets are reasonably similar in their composition. The significant differences that occur in Types 1 and 2 are due primarily to the set of four biologic TSI. There is a tendency also for the three sets of TSI to form Type 4 groupings that span large salinity ranges. The differences are statistically insignificant, however, but further testing with a larger number of lakes would be necessary to evaluate the degree of similarity or dissimilarity.

Biospecies Contrasts. Salinity ranges and mean values for the biospecies classification schemes are depicted graphically in Fig. 43 and summarized statistically in Table 50.

Type 1 groupings occupy highly variable salinity ranges. The largest difference is between the diatom and total net phytoplankton. Each of the four mean values is observably different, but none of them is statistically dissimilar.

Type 2 spans salinity ranges that are dissimilar, especially those occupied by the desmid and the total net phytoplankton. Although in most cases the means are dissimilar, none of them shows statistical dissimilarity.

Type 3 spans large salinity ranges, and, except for the diatom grouping, exhibits mean values that are highly similar. None of the mean levels is dissimilar at P = 0.05. At P = 0.10, however, the diatom grouping does differ from the groupings formed by the other three species suites.

These comparisons reveal that each of the types formed by the four species suites is fairly similar. Despite the observable differences in salinity range and mean value, the only comparison that is statistically significant involves Type 3 lakes, and it is due to the grouping formed by the diatoms.

Contrasts Among Chemical, TSI, and Biospecies Schemes. Direct comparisons among the types that have been generated by the use of major solutes, combinations of TSI, and suites of phytoplankton taxa cannot be made statistically (Figs. 42 and 43). The major solute and TSI classifications generally result in four major types, whereas the species suites give rise to three primary lake groupings. Nevertheless, several generalizations can be made by evaluating the results in a subjective manner.

1. The salinity ranges spanned by Type 1 clusters are nearly identical for the major solutes, TSI (chemical), TSI (chemical

and biological), and net phytoplankton. The salinity ranges occupied by the TSI (biological), desmids, bluegreens and diatoms, however, are much larger and exhibit higher mean levels.

2. The salinity ranges spanned by Type 2 clusters are narrow and reasonably well-separated from adjoining types for the major solutes and the TSI (chemical and biological). The biospecies and the TSI (biological) cluster, however, occupy exceptionally broad salinity ranges and they overlap substantially with other lake groupings.

3. The salinity ranges occupied by Type 3 are extremely large for the desmids, bluegreens, and net phytoplankton. They include or totally eclipse Types 2, 3, and 4 in all of the other analyses.

These observations demonstrate that the lake groupings based on major solutes are reasonably distinct geographically and they are well-separated from one another. Comparatively, the utilization of biological TSI results in lake clusters that occupy larger salinity ranges, and that are not as well-separated from one another. The lake groupings formed by selected suites of phytoplankton taxa exhibit the greatest degree of heterogeneity in their size and geographic composition. Nearly every one of the types overlaps with other groupings.

CHAPTER VI

EVALUATION OF TROPHIC INDICATORS

One of the principal objectives of the present study is to evaluate properties of diatom and phytoplankton communities as indicators of trophic status in Minnesota lakes. The analyses undertaken here are designed specifically to 1) evaluate each variable as a potential indicator of trophy, to 2) identify specific algal expressions that are unique indicators of trophic state, and to 3) detect community properties that may serve as indicators after further, more extensive study. As an integrated part of these evaluations, the results of this investigation are compared with previous studies in Minnesota (Net Phytoplankton Analysis), and they are contrasted with investigations in other north-temperate regions.

The analyses undertaken here can be carried out in a manner that is reasonably quantitative. The previous studies on lake classification provided lake groups that are objective and that are defined in their composition (Chapter V). For the purposes of the present evaluation, I have elected to utilize the types that were established by performing cluster analysis on the suite of major solutes (cf. Fig. 41 and Table 42). These groupings are highly conservative in composition. The mean values of the major solutes are either statistically or observably dissimilar among each of the types (Table 43); the

mean salinity levels of the groups are statistically dissimilar (Table 46); and the salinity ranges occupied by the types are reasonably well-separated from one another (Fig. 41).

In order to maximize the size of the types, five additional lakes were added to the groupings. Lake Goose (No. 25) was placed in Type 1, and Lakes Lillian (No. 35), Stinking (No. 59), School Grove (No. 54), and Albert (No. 1) were added to Type 3. These lakes were not included in the classification scheme based on major solutes because data on the concentrations of major anions and cations were not available. The lakes have COND values, however, that justify their assignment to each of the groups (cf. Tables 12 and 46).

Each type has been assigned trophic designation. This nomenclature, relative to the range of trophic conditions in Minnesota lakes, is satisfactory for the purposes of description. Type 1 (18N) is regarded as a group of oligotrophic lakes. Type 2 (24N) is considered to be a lake group that is mesotrophic to eutrophic in character. Type 3 (21N) is viewed as an assemblage of lakes that is saline and highly eutrophic. Type 4 (5N) is a small group of prairie lakes that is highly saline and "hypereutrophic" in nature (sensu Brezonik et al. 1969).

It should be emphasized that the nomenclature used here is arbitrary, and it may not be comparable to trophic states as defined by investigators in other regions. Despite this fact, I am in agreement with Vallentyne (1969):

> The concept of trophic state as described in the limnological literature (e.g. oligotrophy, mesotrophy, eutrophy) is too multi-dimensional and too susceptible to individual interpretation to be of value to model makers. Nevertheless, limnologists should establish criteria for oligotrophic, mesotrophic, and eutrophic waters, both in terms of lake classification per se and problem-oriented classifications independent on morphometric change. Both have predictive value.

A preliminary rationale for relating salinity levels to nutrient levels and productivity in lakes of this region was presented in Chapter IV, p. 44. The justification for assigning trophic designations to lake groupings that are based on differences in the concentrations of major solutes and salinity is based in part on Moyle's (1954) investigations and partially on data generated in the present study.

Moyle demonstrated that increases in salinity generally are accompanied by increases in the levels of phosphorus, nitrogen, and alkalinity. On a volumetric basis, therefore, the lakes in northeastern Minnesota are lower in nutrients and less productive on the average than the lakes of central Minnesota. The shallow prairie lakes can be considered as representing waters of high nutrient content that are more productive on the average than the lakes in the central part of the state.

Measurements of total phosphorus from seven lakes in northeastern Minnesota and from five saline prairie lakes that were made in this study closely approximate the mean levels of phosphorus that are given by Moyle (1954) for the two regions.

Although the phosphorus estimates are too few in number to investigate the degree of correlation between this nutrient and salinity, it is likely that salinity is in fact a good indirect measure of nutrient level.

In addition to this evidence, the assignment of trophic designations to the lake types can be substantiated by measurements on the standing crop of phytoplankton (SC) and by regional differences in transparency. The estimates of SC exhibit a significant positive correlation with specific conductance (Table 13 and Fig. 32), and they also show significant differences in mean value among the types (Table 54). Similarly, secchi-disc transparency (SD) exhibits a significant inverse correlation with salinity (Table 13). The mean values of SD in the lake groups are:

Type	SD (feet)
1	12.0
2	6.5
3	2.8
4	1.6

The results of an analysis of variance (df = 3, 64) yield an F-statistic of 10.9 (significant at P = 0.01). All of the mean estimates are dissimilar at P = 0.05, as judged by the multiple comparison test of Scheffe (1959).

The statistical procedures and criteria that are used to evaluate each algal variable are presented here in detail.

The initial step in the evaluation is to perform an analysis of variance. This procedure determines if there is at least one combination of mean values that is statistically dissimilar. A mean square ratio of $F = 2.74$ at $P = 0.05$ and $F = 4.10$ at $P = 0.01$ is required to detect a significant mean difference. In these analyses there are 3 and 64 degrees of freedom. If a significant F-statistic at either of these levels is detected, the multiple mean comparison test of Scheffe (1959) is applied. The latter analysis identifies specifically which mean combinations differ from one another. The significance level is set arbitrarily at $P = 0.05$ ($F = 2.74$).

The analysis of variance, coupled with the multiple comparison test, is a procedure that is generally satisfactory. The number of lakes in Type 4 (5N), however, is very small and cannot be regarded as a representative group of lakes. Its incorporation into the above analyses could cause significant mean differences between Types 1, 2, and 3 to escape detection. For some of the evaluations, separate analysis of variance tests were performed by omitting Type 4. The results are presented only if they substantially alter the conclusions. In addition, if reasonably large differences between the mean values of Types 1 and 2 were observed, a separate analysis using only these two groups was performed. A mean square ratio of $F = 4.08$ at $P = 0.05$ and $F = 7.31$ at $P = 0.01$ is required for significance.

The criteria that are used to assess each variable as an indicator of trophic state are: 1) a significant difference between or among mean values in the types; and 2) the trend of the average estimates in each type to increase or to decrease progressively with trophic states of higher order. The assessment of potential or actual indicator value undertaken here also includes a consideration of the criteria outlined by Brezonik and Shannon (1971). Specifically, they suggest that an indicator should be a property that is measureable and quantifiable. Obviously, an estimate of an algal variable that is highly dependent upon sample size or that is difficult to measure accurately because of poor precision detracts from its value as a potential indicator of trophic state. The previous analyses on the bias that can be introduced by dependence on sample size and by counting errors (Chapter II) are integrated with the following evaluations.

Net Phytoplankton Analysis

Species Number

The average value of S in each of the types is statistically dissimilar (Table 51). The mean value of S is highest in the oligotrophic lakes and lowest in the small group of prairie lakes, and it decreases in average value with increasing trophic state of the lake groupings. These observations indicate that S is a good indicator of trophic status in Minnesota lakes.

It is instructive to compare these findings with the results of a previous investigation that was conducted by Brook (1971, unpublished). He sampled 55 lakes during summers 1965-1967 that were distributed among three lake groups within the study region (Table 52). The types utilized by Brook are similar to those of the present study. Type 1 (22N) is composed entirely of lakes in northeastern Minnesota. Type 2 (26N) constitutes the lakes in the central region of the state. Type 3 (7N) is a small group of prairie lakes in Minnesota. The mean COND values of Types 1 and 2 are nearly identical with those of the present study. Type 3, however, has a lower salinity level than Type 3 of this study (Table 43).

Brook's observations differ in two respects from those of the current study. First, the mean values of S in Types 1 and 2 are not statistically dissimilar. Second, in this study the mean estimates of S in Types 1 and 2 are nearly twice as high as those detected by Brook (1971, unpublished).

These disparities are surprising and are somewhat difficult to rationalize. It is plausible that average values of S are higher during fall than during summer. The discrepancy also could be attributed to differences in the thoroughness of sample analysis, or to the fact that some taxa used in the present computations were not utilized by Brook (see Chapter II, p. 11 and Table 57).

Although the findings of this study indicate that S is a good indicator of trophic state, Brook's observations suggest

that the expression may not apply throughout all seasons of the year. Moreover, it is necessary to standardize sample sizes and to define precisely just which species are planktonic and should be included in analysis.

Compound Phytoplankton Quotient

The mean value of CPQ in each of the types is observably different (Table 51). Each estimate increases with increasing trophic status of the lake groupings. Not all of the means, however, are statistically dissimilar. CPQ is low in the oligotrophic lakes, and it differs significantly from all of the other mean estimates. Types 2 and 3 and Types 3 and 4, however, cannot be judged as dissimilar on the basis of these calculations.

These results suggest that CPQ is an indicator that allows the oligotrophic lakes to be distinguished from the mesotrophic to eutrophic lakes in central Minnesota. The quotient, however, does not appear to be an expression that can be used to separate all trophic categories in the study region.

It is instructive to compare the results of this study with those of Brook's investigation (Table 52). The composition of the lake groupings used by him were discussed above. His observations indicate that mean estimates of CPQ in each of the types are statistically dissimilar. The small

group of prairie lakes yields a higher mean value than Type 3 in the present study. This may be an artifact of sample size, however. The mean values of CPQ in Types 1 and 2 of both investigations are nearly identical.

Brook's findings compare favorably with results of the present study. The fact that the mean values in the oligotrophic and mesotrophic to eutrophic lakes are nearly identical indicates that seasonal variability in CPQ is probably minimal. The feasibility of using CPQ to distinguish between Types 1 and 2 is judged here as acceptable. It is supported also by the fact that errors in the estimation of the quotient are small (Chapter II, p. 11).

The above observations reveal that the scale of CPQ values that was proposed by Nygaard (1949) for Danish lakes and used by Brook (1965) in Great Britain does not apply to the lake groupings in Minnesota. Both authors use the following trophic ranges: oligotrophic (0 - 1); mesotrophic (1 - 2.5); and eutrophic (>2.5). In this study the quotient ranges between 0.96 and 5.5 in the oligotrophic lakes ($\bar{x}$ = 2.33), and between 1.92 and 15 ($\bar{x}$ = 5.41) in the mesotrophic to eutrophic lakes of Minnesota. Similarly, Brook's observations in this region reveal that CPQ ranges between 0.6 and 4.0 ($\bar{x}$ = 2.54) in Type 1 and from 1.92 to 15.0 ($\bar{x}$ = 6.78) in Type 2.

The scaling of quotient ranges in Minnesota lakes is markedly displaced toward the eutrophic category. If the trophic spectra

of the above authors is imposed on Minnesota lakes, Type 1 would be judged as mesotrophic to eutrophic, and Type 2 would be ranked as highly eutrophic. This disparity is undoubtedly due to the fact that the oligotrophic lakes in this region are not so chemically dilute as the oligotrophic waters in Britain and Denmark. Brook (1965) gives an average value of 0.07 meq/l $CaCO_3$ for oligotrophic lakes in the English Lake District. Type 1 lakes in this region average 0.374 meq/l $CaCO_3$, a five-fold difference. It is apparent that, if CPQ is to be used as an indicator in north-temperate regions, estimates should be weighted or normalized in some fashion so that realistic comparisons can be made.

Desmids

The average value of DESMID S in each of the types is statistically dissimilar (Table 51). Mean estimates are highest in the oligotrophic lakes, lowest in the small group of saline prairie lakes, and progressively higher with increasing trophic state. These observations indicate that DESMID S is a good indicator of trophic status in this region.

The results of the present study were compared with Brook's investigation (Table 52). His data reveal that the average values of DESMID S are dissimilar between Types 1 and 2, but Type 3 does not differ from Type 2. The latter observation may be real, or it may be an artifact of small size in the prairie

grouping. The major difference between Brook's observations and the present findings is that DESMID S is noticeably higher in each of the three types in this study. This discrepancy could be due to seasonal variability or to the fact that some desmid taxa not utilized by Brook were included in the computations in this study.

Collectively, both studies indicate that DESMID S is a good indicator of trophic state in Minnesota lakes. It is necessary, however, to standardize sample sizes and to identify the specific taxa that should be used in the computations.

Diatom Ratios

Stockner's Ratio

The mean value of A/C_s in each of the types is observably different (Table 53). Average estimates are highest in the oligotrophic lakes and in the small group of prairie lakes. Types 2 and 3 yield lower mean values. None of the estimates, however, is statistically dissimilar. A separate analysis was performed on Types 1 and 2 because of the observable differences in average value. The test revealed a non-significant difference at $P = 0.10$ ($F = 2.75$, df 1, 40).

These observations indicate that A/C_s, as proposed by Stockner, does not reflect trophic conditions in Minnesota lakes. Stockner's trophic scale of 0 - 1 (oligotrophy), 1 - 2 (mesotrophy), and >2.0 (eutrophy) suggests that all

lake groups in this region are highly eutrophic, especially the oligotrophic lakes in northeastern Minnesota. The feasibility of further studies on A/C_s is not promising because of its dependence upon sample size (Figs. 5 and 6), and because precision in its estimation is judged as moderately poor (Table 2).

The components of the ratio do exhibit mean values that are significantly different among some of the types (Table 53). Average estimates of A_s are dissimilar among all types and decrease progressively with higher trophic states. This observation suggests that A_s may, in fact, represent an expression that can be used to distinguish lakes of dissimilar trophic status. Further studies, however, would be necessary to verify the present observations.

C_s also exhibits mean values that are significantly different among some lake groups. Average estimates are higher in Types 2 and 3 and lower in the oligotrophic and saline prairie lakes. This trend is difficult to interpret. C_s is judged here as an indicator that has little value in separating lake groupings of dissimilar trophic state.

Nygaard's Ratio

The mean value of C/P in each type is observably different (Table 53). Estimates are relatively similar in Types 1, 2, and 3, and the ratio is low in the saline prairie lakes. The average values, however, are not statistically dissimilar.

These observations suggest that the ratio cannot be used as an indicator of trophic state in Minnesota lakes. In addition, if Nygaard's scale is used (< 0.75 indicates mesotrophy), all of the lake groupings would be in the category of oligotrophic to mesotrophic. The feasibility of further investigations on C/P is not promising because of its dependence on sample size (Fig. 7 and 8), and because precision in its estimation is judged as relatively poor (Table 4).

Similarly, the components of the ratio appear to have limited value as indicators (Table 53). Average estimates of P in each of the types are not statistically dissimilar. Mean estimates of C are comparable in Types 1, 2, and 3. The significant F-statistic is due to the low value in the small group of prairie lakes and is inconsequential.

Modified Ratios

The mean values of A/C_t are nearly equal in each of the types (Table 53). None of the average values is statistically dissimilar. Similarly, the components of the ratio do not yield mean values that produce significant differences among the types. The significant F-statistic generated by C_t estimates is due to the low mean value in the small group of prairie lakes. This difference is judged as inconsequential.

This ratio and its components appear to have little value as indicators of trophic state in this region. The feasibility

of further studies on the distribution of the ratio are judged as impractical. The ratio is highly dependent upon sample size (Figs. 9 and 10), and it cannot be estimated with a high degree of precision (Table 3).

The "alternative ratios" that were generated by using each diatom group alternatively as numerator and denominator (Chapter IV) were tested for significant differences among the types. The results are similar to those of A/C_s, C/P, and A/C_t (Table 53). No significant differences that have indicator value were detected.

Quantitative Analysis

Standing Crop

The mean estimates of SC in each of the types are statistically dissimilar (Table 54). Average values are low in the oligotrophic lakes, high in the small group of saline prairie lakes, and progressively higher with increasing trophic status of the lake groupings. These observations, coupled with the high degree of precision in estimation (Table 5), provide evidence that SC is a good indicator of trophic state in Minnesota lakes.

Net/Nannoplankton

The mean estimates of NET SC in each of the types are statistically dissimilar (Table 54). The values are low in

the oligotrophic lakes and progressively higher with increasing trophic status of the lake groupings. These observations provide evidence that this component of total SC is also a good indicator of trophic state in the study region.

The mean values of NANNO SC in each of the types are observably different (Table 54); however, none of the estimates is statistically dissimilar. The failure of this fraction of standing crop to exhibit significant differences among the types is due to the high degree of variance associated with each of the means. The observable difference between Types 1 and 2 was tested separately because of the large difference between the two means. The estimates, however, are not dissimilar ($F = 0.71$, $df = 1, 40$).

These observations suggest that NANNO SC is observably different among the lake groupings, but its value as an indicator of trophic state is minimal because of the high degree of variability within each of the lake groups.

Community Structure Analyses

Diatom Diversity

The mean values of the indices D and H and the related statistics S and J exhibit observable differences among each of the types (Table 55). None of these expressions, however, is statistically dissimilar. The relatively large difference between the mean values of D and H in Types 1 and 2 prompted a separate test involving only these two groups of lakes.

The results of analysis, however, indicate that the mean values are not dissimilar (H:F = 2.00, df = 1, 40; D:F = 0.999, df = 1, 40).

These observations provide evidence that species diversity in diatom communities is not an indicator of trophic state in Minnesota lakes. The failure of the indices to exhibit significant differences among the lake groupings cannot be attributed to the effects of sample size (Figs. 18 and 19) or to biases that are introduced by the lack of good precision (Tables 7 and 8). Although both D and S are dependent upon sample size, this problem has been circumvented by using a reasonably constant count size throughout the entire study (Table 24).

It is instructive to compare the values of D and H in this study with the trophic spectra given by Margalef. The mean value of D in the four lake groups indicates that each type would be recognized as mesotrophic (2.5 - 3.5) or oligotrophic (>3.5). The estimates of H, however, suggest that each group would be recognized as eutrophic (< 2.5). These estimates do not conform to the ranges that would be anticipated for lakes of this region.

Phytoplankton Diversity

The mean values of the indices H and D and the related properties J and S exhibit observable differences among the types (Table 56). Some of these contrasts are statistically

dissimilar, whereas others are not. These indices and properties will be examined individually.

The average estimates of D in each of the types are observably different. The oligotrophic lakes, however, do not differ from the mesotrophic to eutrophic lakes of central Minnesota, and the two groups of prairie lakes do not exhibit mean values that are statistically dissimilar. The relatively large observable difference between Types 1 and 2 prompted a separate test involving only these two groups. The results of the analysis, however, indicate that the means are not dissimilar ($F = 1.597$, $df = 1, 40$).

These findings indicate that D has limited value as an indicator of trophic state in Minnesota lakes. The results of these analyses are not biased by a lack of precision in the estimation of D (Table 8). Estimates of D, however, are dependent upon sample size (Fig. 24). The use of a reasonably consistent sample size throughout the study, however, minimizes this bias.

The average estimates of H in each of the types are observably different. The oligotrophic lakes, however, do not differ from the mesotrophic to eutrophic lakes in central Minnesota nor are they dissimilar from the small group of highly saline prairie lakes. Similarly, the mean values of the two groups of prairie lakes are not statistically dissimilar. The moderately large difference between estimates of H in

Types 1 and 2 prompted a separate test involving only these two groups of lakes. The results of the analysis indicate, however, that the means are not dissimilar ($F = 2.061$, $df = 1, 40$). These observations provide evidence that, although observable differences in H do occur among the types, the index has limited value as an indicator of trophic state in this region. The present findings are not biased by a lack of precision in the estimation of H (Table 10), nor are they biased by the effects of sample size (Fig. 23).

The evenness component of H diversity does exhibit observable differences in all of the types. The mean values of J are similar in Types 1, 2, and 3. The significant F-statistic is due to the relatively low mean value that was detected in the highly saline prairie lakes.

These observations indicate that J is not an indicator of trophic state in Minnesota lakes. The results of the analyses are not biased by poor precision or by the effects of sample size. Precision and the influence of count size on evenness are comparable to those already presented for H.

The mean values of S in each of the types are statistically dissimilar. The average number of taxa is highest in the oligotrophic lakes and lowest in the small group of saline prairie lakes, and decreases with increasing trophic status of the lake groupings.

These observations indicate that S in samples of whole water is a good indicator of trophic state in Minnesota lakes.

S, however, is dependent upon sample size. It can be used effectively only if the size of the count is reasonably constant.

It is instructive to compare the range of values of D and H obtained in this study with the trophic spectra given by Margalef. On the basis of D, each of the types in Minnesota would be ranked as oligotrophic (> 3.5), and Types 1 and 2 would be considered as lake groups that are "ultraoligotrophic". The scale of diversity values proposed by Margalef does not appear to be applicable to a description of the trophic status of Minnesota lakes.

Conversely, the average estimates of H in the lake groupings fit Margalef's trophic ranges reasonably well. The mean value of the index in Type 1 is very close to the expected value of 3.5 for oligotrophic lakes. Type 2 would represent a group of lakes that is mesotrophic. The two groups of prairie lakes would be judged as eutrophic or bordering on mesotrophy.

Although D and H have been judged in this study as indicators of limited value in Minnesota lakes, the observable differences in average value in each of the types suggest that further studies are needed. If the number of lakes sampled in each group is increased, it is possible that significant differences might be detected among most of the lake groupings.

Net/Nannoplankton Diversity

The average estimates of NET H, NANNO H, and the number of species in the two fractions exhibit observable differences

among the types (Table 56). Several of the mean estimates are statistically dissimilar, whereas others are not.

The average values of NET H and NET S are dissimilar among all of the types, except between the oligotrophic lakes and the mesotrophic to eutrophic lakes in central Minnesota and between the two groups of prairie lakes.

NANNO H exhibits average values in each group that are very similar. The significant F-statistic is due to the relatively high mean estimate in the oligotrophic lakes and the moderately low value in the large group of prairie lakes. In these analyses Types 1 and 2 are observably different, but they are not recognized as statistically dissimilar. A separate test involving only these two groups was performed. The results of the analysis indicate that the mean values are in fact dissimilar ($F = 4.50^*$, df = 1, 40).

The mean estimates of NANNO S in all of the types are observably dissimilar. The highest average value occurs in the oligotrophic lakes and the lowest in the small group of saline prairie lakes, and there is a progressive decrease in value with increasing trophic status of the lake groupings. All of the contrasts are dissimilar, except for Types 2 and 3 and Types 3 and 4.

The present findings suggest that species diversity in communities of net- and nannoplankton cannot be used effectively as trophic indicators in Minnesota lakes. The fact that some types exhibit mean values of H and S that are dissimilar,

however, suggests that further studies should be undertaken. It is plausible that by increasing the number of lakes in each group, species diversity in net- and nannoplankton might yield significant differences among most of the types.

NET SC and NANNO SC, expressed as percentage estimates, were tested for dissimilarity among the types. Mean percentage values in the four groups of lakes do not result in significant differences (Table 54). Types 1 and 2, however, exhibit relatively large differences in mean value. These two groups were tested separately for dissimilarity. The results of the analysis indicate that the oligotrophic lakes and the mesotrophic to eutrophic lakes in central Minnesota are dissimilar ($F = 9.442^{**}$, $df = 1, 40$). These observations suggest that NET SC and NANNO SC can be used as indicators to distinguish between these types, but it is doubtful that the expressions will apply to the entire region.

CHAPTER VII

EVALUATION OF INDICATOR SPECIES

One of the objectives of the present study is to evaluate species of net phytoplankton as indicators of the trophic status of lakes in Minnesota. Specifically, the analyses undertaken here are designed to 1) evaluate all of the species as potential indicators of trophy, to 2) identify species that are unique indicators of lakes of dissimilar trophic state, and to 3) detect taxa that may be found to have trophic preferences after further, more extensive study.

There have been numerous attempts to identify taxa that exhibit trophic preferences, and to use them to assess the trophic state of lakes (cf. review by Hutchinson 1967). The practice of utilizing indicator species, however, generally has met with limited success. A taxon that appears to be a reliable indicator in one lake district either exhibits no apparent trophic preference in another region, or it exhibits a preference for a different trophic state. Teiling (1955), for example, claims that indicators of oligotrophy and eutrophy in European lakes are not distinct, but he suggests that certain taxa are indicators of mesotrophy. Rawson (1956) suggests that there may be few, if any, species in lakes of western Canada that can be used with confidence in assessing trophic status. Järnefelt's (1952) investigations on more than 300

lakes in Finnland reveal that few taxa can be judged as indicators of oligotrophy, and only 30 taxa are found exclusively in lakes that are of high nutrient status.

It is pertinent to this investigation to consider the basic difficulties that can be encountered in evaluating species as indicators of trophic status. There are four problems that can introduce bias into such assessments. 1. The nomenclature used by various investigators frequently differs. Confusion can result therefore because of synonomies and other taxonomic inconsistencies. 2. A species may occur in lakes that are dissimilar in their trophic status. Although the species may be indistinguishable morphologically in each group, it may exhibit physiological differences that allow both forms to tolerate different conditions of trophy. 3. The trophic status of the lake groups used by various investigators is not always well-defined, and frequently the groupings have not been established in an objective manner. It is difficult, therefore, to compare indicators of "oligotrophy" in one lake district with indicators of "oligotrophy" in another region. 4. The criteria that have been used to assess a species trophic preference rarely have been defined in a manner that is quantitative. How many times must a species occur in a group of lakes before it can be regarded as exhibiting a trophic preference? Furthermore, it is conceivable that one investigator would judge a species to be an indicator, whereas another

would consider the taxon to be of limited value in distinguishing among states of trophy.

The analyses undertaken here are designed to minimize the degree of subjectivity that is normally encountered in assessing the indicator value of planktonic algae. The taxonomic nomenclature used in this study is internally consistent (Chapter II). The possible existence of identical phenotypes with dissimilar physiology, however, cannot be evaluated in the present investigation. The lake types utilized here are those that have been established by performing cluster analysis on the suite of major solutes (Fig. 41, Table 42). The types have been derived objectively, they are well-defined in their composition, and they represent lake groups of dissimilar trophic status. A rationale for their use has been presented in Chapter VI.

The method that is used here to evaluate the trophic preference of a species is a measure of fidelity (Fager 1963). An ideal or unique indicator is a species that occurs in all of the lakes of one group and in no other lakes. Species, however, respond to complex gradients, and rarely, if ever, do they occur solely within a single type of community (Whittaker 1967). The present study has demonstrated indirectly that species occurrences extend into different lake groupings, and there is overlap in some of their distributions (Chapter V).

I have elected to use numerical procedures that are objective and reasonably quantitative. The first step in the evaluation

is to "screen" each species by simply examining the number of occurrences within each lake group. Species that are found in two or more of the types with relatively similar occurrence values are ignored as potential indicators of trophic state. Species that occur principally within a particular lake group are evaluated by frequency (FR) and preference (PR) calculations. FR is the number of occurrences of a species in one lake group divided by the number of lakes in that group. PR is the number of occurrences of a species in a lake group divided by its total number of occurrences in all groups. A unique indicator, i.e. a species that occurs only in one lake group and in all of the lakes of that group, would have FR and PR values of 1.0. FR and PR are not necessarily related. A taxon may have a relatively low FR value and a reasonably high PR value. Similarly, a species may exhibit high FR values and moderately low PR estimates. If either of these expressions is used individually, assessments of indicated value could be strongly biased. By using the expressions simultaneously, it is possible to evaluate the trophic preferences of selected species. The numerical values of FR and PR that are required to judge a species as an indicator of trophic state cannot be stated explicitly. The assessment of indicator value is based on combined estimates of both measures in each of the types. Species with FR and PR < 0.50, however, would appear to have little value as indicators.

The taxa utilized in these studies are set out in Table 57. The total number of occurrences of each taxon in the 68 lakes

is given along with its number of occurrences in each of the lake types. Few comparisons will be made with the results of other investigators, primarily because of the difficulties discussed above. A number of general comparisons, however, can be drawn between diatom indicators and the findings of previous studies in Minnesota lakes.

Chlorophyta

The chlorophyte flora, exclusive of the desmids, is represented by 62 taxa. Four of the species are nearly cosmopolitan in their distribution, occurring in at least 40 lakes (Botryococcus braunii Kütz., Dictyosphaerium pulchellum Wood, Pediastrum boryanum (Turp.) Menegh., and P. duplex Meyen). Each of these taxa exhibits relatively high FR values (> 0.60) in two or more types; however, PR values are < 0.50. These species cannot be judged as having indicator value.

Forty of the taxa occur infrequently (< 10 occurrences). An examination of Table 57 reveals that, although many of these species have high PR values (> 0.60) in a particular lake grouping, they also exhibit relatively high PR values in at least one of the other types. In all cases, however, FR values are low. Most of these taxa appear to be of little actual or potential value as indicators of trophy.

There are only five chlorophytes that appear to exhibit some degree of trophic preference. One species occurs primarily in the oligotrophic lakes, but it is present in less than

one-half of them:

	FR	PR
Asterococcus limneticus Smith	0.39	0.78

Three taxa in the Type 2 lakes have values of FR and PR that suggest a preference for mestrophic to eutrophic conditions:

	FR	PR
Ankistrodesmus falcatus (Corda) Ralfs	0.50	0.50
Oocystis lacustris Chodat	0.58	0.61
Pediastrum simplex (Meyen) Lemm.	0.50	0.60

In addition, Nephrocytium agardhianum Näg. (FR = 0.29, PR = 0.64) exhibits a high PR value, but it occurs in less than one-half of the lakes.

On the basis of the present observations, none of the chlorophytes can be judged as exhibiting a pronounced trophic preference. The five species that have moderately high PR values in Types 1 or 2 also have low FR values. Further observations would be necessary to evaluate the trophic preferences of these species.

Desmids

The desmid flora is represented by 55 taxa. In contrast with the other chlorophytes, few species in this group were recorded in more than 30 lakes. Staurastrum chaetoceros (Schrod.) G. M. Smith, S. cingulum (West et West) G. M. Smith, and S. pingue Teil. have the widest distributions, occurring in all of the types. Over one-half of the species, however, are markedly restricted in their distribution. They occur

in fewer than 10 lakes.

The desmid flora does contain species that exhibit pronounced trophic preferences, especially in Types 1 and 2. In addition, several taxa in these two trophic categories appear to have potential indicator value.

There are six planktonic species that can be regarded as indicators that are nearly unique to the oligotrophic lakes. They all yield FR values that are > 0.50 and PR estimates that are > 0.69:

	FR	PR
Cosmarium contractum Kirch.	0.50	0.75
Spondylosium planum (Wolle) West et West	0.61	0.92
Staurastrum longipes (Nordst.) Teiling	0.50	0.74
Staurodesmus cuspidatus (de Breb.)	0.61	0.69
S. curvatus (West) Thunm.	0.67	0.86
S. megacanthus (Lund) Thunm.	0.50	0.90

Several additional taxa are judged here as potential indicators of oligotrophy. Four of them occur exclusively but with relatively lower frequency in Type 1.

	FR	PR
Staurastrum arctiscon (Ehrbg.) Lund	0.22	1.0
S. pentacerum (Wolle) G. M. Smith	0.45	1.0
Xanthidium antilopeum (de Breb.) Kütz	0.33	1.0
X. subhastiferum West	0.33	1.0

Three species are distributed in Types 1 and 2, but they exhibit very high PR values in the oligotrophic lakes:

	FR	PR
Staurastrum avicula de Breb.	0.28	0.71
Cosmarium depressium (Näg.) Lund	0.60	0.83
Staurodesmus subtriangulus (West et West) Teil.	0.45	0.89

A number of species occurs with relatively high FR and PR values in the mesotrophic to eutrophic lakes in central Minnesota. Although some of them also occur in Types 1, 3, or 4, they are judged here as moderately good indicators of Type 2 lakes:

	FR	PR
Closterium aciculare West et West	0.50	0.71
C. acutum v. variabile de Breb.	0.50	0.86
S. chaetoceras	0.75	0.60
S. pingue	0.79	0.54
S. planctonicum Teil.	0.50	0.60

Two additional taxa appear to have some value as potential indicators. They occur in the other lake groupings, but they exhibit relatively high PR values in Type 2:

	FR	PR
Staurastrum contortum G. M. Smith	0.37	0.53
S. leptocladum Nordst.	0.33	0.73

The present observations suggest that there are no indicators of the saline, eutrophic conditions in the prairie, nor are there indicators of the small group of highly saline, hypereutrophic lakes. S. chaetoceras, S. contortum, and S. pingue occur in

Type 3, but all of the PR values are < 0.40. S. cingulum (West et West) G. M. Smith exhibits a FR value of 0.39 and a PR value of 0.57; however, it also occurs in Types 1 and 2. These four taxa apparently are tolerant of relatively high states of eutrophy and of high salinity levels as well.

Cyanophyta

The cyanophyte flora is composed of 39 taxa. Six of the species are widespread in their distribution, occurring in at least 30 of the lakes (Aphanizomenon flos-aquae Ralfs, Anabaena flos-aquae (Lyngb.) de Breb., Chroococcus limneticus Lemm., Coelosphaerium naegelianum Unger, Gomphosphaeria lacustris Chodat, Microcystis aeruginosa (Kütz.) Elenkin). Most of these taxa are found in all of the lake groups; however, two of them do have value as trophic indicators (see below). Nearly one-half of the species occur in fewer than 10 lakes.

The cyanophyte flora does contain several taxa that are either reasonably good indicators of a specific lake group or appear to have some value as indicators.

There is only one species that can be judged as an indicator of oligotrophy in this region:

	FR	PR
Aphanocapsa elachista West et West	0.67	0.71

This species is found in Type 2 lakes, but it is limited in its occurrence to those of low salinity. Two additional taxa exhibit relatively low FR values, but they may be considered as

potential indicators of Type 1 lakes.

	FR	PR
Rhabdoderma lineare Schm. et Laut.	0.36	0.83
Aphanothece nidulans Richter	0.44	0.62

The occurrence of these taxa in Type 2 lakes is limited primarily to those that are of low salinity.

Three species are judged here as primary indicators of the mesotrophic to eutrophic lakes. Although each of them occurs in the other lake groupings they all exhibit relatively high FR and PR values in Type 2.

	FR	PR
Anabaena spiroides v. crassa Lemm.	0.83	0.77
Chroococcus dispersus (Keissl.) Lemm.	0.67	0.62
Gomphosphaeria lacustris	0.71	0.53

In addition to these species, two cyanophytes have relatively high values of FR and PR and can be regarded as potential indicators of Type 2.

	FR	PR
Anabaena flos-aquae	0.75	0.53
Lyngbya birgei G. M. Smith	0.58	0.61

The present observations suggest that there are no species that can be judged as good indicators of Type 3 or Type 4. One taxon, however, does exhibit relatively high PR value in Type 3, and it is also found in two of the five hypereutrophic lakes:

	FR	PR
Lyngbya contorta Lemm.	0.24	0.63

This species apparently tolerates high degrees of trophy and high salinity levels as well. It is markedly limited in its distribution, occurring only in the prairie lakes (No's. 1, 2, 18, 30, 35, 44, 50, 67).

Chrysophyta

Chrysophytes

The chrysophyte flora is represented by 18 taxa. Only four species occur in more than 20 lakes, whereas seven taxa are found in less than 10 of the samples. An examination of Table 57 indicates that most of the occurrences of these species is limited to the Type 1 and Type 2 lake groupings. Several chrysophytes exhibit marked trophic preferences or can be regarded as potential indicators of trophy. Most of them are limited to Type 1 lakes.

There are five taxa that are unique or near-unique indicators of oligotrophy. Each of the species exhibits FR values > 0.50 and preference estimates > 0.80.

	FR	PR
Chrysocapsa planctonica (West et West) Pasch.	0.61	0.92
Chrysosphaerella longispina Laut. em Korsh.	0.50	0.90
Dinobryon bavaricum Imhof	0.78	0.82
Stichogloea doederleinii (Schmidle) Wille	0.78	0.78
Synura uvella Ehrbg. em Korsh.	0.61	0.85

Each of these taxa also occurs in the mesotrophic to eutrophic lakes; not one of them, however, occurs more than four times in the Type 2 grouping.

Three additional taxa may be judged as potential indicators of oligotrophy. Each of them exhibits relatively high PR values in Type 1, but they either occur in Type 2 lakes with relatively higher FR values than the above species or they have lower FR estimates in the oligotrophic lakes.

	FR	PR
Dinobryon divergens Imhof	0.78	0.61
Dinobryon sertularia Ehrbg.	0.39	0.78
Dinobryon cylindricum Imhof	0.56	0.56

There are no species that exhibit marked trophic preferences in Types 2, 3, or 4. The only taxon that can be regarded as a potential indicator of the mesotrophic to eutrophic lakes is Mallomonas tonsurata Teil. (FR: 0.54, PR: 0.54). The species also occurs in Types 1 and 3, but with extremely low FR and PR values.

Diatoms

The diatom flora is represented by 27 taxa. The most abundant taxa in each of the study lakes are listed in Table 22. Four species are nearly cosmopolitan in their distribution, occurring in more than 40 lakes (Melosira granulata (Ehr.) Ralfs, Stephanodiscus niagarae Ehr., Fragilaria crotonensis

Kitton, Asterionella formosa Hassall). These species occur with relatively high FR values in most of the lake groups, and therefore have little value as indicators of specific trophic types (cf. Table 58). Only six taxa are limited in their distribution, occurring in < 10 lakes.

Several planktonic diatoms exhibit marked preferences for the trophic conditions of Type 1 and Type 3 lakes, and a number of taxa can be judged as having some degree of indicator value in the lake groupings.

Two taxa can be judged as good indicators of oligotrophy in this region.

	FR	PR
Cyclotella comta (Ehr.) Kütz.	0.61	0.65
Tabellaria flocculosa v. flocculosa Knud.	0.95	0.59

Both of these species occur in Types 2 and 3; however, their FR and PR values in each of the groups are extremely low. Two other species exhibit combined values of FR and PR that suggest a preference for oligotrophic conditions.

	FR	PR
Melosira distans (Ehr.) Kütz.	0.39	1.0
Cyclotella stelligera Cl. v. Grun.	0.61	0.5

Although M. distans exhibits a low FR value, it is found exclusively in Type 1. The occurrence of C. stelligera in Types 2 and 3 is due largely to its variety C. stelligera v. tenuis. Consequently, C. stelligera is limited almost exclusively in its distribution to the oligotrophic lakes.

The present observations reveal that there are no species that can be judged as good indicators of the mesotrophic to eutrophic lakes of central Minnesota. Two taxa do occur with moderately high PR values in Type 2; however, FR estimates are relatively low and the species are also found in Type 3 lakes.

	FR	PR
Fragilaria capucina Desmaz.	0.42	0.56
F. capucina v. mesolepta (Rabh.) Grunow	0.42	0.59

The species may be potential indicators of Type 2, but apparently they are tolerant of high degrees of eutrophy and salinity as well.

There are two species that can be judged as moderately good indicators of the eutrophic, saline prairie lakes. Both of them occur in at least one of the other types; however, they exhibit relatively high PR values.

	FR	PR
Cyclotella striata (Kütz.) Grun.	0.43	0.75
C. meneghiniana Kütz.	0.53	0.85

The only diatom that exhibits a preference for the group of highly saline, hypereutrophic lakes is Chaetoceros muelleri Lemm. (FR: 0.60, PR: 0.60). The distribution of this species appears to be limited to lakes of high salinity. It is also found in two of the Type 3 lakes (Mineral No. 44 and Waubay No. 67), both of which have high COND levels (Table 13).

It is instructive to compare the distribution and relative trophic preferences of selected diatom taxa (Table 58) with the studies of Bright (1968 and unpublished), Bradbury and Megard (1972), and Bradbury and Waddington (1973). Bright's investigations on the regional distribution patterns of planktonic diatoms have shown that certain taxa are widely distributed throughout the region, whereas others are limited in their occurrence to unpolluted or to enriched lakes. Similarly, stratigraphic investigations by Bradbury on Shagawa Lake (No. 55) have documented changes in species composition of diatom communities that can be related to past nutrient conditions in the lake.

Bright's observations indicate that C. comta occurs with highest frequency in unpolluted lakes. Its distribution is confined primarily to the oligotrophic lakes and to other lakes in northern Minnesota that are low in nutrients. M. granulata, A. formosa, and S. niagarae are widely distributed, but they occur most frequently in mesotrophic and especially in eutrophic lakes. The distribution of M. ambigua is intermediate between that of C. comta and M. granulata. The species tendsto occur with highest frequency in the mesotrophic lakes of northern and central Minnesota.

The stratigraphic analysis of diatom succession in Shagawa Lake demonstrates that, prior to nutrient enrichment, the community is characterized by C. comta. Commensurate with sustained increases in nutrient level, the relative percentages of

F. crotonensis, F. capucina, M. ambigua, M. granulata, and A. formosa increase dramatically. The diatom community in the surficial sediments, representing the present condition of a high state of eutrophy, is characterized by Stephanodiscus minutulus, A. formosa, F. crotonensis, F. capucina, S. hantzschii Grun., and S. hantzschii v. pusilla (Grun.) Krieger.

The findings of the present study (Table 58) are in general agreement with those of Bright and Bradbury. C. comta is a predominant component of diatom communities in the oligotrophic lakes, and it occurs infrequently in lakes of higher trophic status. The distribution of M. ambigua is, in fact, intermediate between that of C. comta and M. granulata. It occurs in the oligotrophic lakes and exhibits a maximum PR value in the mesotrophic to eutrophic lakes, and its FR and PR values are lower in the Type 3 lakes. F. capucina, F. capucina v. mesolepta, F. crotonensis, M. granulata, S. astrea v. minutula (Kütz.) Grun. (taxonomic equivalent of S. minutulus), and S. hantzschii Grun. exhibit higher PR values in Types 2 and 3 than in Type 1.

The relative trophic preferences of some of the more widely distributed diatoms are reflected almost exactly in the historical sequence of species succession in Shagawa Lake. Despite the obvious parallels among these three investigations, however, species such as A. formosa, F. capucina, F. capucina v. mesolepta, F. crotonensis, M. ambigua, M. granulata, and S. astrea v. minutula cannot be judged as indicators of specific trophic states. They exhibit a tolerance to a broad range of trophic conditions, and collectively they tend to overlap in their distribution.

Pyrrophyta/Euglenophyta

The pyrrophytes and euglenoids are represented by relatively few species. They are treated together here. The dinoflagellate flora consists of seven species. Ceratium hirundinella (O.F.M.) Schrank and Peridinium willie Huitfeld-Kaas are distributed throughout the study region. Both taxa exhibit moderate to high FR values in Types 1 and 2; however, their PR values in the lake groupings never exceed 0.50. The only species that might be regarded as a potential indicator is P. wisconsinense Eddy. It occurs almost exclusively in the oligotrophic lakes (PR = 0.86); however, the FR value is very low.

The euglenoid flora is represented by six species. Each of the taxa occurs infrequently (< 10 occurrences), and there is no evidence of a species exhibiting a trophic preference.

CHAPTER VIII

SUMMARY

Lakes in Minnesota and eastern North Dakota and South Dakota exhibit a wide range of trophic conditions. This study was undertaken to 1) delineate patterns in phytoplankton distribution, to 2) investigate schemes of lake classification based on chemical and biological criteria, and to 3) evaluate properties of net phytoplankton, diatom assemblages, and whole-water phytoplankton communities as indicators of trophic state in lakes of Minnesota. The results of the study are compared with previous investigations in Minnesota and with observations in other north-temperate regions.

Sixty-eight lakes, ranging from unproductive waters of low salinity in northeastern Minnesota to highly saline, productive lakes in the prairie, were sampled during fall 1970 and 1971. Measurements of specific conductance, transparency, and temperature were made on each lake, and samples of surface water from selected lakes were used to determine the concentration of major anions and cations. Phytoplankton samples were taken by plankton haul and by integrating a column of water from the euphotic zone of each lake. Samples of net phytoplankton were used to compile a species inventory and as source material for a semi-quantitative analysis of diatom communities. Whole-water samples were examined quantitatively by the inverted microscope technique.

These data were used to compute algal expressions that have been proposed as indicators of trophic state in north-temperate lakes. Specifically, the analysis of net phytoplankton was used to calculate the total number of taxa (S), the compound phytoplankton quotient (CPQ), and the number of desmids (DESMID S). The diatom analysis was utilized to compute the ratios of Stockner (A/C_s), Nygaard (C/P), a number of "trial" ratios, and several indices of community structure. Analyses of whole-water samples were used to derive estimates of the standing crop of total phytoplankton (SC), net phytoplankton (NET SC), and nannoplankton (NANNO SC) and to calculate indices of community structure. The species diversity of diatom and whole-water communities was computed by using Margalef's index (D), and Shannon-Weaver function (H), the evenness component of diversity (J), and the number of taxa (S) in each sample.

The investigation was carried out by following a sequence of integrated procedures. Initially, selected physical, chemical, and biological measurements were used to define the range of trophic conditions in the region. These parameters serve as a framework against which to investigate patterns in the regional distribution of algal variables. The results of these analyses are incorporated partially into a series of studies on lake classification and comparative lake-typology. The lake clusters identified in one of the classification schemes were utilized as lake types of dissimilar trophic state. They serve

as a framework within which to assess algal variables and species occurrence as indicators of trophic state. The salient observations of these studies are presented here.

Regional Distribution of Phytoplankton. The regional distribution of each algal expression was investigated by using it as a dependent variable and performing simple and multiple correlation analyses with gradient parameters (GP). The parameters that were selected as defining the range of trophic conditions are: specific conductance (COND), alkalinity (ALK), a summation of calcium and magnesium ($\sum$Ca + Mg), secchi-disc transparency (SD), and the standing crop of phytoplankton (SC). The values in parentheses after each algal variable are range and mean estimates based on 68 lakes.

The net phytoplankton expression S, CPQ, and DESMID S exhibit relatively large ranges in extreme values, and each of them is significantly correlated with the gradient. S (4 - 79, $\bar{x}$ = 39) and DESMID S (0.96 - 15.0, $\bar{x}$ = 7.4) are high in the northeastern lakes and decrease over the gradient. CPQ is low in the northeastern lakes and increases in value over the gradient. These observations are in general agreement with previous investigations in Minnesota and are in accord with the general belief that each of the expressions is sensitive to trophic conditions.

The diatom ratios A/C_s (0.002 - 142, $\bar{x}$ = 9.8), C/P (0.038 - 2.33, $\bar{x}$ = 0.478), and the "trial" ratios do not exhibit

significant correlations with most GP, and none of the multiple correlation coefficients between the ratios and GP is statistically significant. The relative abundance of the Araphidineae (A_s), however, generally is high in the northeastern lakes and low in the prairie and exhibits significant correlations with most GP. Although diatom ratios may not respond to the gradient, A_s appears to be sensitive to trophic conditions.

Estimates of total standing crop and the standing crop of net- and nannoplankton (individuals/ml) exhibit large ranges in value, and they are significantly correlated with the gradient. SC (89 - 404,000, $\bar{x}$ = 20,000) and NET SC (8 - 306,000, $\bar{x}$ = 12,000) are low in the northeastern lakes and increase over the gradient. NANNO SC (75 - 130,000, $\bar{x}$ = 8,000) tends to increase with increasing nutrient conditions, but the correlations with GP are not so pronounced as those with SC and NANNO SC. The standing crop of total phytoplankton and its components are sensitive to trophic conditions in this region.

Structural properties of diatom and of whole-water communities do not respond to the gradient in the same manner. The indices D (0.48 - 10.8, $\bar{x}$ = 3.37), H (0.08 - 4.57, $\bar{x}$ = 2.21), J (0.04 - 0.78, $\bar{x}$ = 0.05), and S (4 - 73, $\bar{x}$ = 22.3) of diatom assemblages are not correlated with the gradient. Apparently, the diversity of diatoms is not sensitive to trophic conditions. Each index of species diversity of whole-water communities, however, exhibits significant correlations with most GP.

D (1.24 - 12.4, $\bar{x}$ = 5.56), H (0.81 - 4.62, $\bar{x}$ = 2.92), J (0.18 - 0.81, $\bar{x}$ = 0.58), and S (10 - 70, $\bar{x}$ = 34.3) generally are high in the northeastern lakes and low in the prairie and decrease in value over the gradient. D, H, and especially S are sensitive to trophic conditions. These observations support the general contention that species diversity of phytoplankton communities is inversely correlated with increasing levels of nutrient enrichment.

Lake Classification. The lakes were classified objectively by performing cluster analysis on the concentrations of major solutes, on combinations of eight trophic-state indicators (TSI), and on suites of phytoplankton taxa. The lake clusters formed by the use of major solutes are geographically distinct. They consist primarily of 1) lakes of low salinity in northeastern Minnesota, 2) lakes of intermediate salinity in the central region of the state, and 3) saline lakes of the prairie. A small group of prairie lakes of high salinity was detected as a residual cluster. The salinity range occupied by each type does not overlap substantially with other types, and the mean salinity levels of the types are statistically dissimilar.

Typological schemes based on combinations of TSI generally result in four major lake types, but the size and composition of the clusters differ from one another. The lake grouping formed by physical-chemical TSI (COND, ALK, $\sum$Ca + Mg, and SD) are similar to those established by major solutes, but they differ in their composition from the clusters generated by the

biological TSI (Sc, CPQ, H, and S). The composition of the lake types formed by all eight TSI are intermediate between the groupings formed by the physical-chemical TSI and the biological TSI. The use of biological TSI as classificatory variables results in lake clusters whose salinity ranges overlap and whose mean salinity levels are not all statistically dissimilar.

The utilization of four suites of algal species as classificatory variables results in three major lake groupings. The size and composition of the clusters formed by the diatoms and the desmids vary substantially. The salinity ranges occupied by the types overlap, and the mean salinity levels of the groups are not all statistically dissimilar. These results are attributed to species that are nearly cosmopolitan in their distribution and to taxa that occur in two or more regions. The total plankton and the bluegreen flora result in lake groupings that overlap in their salinity ranges, but the mean salinity levels of each type are statistically dissimilar.

Evaluation of Trophic-State Indicators. The evaluation of algal variables as indicators of trophic state in Minnesota lakes was carried out by using the lake clusters based on major solutes. Types 1, 2, 3, and 4 are regarded as oligotrophic, mesotrophic to eutrophic, saline-eutrophic, and "hypereutrophic", respectively. The criteria that are used to assess indicator value are: 1) mean values that are significantly different among the lake types, and 2) the bias introduced by variations in precision of estimation and by dependence upon sample size.

Mean estimates of the net plankton expressions S and DESMID S are highest in the oligotrophic lakes and decrease with increasing trophic status of the lake groupings. The average values are statistically dissimilar among all of the types. The variables are judged as good indicators of trophy. Average estimates of CPQ increase observably with trophic states of higher order, but they can be used only to distinguish between the oligotrophic lakes and the mesotrophic to eutrophic lakes. The range in value and the mean estimates of CPQ in Types 1 and 2 are much higher than in many of the oligotrophic and mesotrophic to eutrophic lakes in Europe. It is suggested that these lake types in Minnesota are of higher trophic status than those in Europe.

The mean values of the diatom ratios A/C_s, C/P, and the "trial" ratios are observably but not statistically dissimilar among the lake types. These observations, coupled with poor precision and dependence of estimation on sample size, suggest that diatom ratios have limited value as indicators of trophic state. The A_s component, however, exhibits average values that are high in the oligotrophic lakes, low in the prairie lakes, and decrease progressively with higher states of trophy. The component may serve as an indicator of trophy in Minnesota lakes.

The quantitative estimates of SC, NET SC, and MANNO SC exhibit observable differences among the lake types. The mean values of SC and NET SC are lowest in the oligotrophic lakes,

highest in the hypereutrophic lakes, and increase progressively with higher states of trophy. Both expressions are statistically dissimilar among all of the types. They are considered as good indicators of trophic status. Although NANNO SC increases with trophic state, none of the mean estimates among the types is statistically dissimilar. The variable has limited value as an indicator.

The mean values of species diversity expressions in communities of diatoms and phytoplankton exhibit observable differences among all of the types. None of the indices of diatom assemblages exhibits a mean value that is statistically dissimilar from another average estimate. Diatom diversity apparently is not an indicator of trophic state in Minnesota lakes.

The structural properties of whole-water phytoplankton communities exhibit mean values among some types that are statistically different. Average estimates of D, H, and J can be used to distinguish between the mesotrophic to eutrophic lakes and the group of saline, eutrophic prairie lakes. The mean values of these indices are not dissimilar between the oligotrophic and the mesotrophic to eutrophic lakes. These indices are judged as having limited values as indicators of trophy. The average values of the related statistic S are dissimilar among all of the lake groupings. It is considered as the only index that can be used as an indicator of trophic state in the region.

Evaluation of Indicator Species. The composition of the net phytoplankton flora, consisting of 214 taxa, was examined for species that are indicators of trophy. The value of a taxon as an indicator was assessed by frequency and preference computations. The Chlorococcales, dinoflagellates, and euglenoids contain few species that are indicators of trophy. Desmids, bluegreens, chrysophytes, and diatoms contain taxa that are indicators of specific trophic states.

The species judged as primary indicators of oligotrophy are: Cosmarium contractum, Spondylosium planum, Staurastrum longipes, Staurodesmus cuspidatus, S. curvatus, S. megacanthus, Aphanocapsa elachista, Chrysocapsa planctonica, Chrysosphaerella longispina, Stichogloea doederleinii, Synura uvella, Cyclotella comta, Tabellaria flocculosa v. flocculosa.

The taxa judged as primary indicators of the mesotrophic to eutrophic lakes in central Minnesota are: Closterium aciculare, C. acutum v. variabile, Staurastrum chaetoceras, S. pingue, S. planctonicum, Anabaena spiroides v. crassa, Chroococcus dispersus, Gomphosphaeria lacustris, Mallomonas tonsurata.

Two diatoms are the only taxa that can be judged as indicators of the saline, eutrophic lakes in the prairie: Cyclotella striata, C. meneghiniana.

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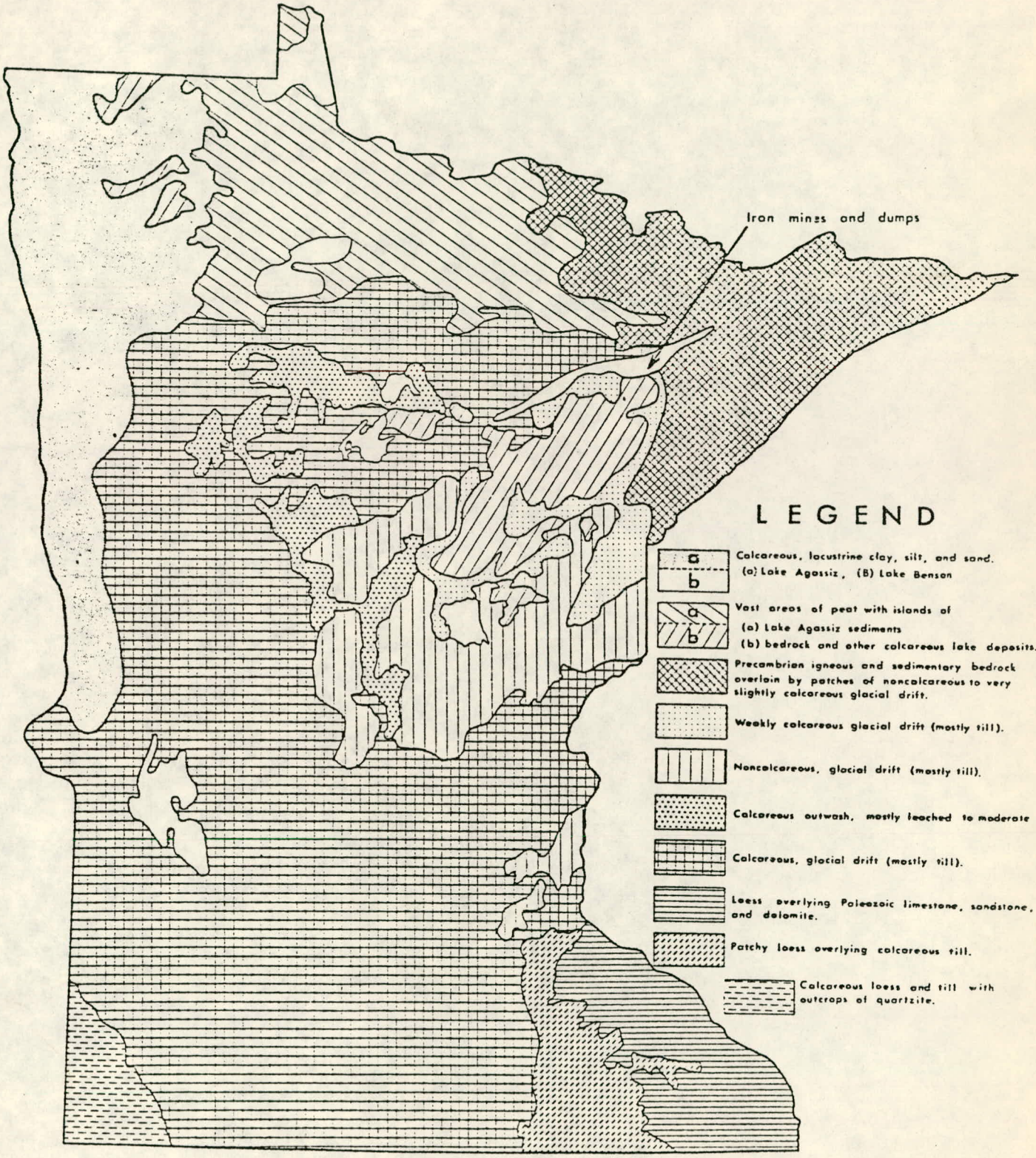

GENERALIZED DISTRIBUTION OF SURFICIAL DEPOSITS

Fig. 1. A map of Minnesota showing the generalized distribution of surficial deposits (modified from Arneman 1963).

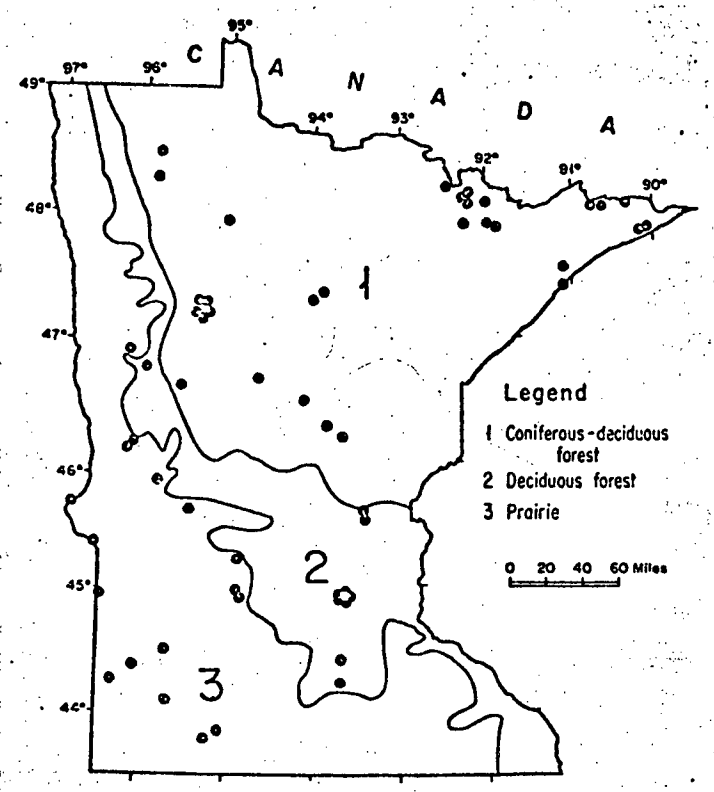

Fig. 2. A map of Minnesota showing the main vegetation types and the location of the lakes (Pre-settlement vegetation map from Minn. Geol. Bull. 12).

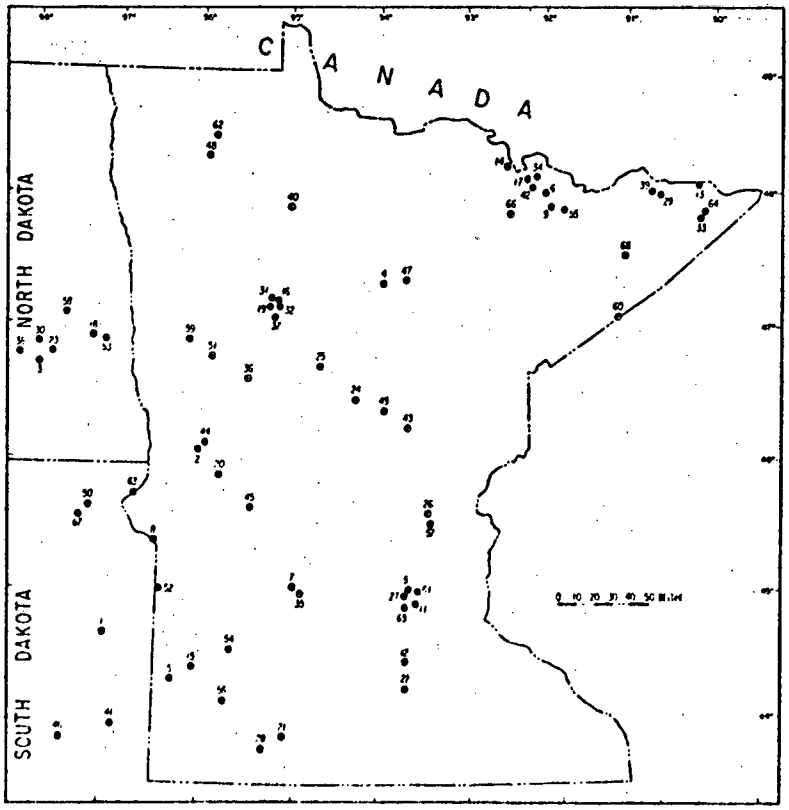

Fig. 3.

A map of Minnesota and eastern North Dakota and South Dakota showing the location of the 68 lakes studied. Each lake is represented by an arbitrarily assigned number.

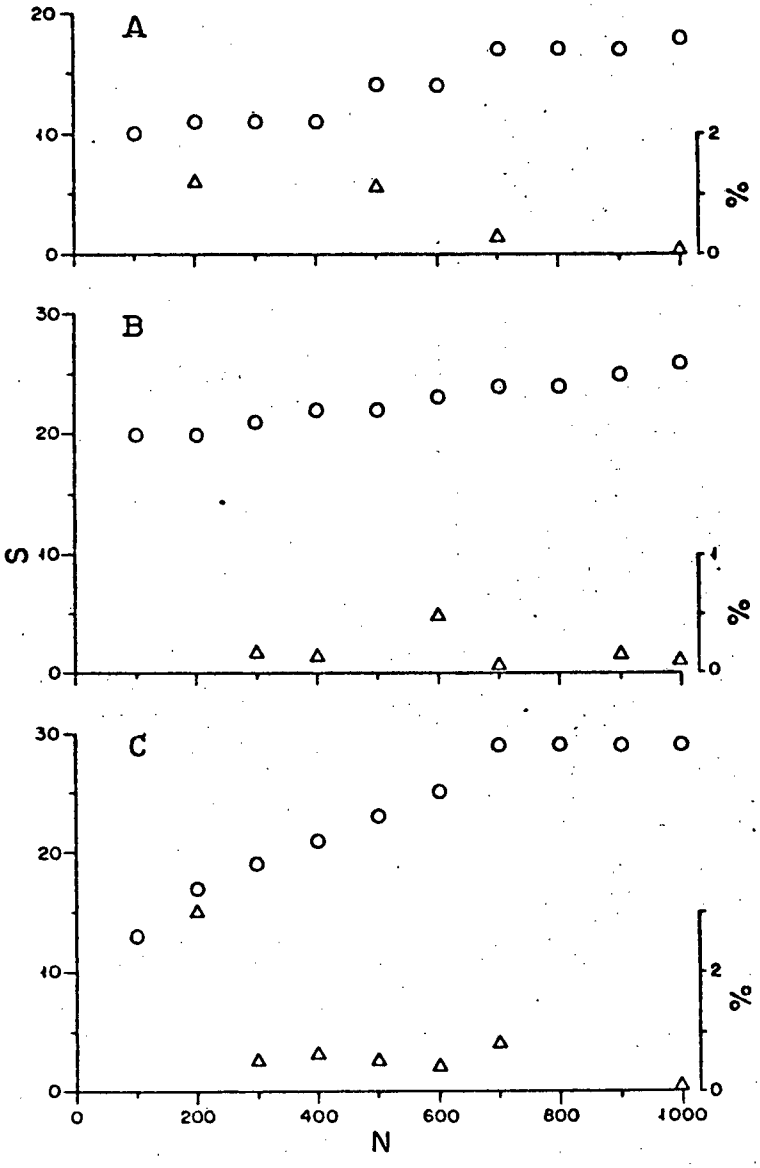

Fig. 4.

The effects of sample size (N) on the number of diatom species (O) and on the per cent contribution of less abundant species (Δ) in the community. Specimens are tallied to a level of 100, assigned to species, and the procedure continued in cumulative increments of 100 until 1000 cells are recorded. Per cent values on the right-hand ordinate represent the community contribution of individuals of newly encountered species in each 100-individual increment. See text for discussion. Lakes Pickerel (A), Salt (B), and Spiritwood (C).

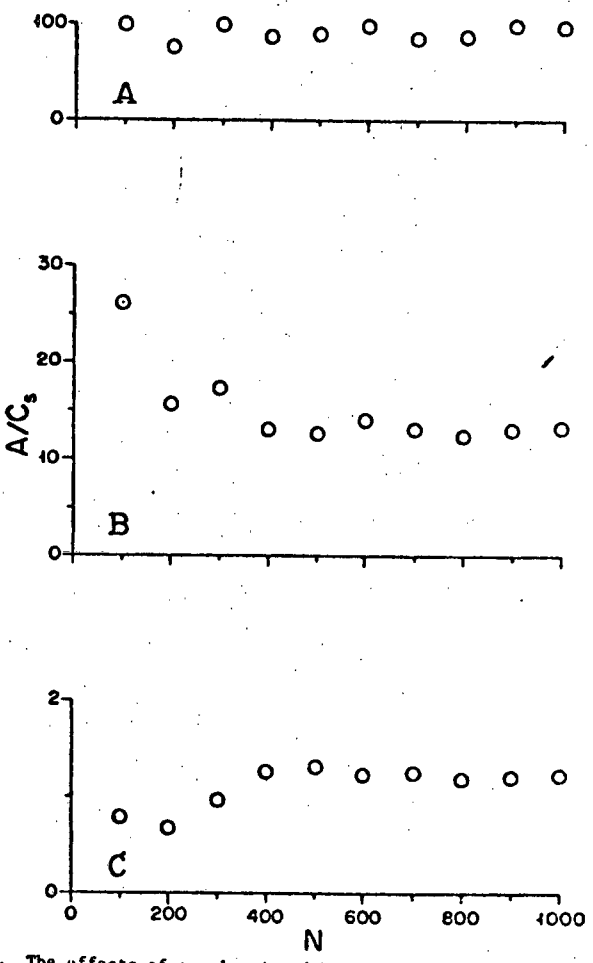

Fig. 5. The effects of sample size (N) on the value of the A/C$_s$ ratio (Stockner). Ratio values are calculated at each cumulative 100-individual increment. See text for discussion. Lakes Trout (A), Burntside (B), and Shagawa (C).

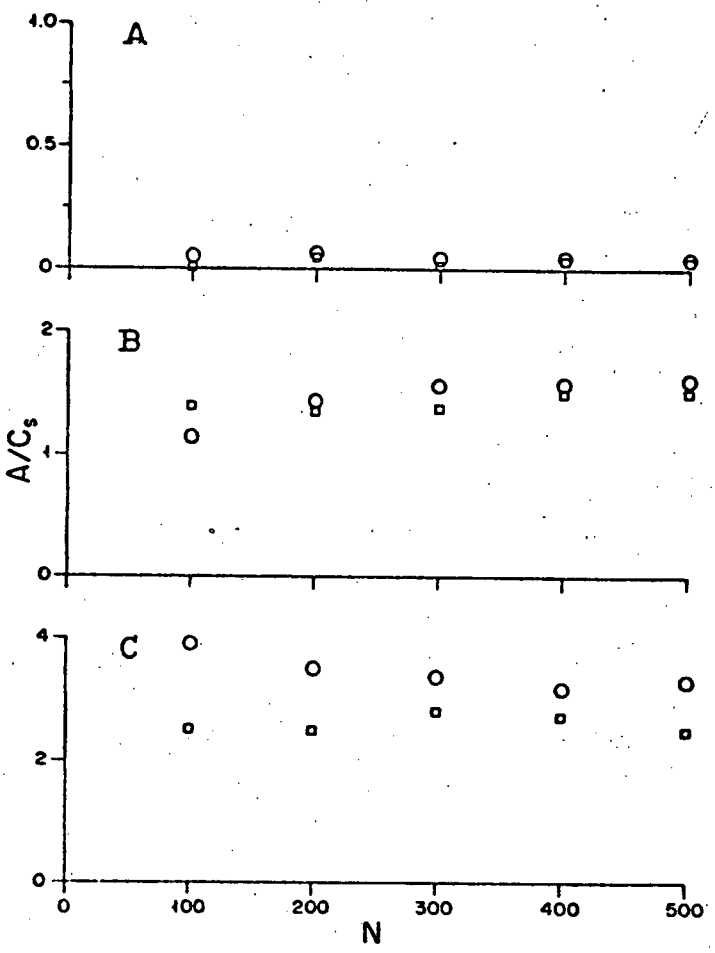

Fig. 6. The effects of sample size (N) on replicated estimates of the A/C_s ratio (Stockner). Ratio values are calculated at each cumulative 100-individual increment. See text for discussion. Lakes Spiritwood (A), Pickerel (B), and Salt (C).

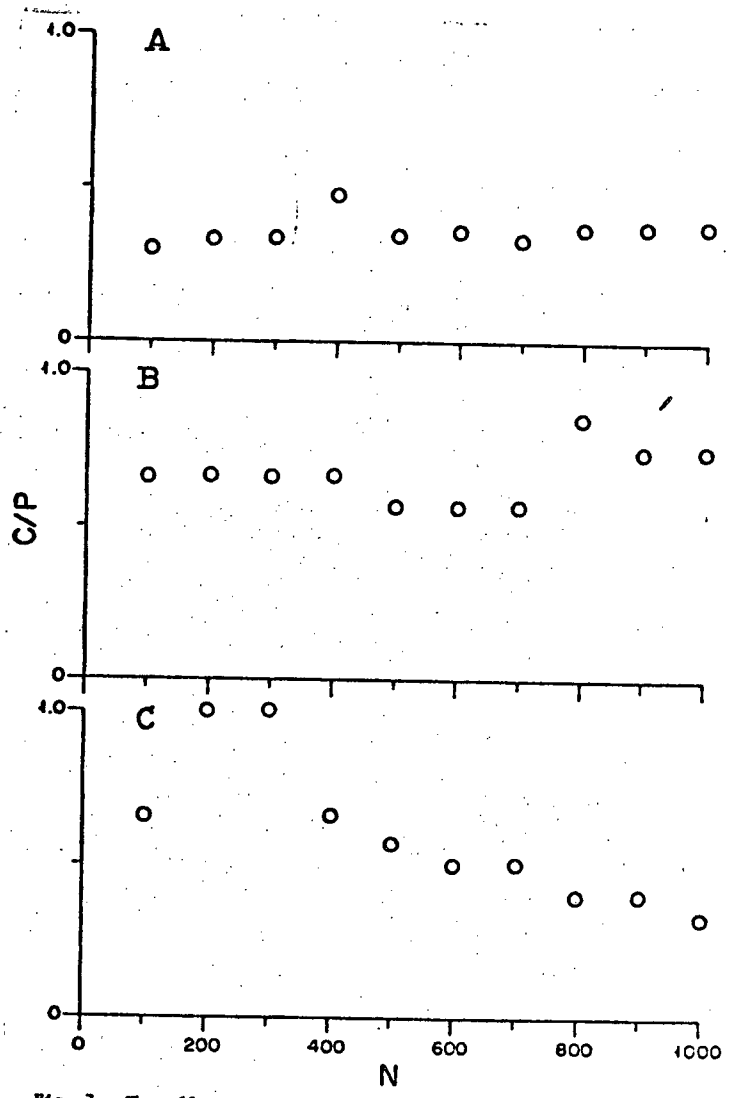

Fig. 7. The effects of sample size (N) on the value of the C/P ratio (Nygaard). Ratio values are calculated at each cumulative 100-individual increment. See text for discussion. Lakes Burntside (A), Shagawa (B), and Trout (C).

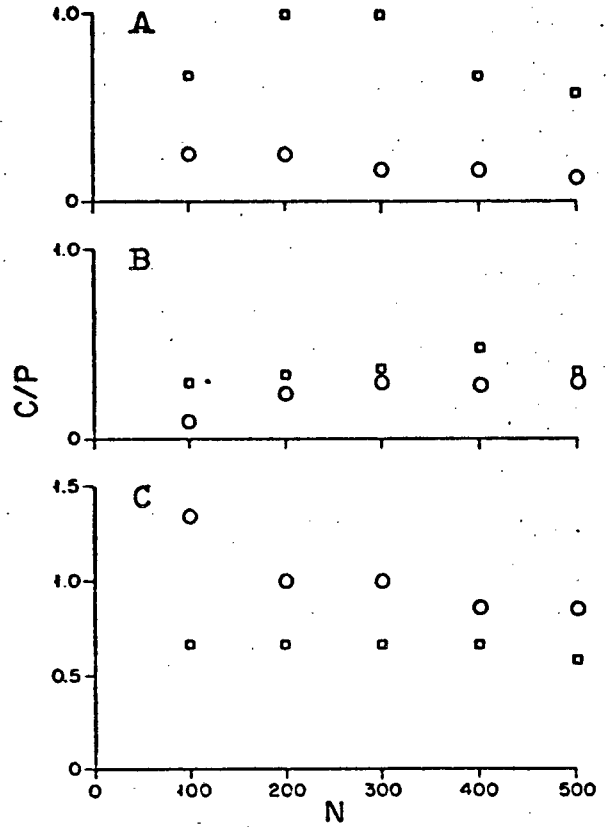

Fig. 8. The effects of sample size (N) on replicated estimates of the C/P ratio (Nygaard). Ratio values are calculated at each cumulative 100-individual increment. See text for discussion. Lakes Trout (A), Burntside (B), and Shagawa (C).

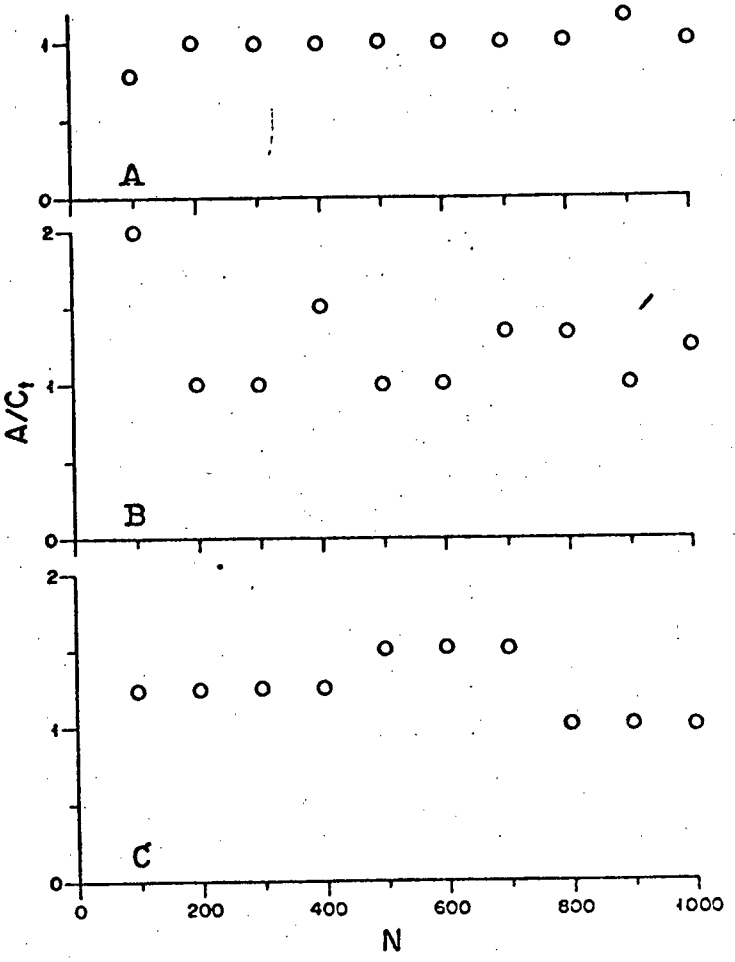

Fig. 9. The effects of sample size (N) on the value of the A/C_t ratio. Ratio values are calculated at each cumulative 100-individual increment. See text for discussion. Lakes Pickerel (A), Elk (B), and Shagawa (C).

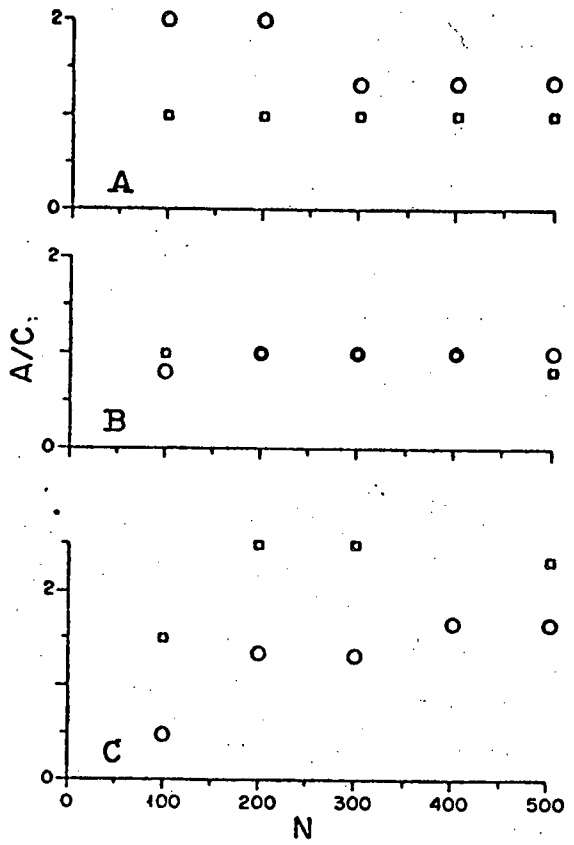

Fig. 10. The effects of sample size (N) on replicated estimates of the A/C_t ratio. Ratio values are calculated at each cumulative 100-individual increment. See text for discussion. Lakes Salt (A), Pickerel (B), and Spiritwood (C).

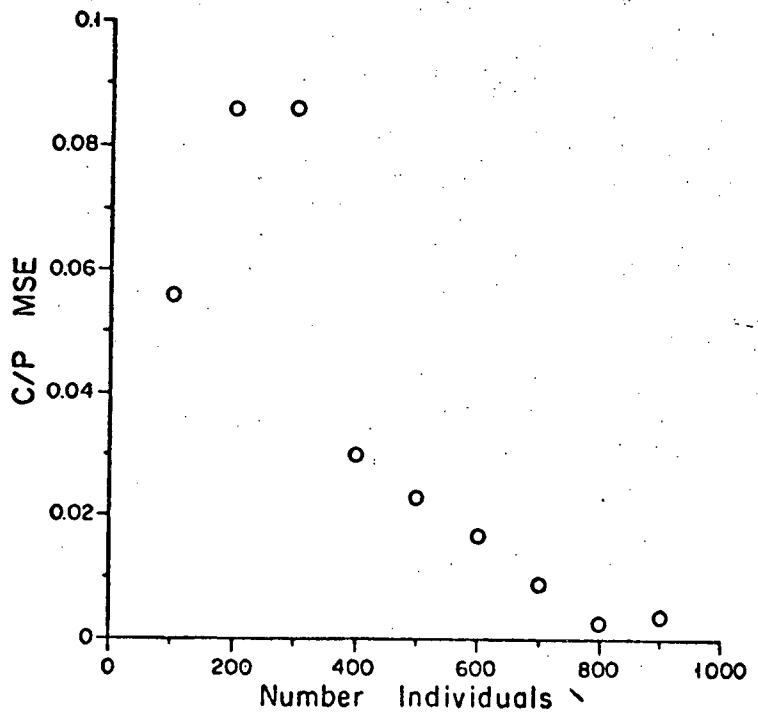

Fig. 11. The effects of sample size (N) on estimates of the C/P ratio (Nygaard) in nine lakes, as assessed by the mean square error statistic (MSE). Decreasing MSE values for cumulative 100-individual increments indicate the rate at which the error in estimation of the ratio is undergoing reduction. See text for discussion.

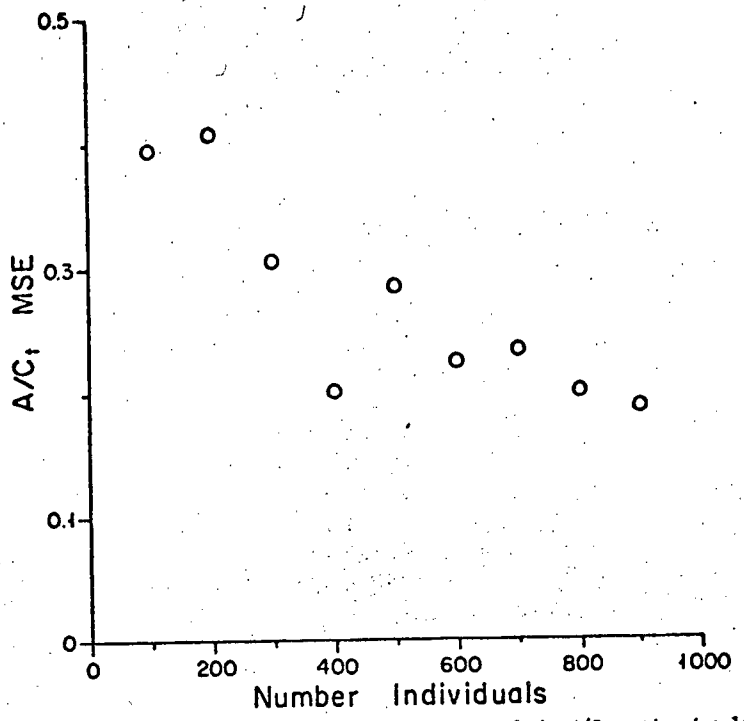

Fig. 12. The effects of sample size (N) on estimates of the A/C_t ratio nine lakes, as assessed by the mean square error statistic (MSE). Decreasing MSE values for cumulative 100-individual increments indicate the rate at which the error in estimation of the ratio is undergoing reduction. See text for discussion.

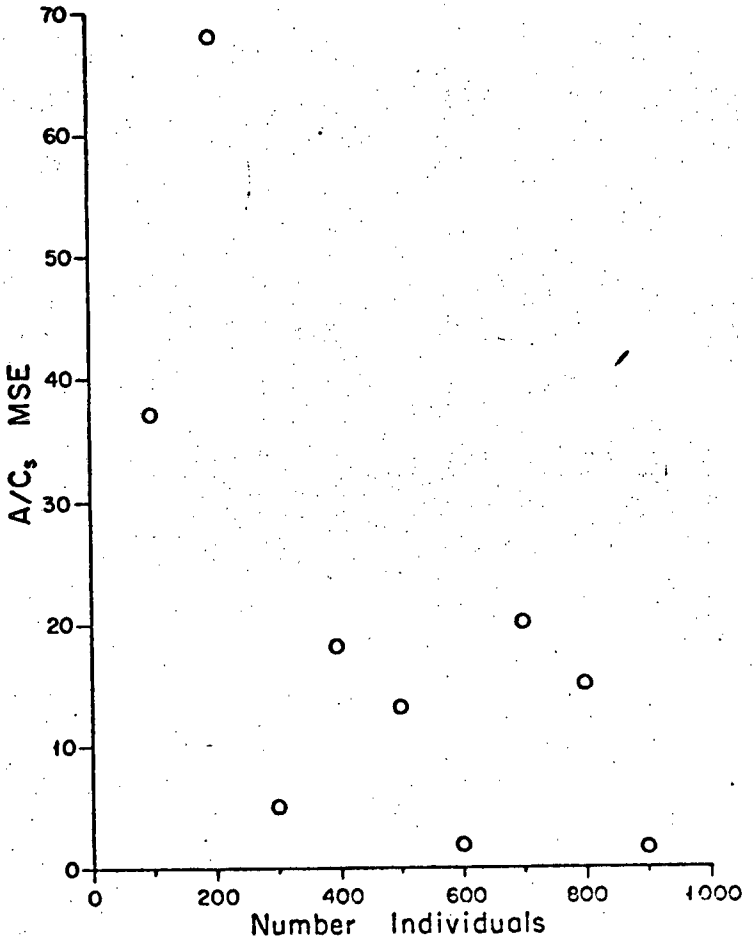

Fig. 13. The effects of sample size (N) on estimates of the A/C_s ratio (Stockner) in nine lakes, as assessed by the mean square error statistic (MSE). Decreasing MSE values for cumulative 100-individual increments indicate the rate at which the error in estimation of the ratio is undergoing reduction. See text for discussion.

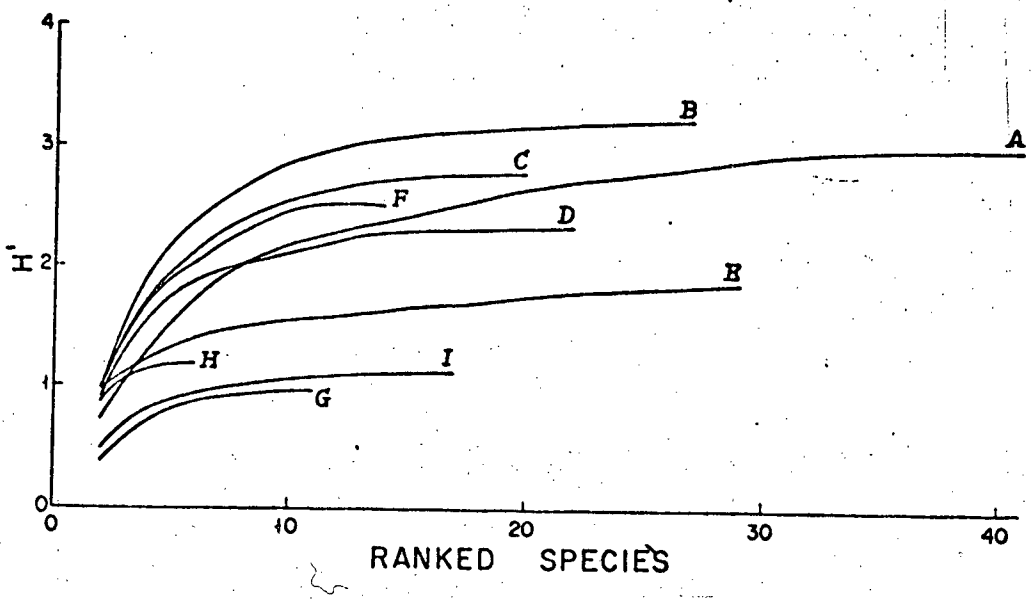

Fig. 14.

The effects of relative species abundance on the value of H (Shannon) in nine diatom analyses. The species in each sample are ranked from most to least abundant, and are incorporated sequentially into the calculation of H. After the 10 to 15 most abundant species in each sample are incorporated into the estimate, addition of the 'rare' species in the sample contributes minimally to the final value of H. The lakes in curves A through I and their respective H values, sample size, and species number are:

Lake	H	Sample Size	Species
A School Grove	3.056	623	41
B Vermilion	3.267	629	27
C Alkali	2.796	570	20
D Salt	2.403	599	22
E Minnewaska	1.926	514	29
F George	2.197	512	14
G Fish	0.960	560	11
H Upper Minnetonka	1.188	553	6
I Dogfish	1.156	541	17

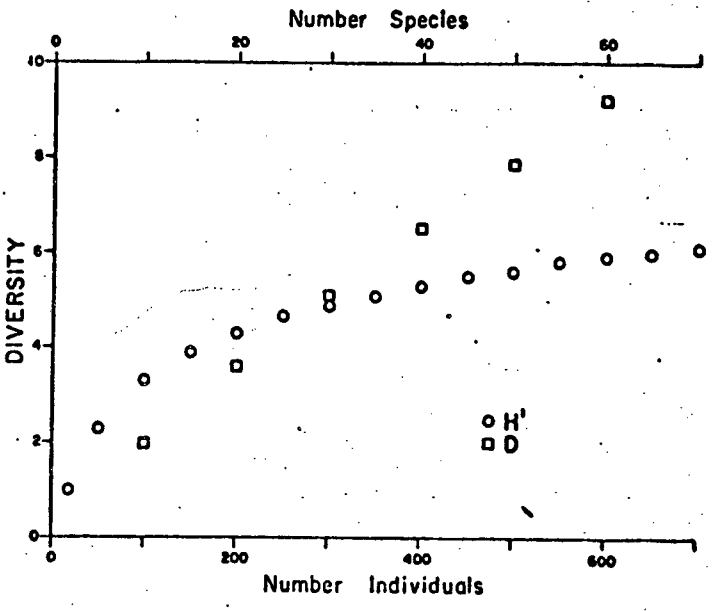

Fig. 15.

A comparison of the values of D (Margalef) and H (Shannon) diversity in a hypothetical population (H' = Hmax, i.e. the distribution of individuals among species is equal). H is greater than D in communities with 'small' species numbers, whereas D is greater than H in communities with large species numbers.

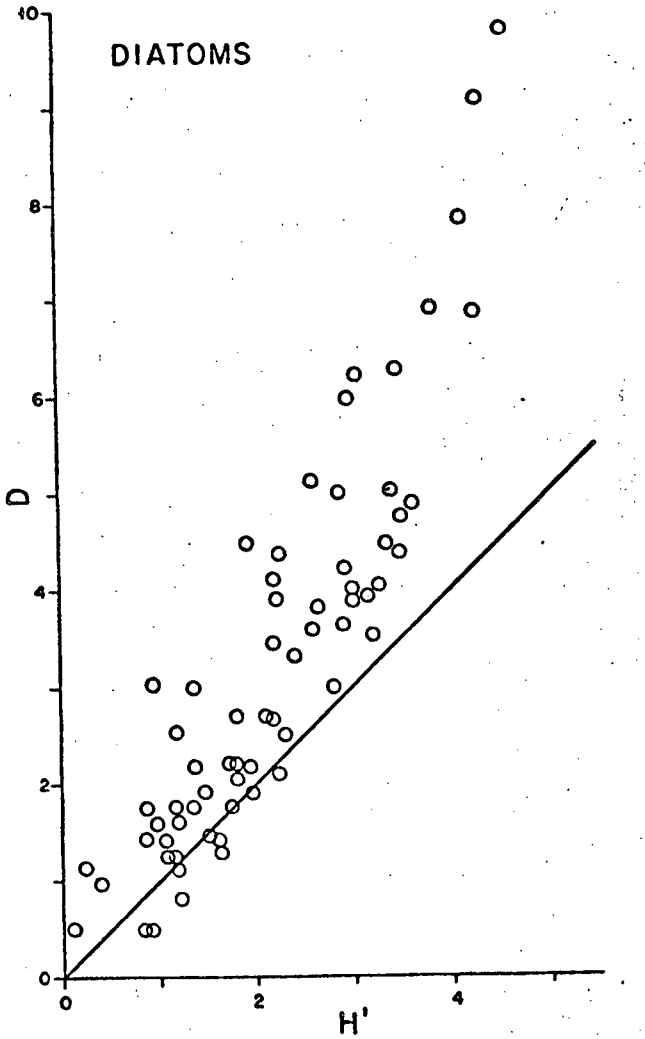

Fig. 16. Diatoms. Correlation between estimates of D (Margalef) and H (Shannon) diversity for 68 paired observations in Minnesota lakes. The solid line represents a theoretical one-to-one relationship.

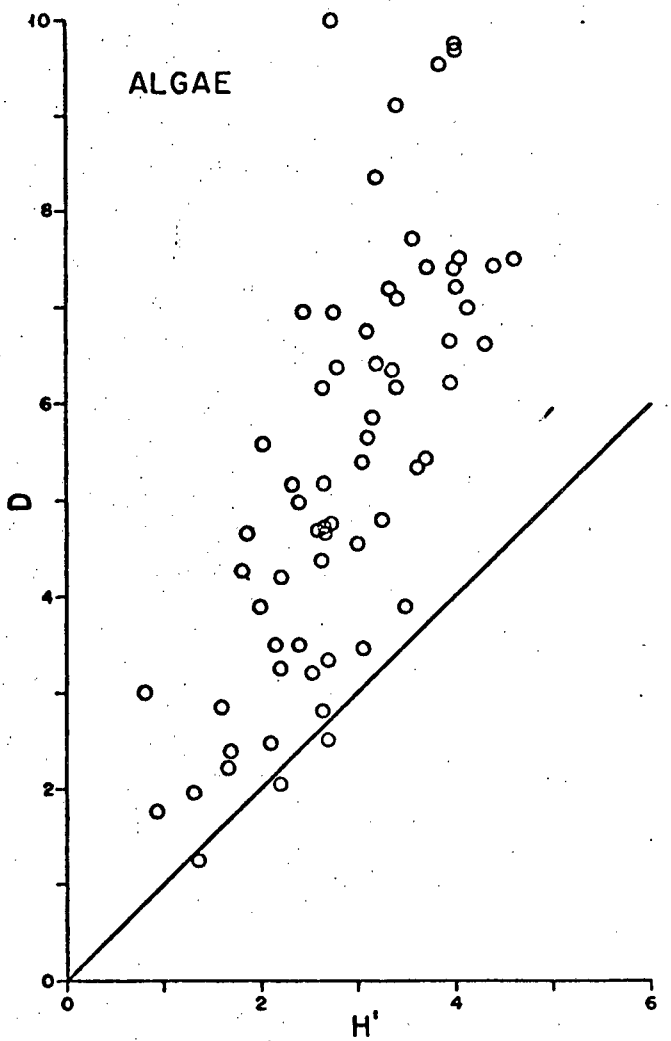

Fig. 17. Whole-water samples. Correlation between estimates of D (Margalef) and H (Shannon) diversity for 68 paired observations in Minnesota lakes. The solid line represents a theoretical one-to-one relationship.

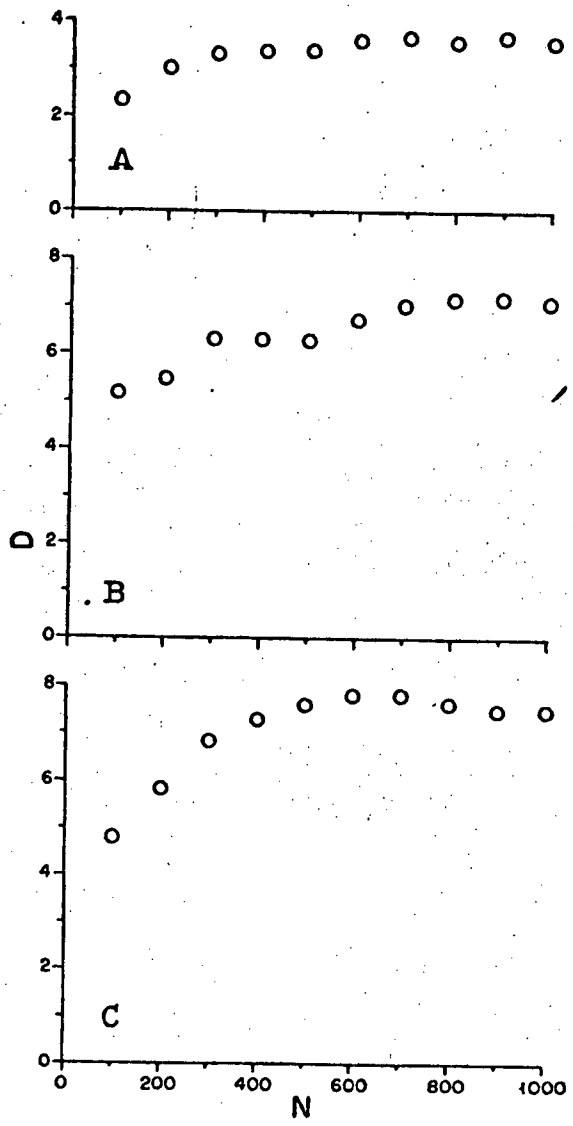

Fig. 18.

Diatoms. The effects of sample size (N) on the value of D (Margalef) diversity. Values of the index are calculated at each cumulative 100-individual increment. See text for discussion. Lakes Trout (A), Shagawa (B), and Burntside (C).

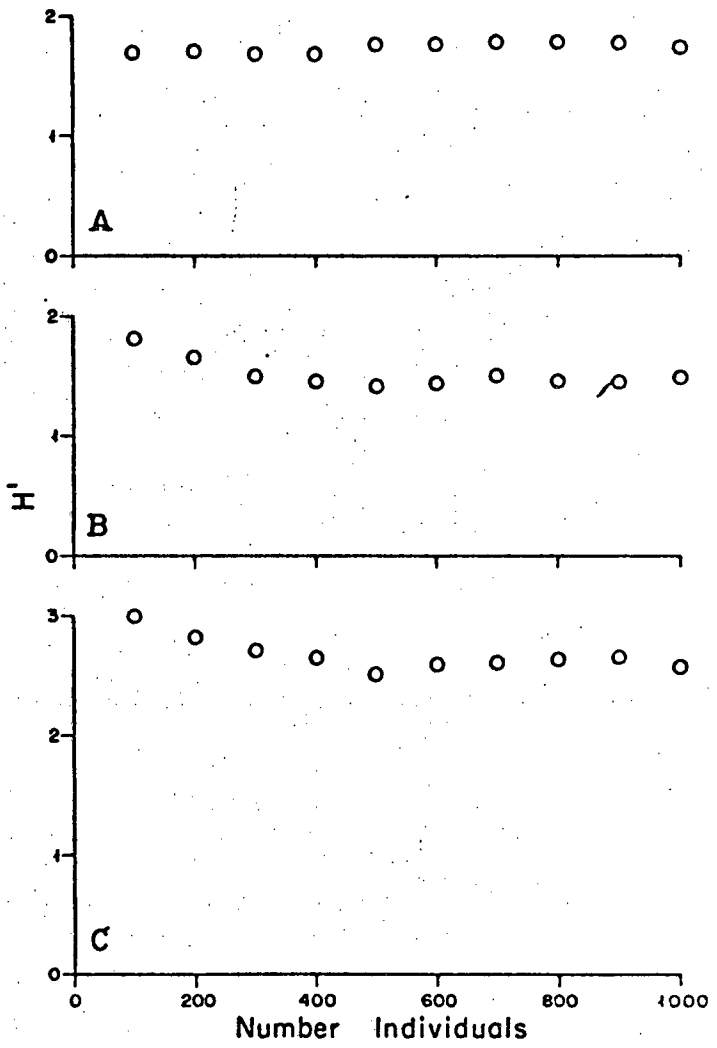

Fig. 19.

Diatoms. The effects of sample size (N) on the value of H (Shannon) diversity. Values of the index are calculated at each cumulative 100-individual increment. See text for discussion. Lakes Pickerel (A), Spiritwood (B), and Salt (C).

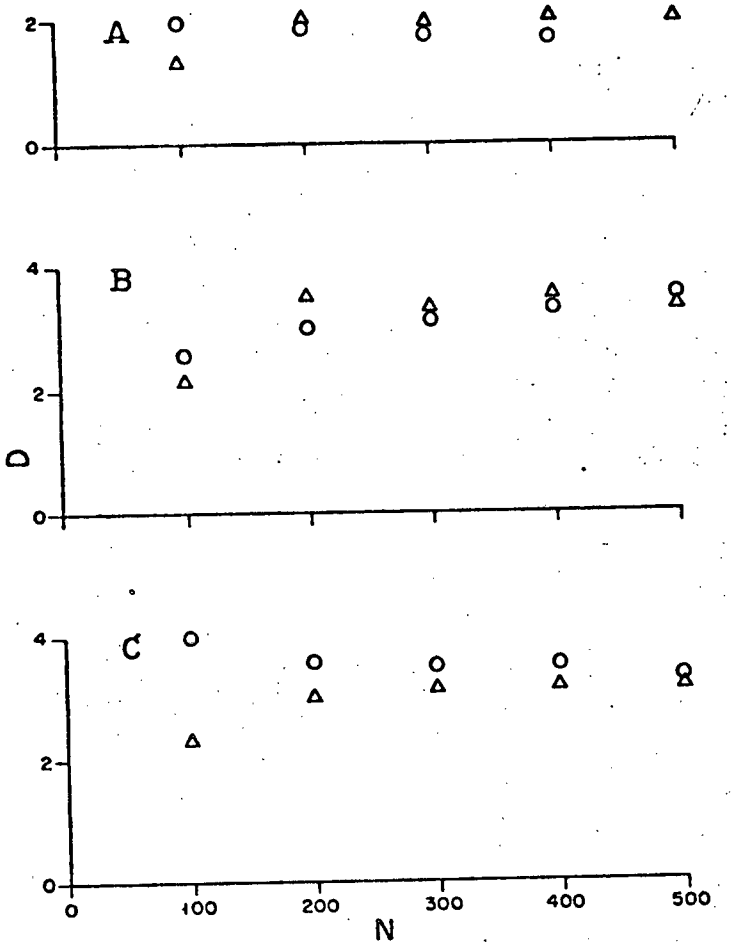

Fig. 20. Diatoms. The effects of sample size (N) on replicated estimates of D (Margalef) diversity. Values of the index are calculated at each cumulative 100-individual increment. See text for discussion. Lakes Pickerel (A), Spiritwood (B), and Salt (C).

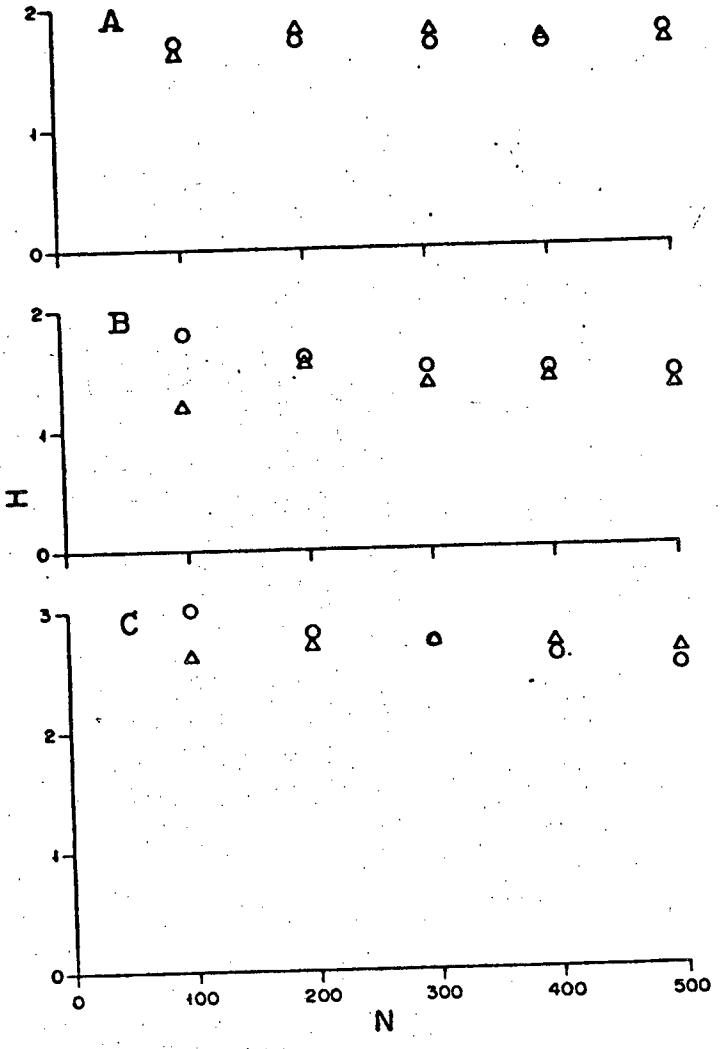

Fig. 21.

Diatoms. The effects of sample size (N) on replicated estimates of H (Shannon) diversity. Values of the index are calculated at each cumulative 100-individual increment. See text for discussion. Lakes Pickerel (A), Spiritwood (B), and Salt (C).

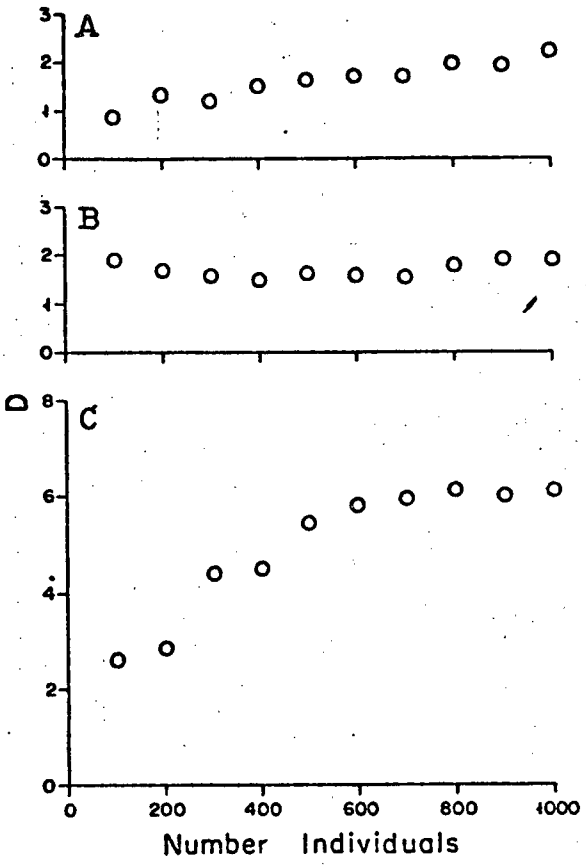

Fig. 22. Whole-water communities. The effects of sample size (N) on the value of D (Margalef) diversity. Values of the index are calculated at each cumulative 100-individual increment. See text for discussion. Lakes Nokay (A), Itasca (B), and Minnetonka (C).

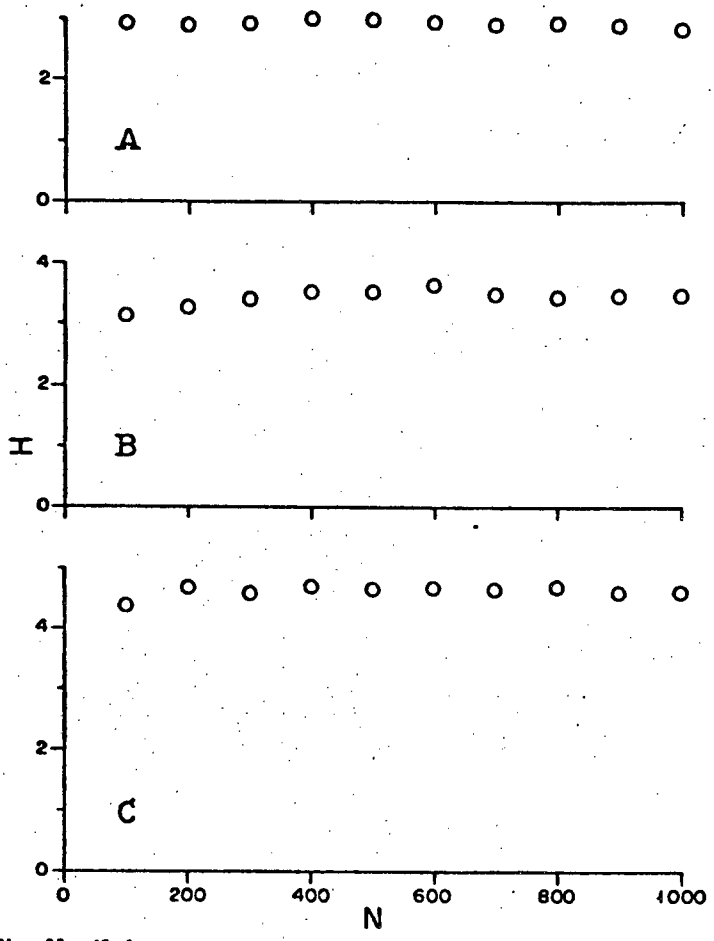

Fig. 23. Whole-water communities. The effects of sample size (N) on the value of H (Shannon) diversity. Values of the index are calculated at each cumulative 100-individual increment. See text for discussion. Lakes Elk, Grant Co. (A), Minnewaska (B), and Pickerel (C).

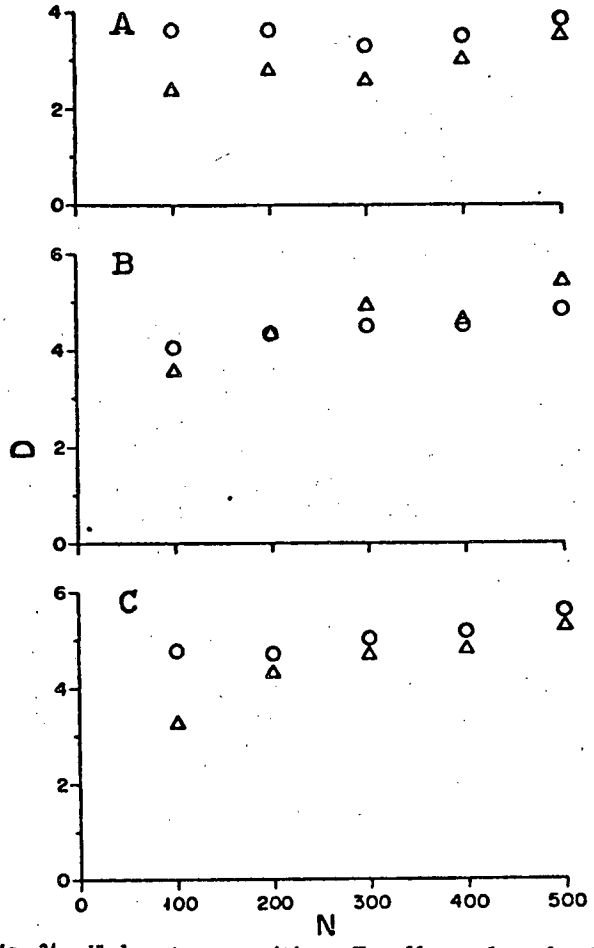

Fig. 24. Whole-water communities. The effects of sample size (N) on replicated estimates of D (Margalef) diversity. Values of the index are calculated at each cumulative 100-individual increment. See text for discussion. Lakes Shagawa (A), Vermilion (B), and Loon (C).

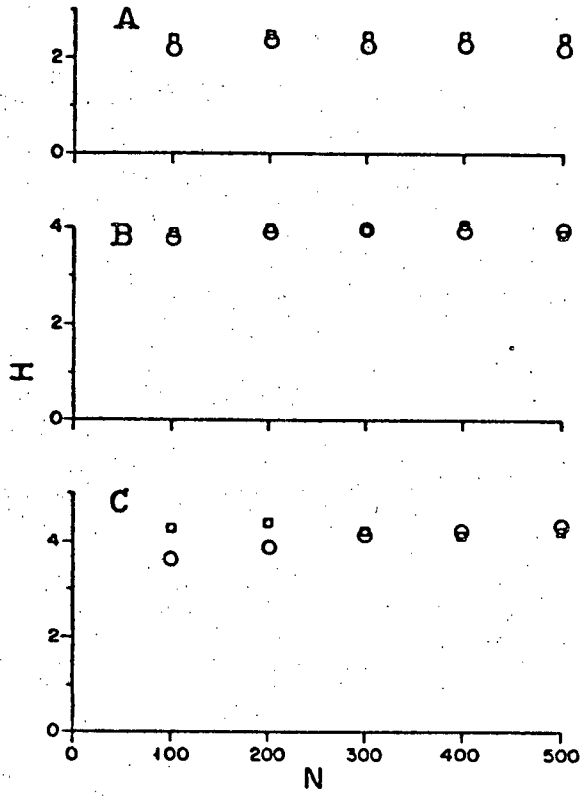

Fig. 25. Whole-water communities. The effects of sample size (N) on replicated estimates of H (Shannon) diversity. Values of the index are calculated at each cumulative 100-individual increment. See text for discussion. Lakes Minnetonka (A), Itasca (B), and Nokay (C).

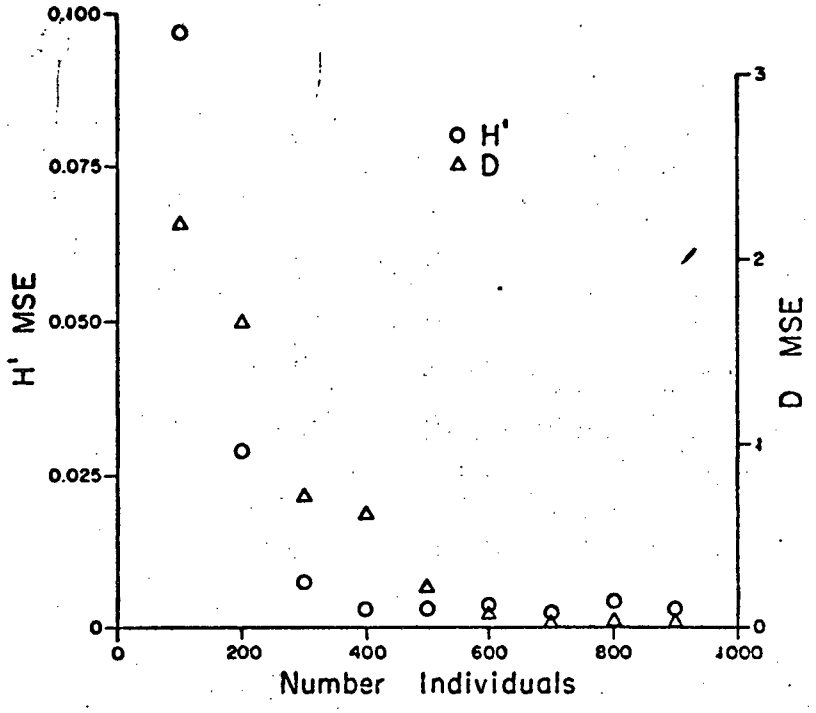

Fig. 26. Diatoms. The effects of sample size (N) on estimates of D (Margalef) and H (Shannon) diversity in nine lakes as assessed by the mean square error statistic (MSE). Decreasing MSE values for cumulative 100-individual increments indicate the rate at which the error in estimation of the index undergoes reduction. See text for discussion.

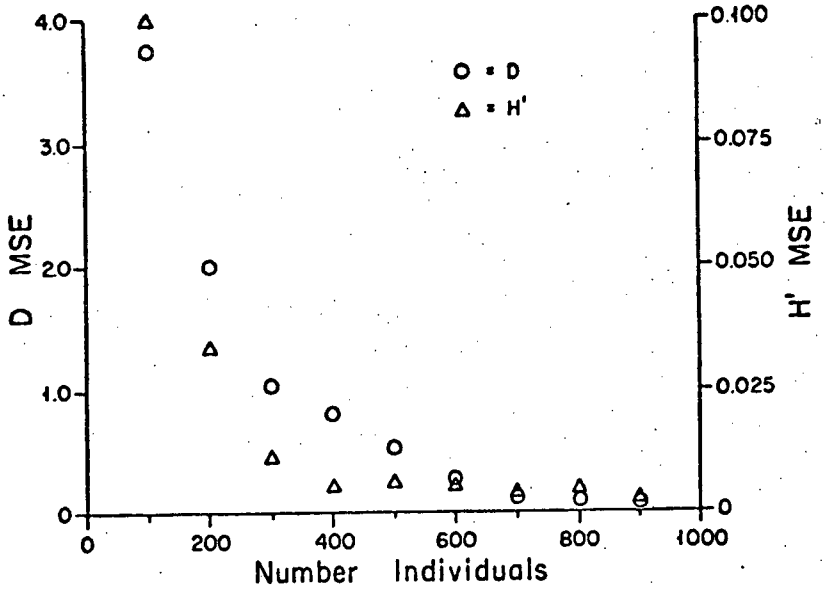

Fig. 27. Whole-water communities. The effects of sample size (N) on estimates of D (Margalef) and H (Shannon) diversity in nine lakes as assessed by the mean square error statistic (MSE). Decreasing MSE values for cumulative 100-individual increments indicate the rate at which the error in estimation of the index undergoes reduction. See text for discussion.

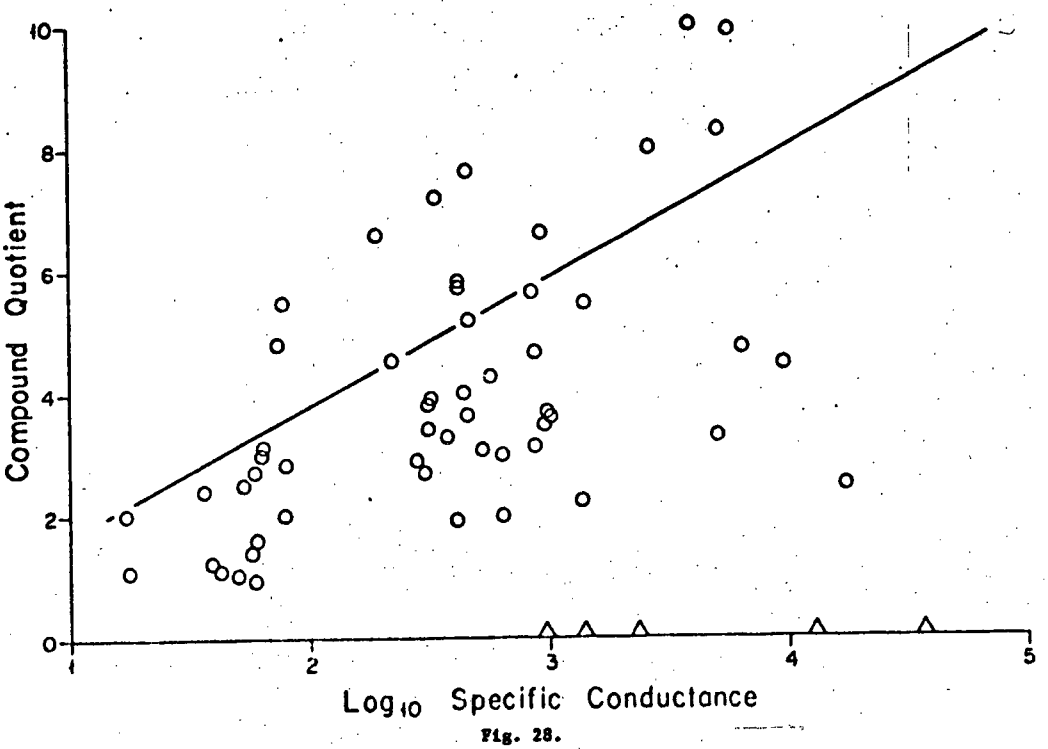

Fig. 28.

A regression of the compound phytoplankton quotient (CPQ) on $\log_{10}$ specific conductance (COND) in umho cm^{-1} at 25C for 68 study lakes in Minnesota. CPQ estimates >10.0 are omitted from the graph and quotients with a zero term in the denominator are plotted on the x axis. See Table 19 for CPQ computations. The equation relating CPQ to specific conductance is: $y = 2.129(\text{COND}) - 0.471$.

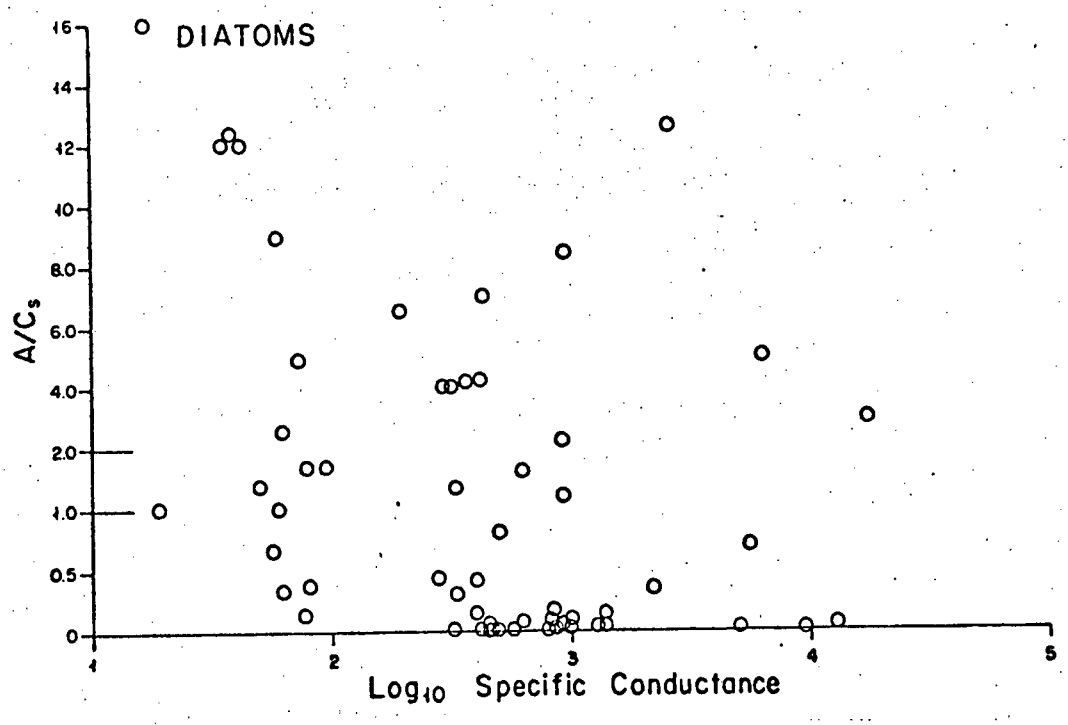

Fig. 29.

A plot of Stockner's diatom ratio (A/C_s) versus $\log_{10}$ specific conductance in umho cm^{-1} at 25C for 60 study lakes in Minnesota. Eight ratios >16.0 are omitted from the graph. See Table 23 for A/C_s computations.

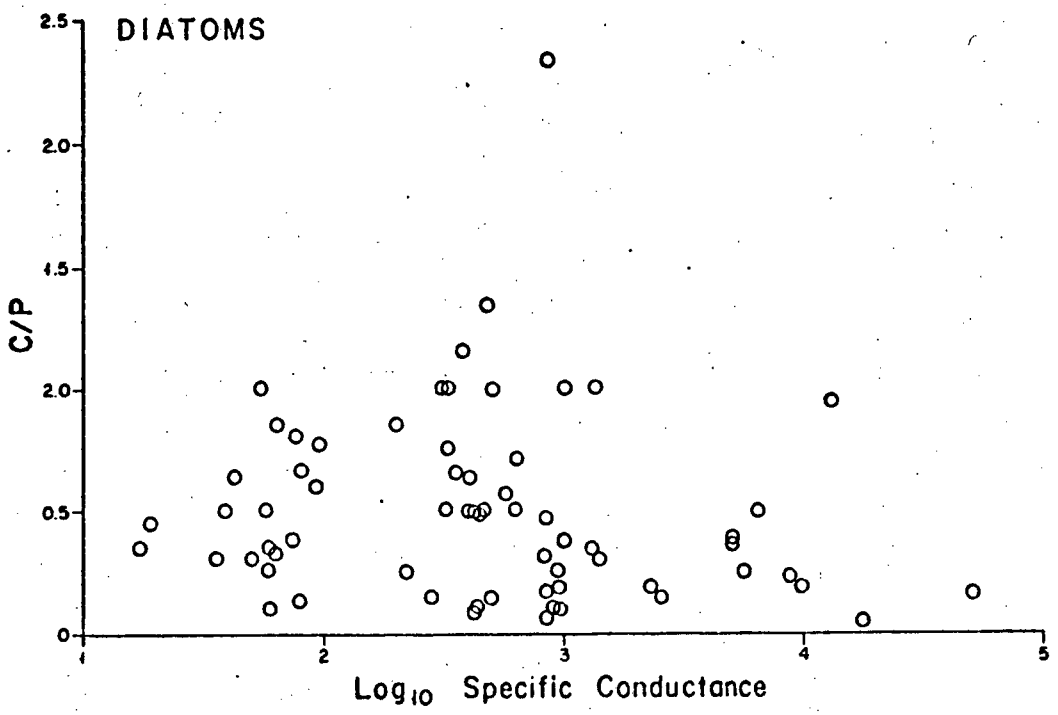

Fig. 30.

A plot of Nygaard's diatom ratio (C/P versus $\log_{10}$ specific conductance in umho cm^{-1} at 25C for 66 study lakes in Minnesota. Two ratios with a zero term in the numerator are omitted from the graph. See Table 23 for C/P computations.

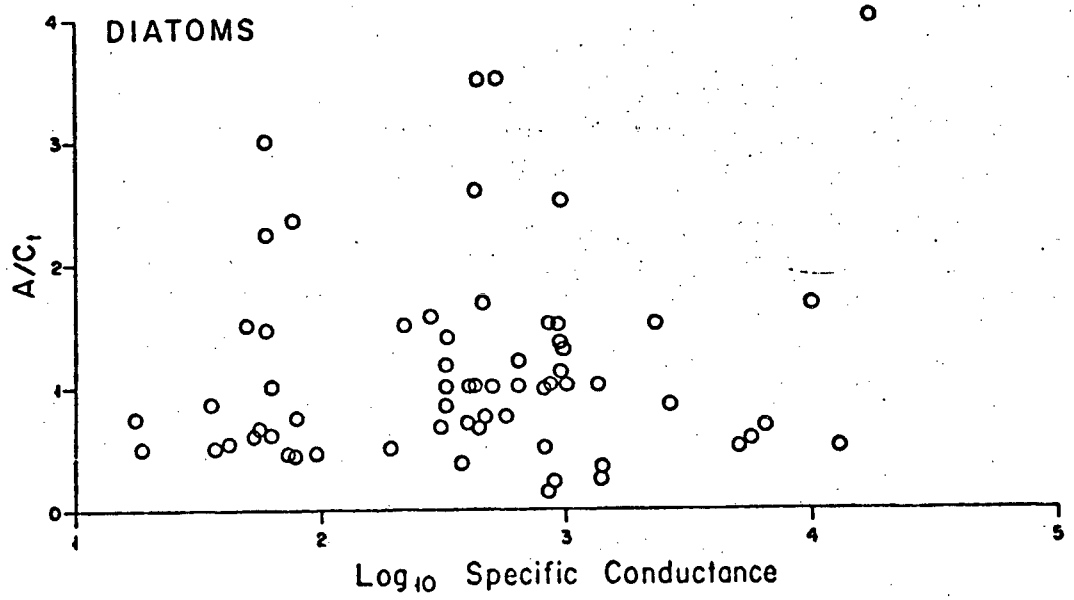

Fig. 31. A plot of a modified version of Stockner's ratio (A/C_t) versus $\log_{10}$ specific conductance in umho cm^{-1} at 25C for 63 study lakes in Minnesota. Five ratios with a zero term in the numerator or denominator are omitted from the graph. See Table 23 for A/C_t computations.

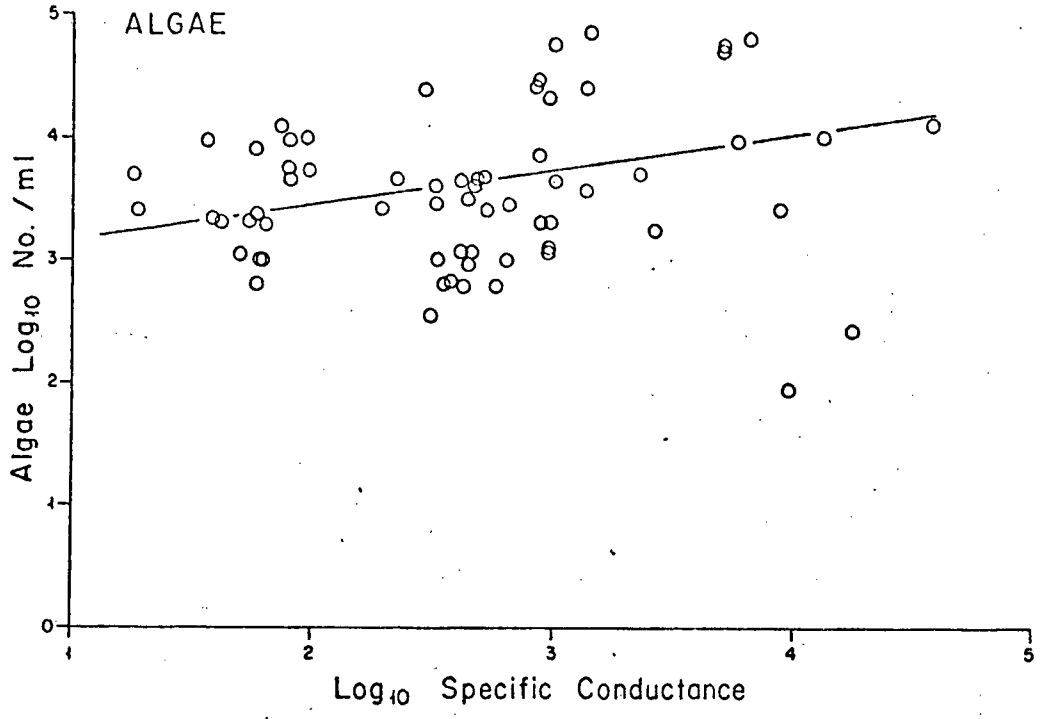

Fig. 32.

A regression of phytoplankton standing crop (Algae $\log_{10}$ No./ml) on $\log_{10}$ specific conductance (COND) in umho cm^{-1} at 25C for 68 study lakes in Minnesota. Three lakes >5.0 Algae $\log_{10}$ No./ml are omitted from the graph. These lakes and their standing crops as $\log_{10}$ estimates are Heron 5.278, Isabel 5.174, and Eckelson 5.606. The equation relating $\log_{10}$ phytoplankton standing crop to specific conductance is: $y = 0.263(\text{COND}) + 2.94$.

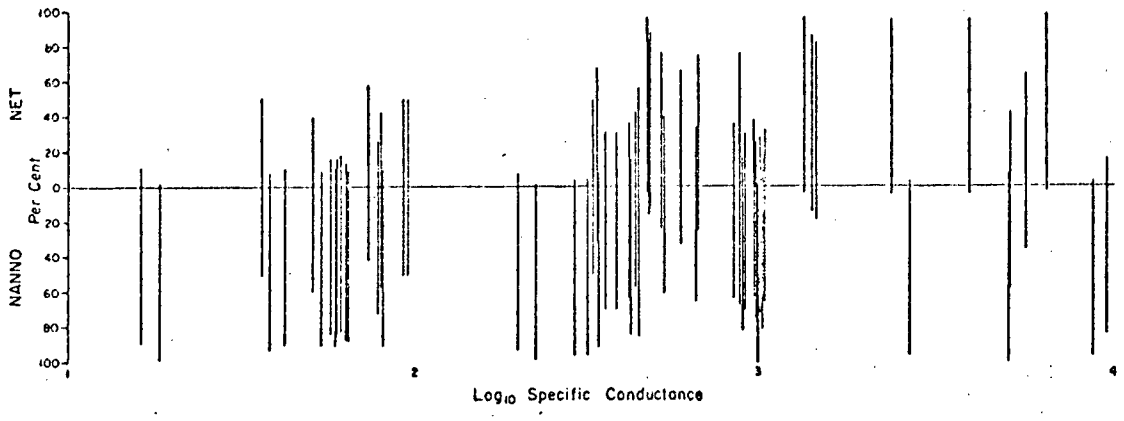

Fig. 33. A plot of net phytoplankton (NET) and nannoplankton (NANNO) standing crop as a percentage of the total phytoplankton standing crop (individuals/ml) versus $\log_{10}$ specific conductance (COND) in umho cm^{-1} at 25C for 63 study lakes in Minnesota. Five lakes with COND $>10^4$ are omitted from the graph (Table 12). These lakes and their percentage values of NET and NANNO are Alkali (3/97), Alkaline (17/83), Eckelson (76/24), George (92/8), and Salt (3/97).

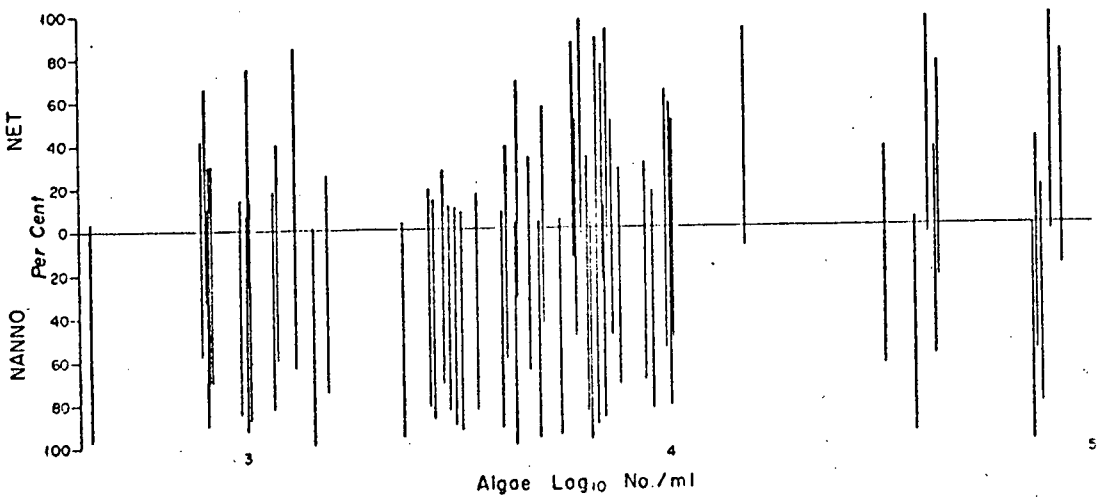

Fig. 34.

A plot of net phytoplankton (NET) and nannoplankton (NANNO) standing crop as a percentage of the total phytoplankton standing crop (individuals/ml) versus phytoplankton standing crop (Algae $\log_{10}$ No./ml) for 64 study lakes in Minnesota. Four lakes < 2.4 and >5.0 Algae $\log_{10}$ No./ml are omitted from the graph. These lakes and their percentage values of NET and NANNO and Algae $\log_{10}$ No./ml in parentheses are Isabel 96/4 (5.174), Spiritwood 16/84 (1.949), Eckelson 76/24 (5.606), and Heron 32/68 (5.278).

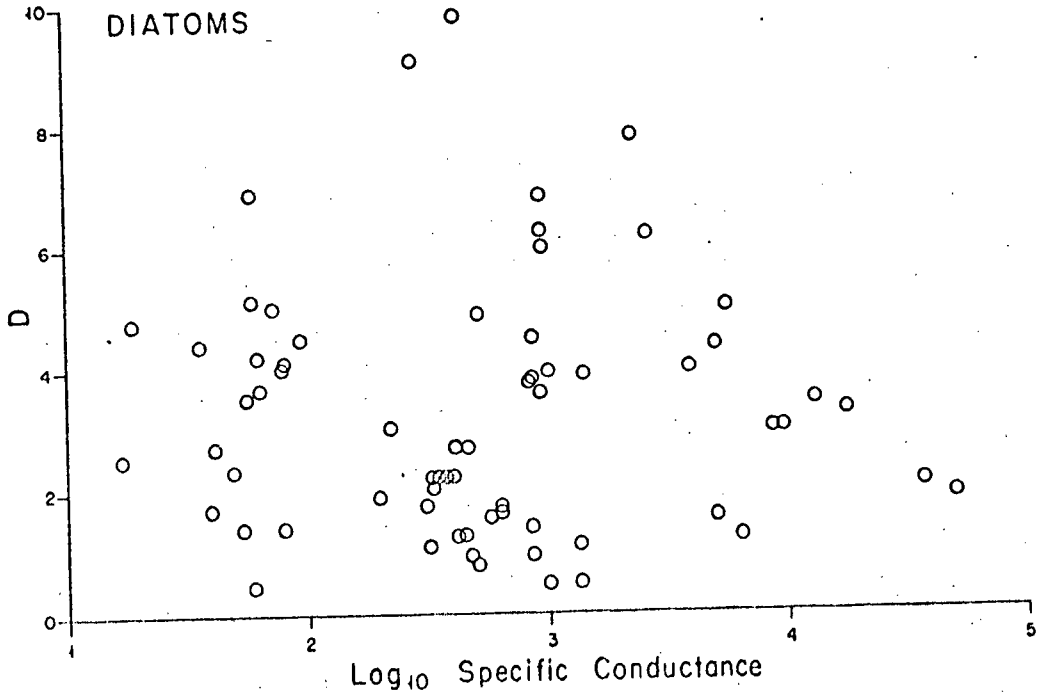

Fig. 35.

A plot of species diversity D (Margalef) in diatom communities versus $\log_{10}$ specific conductance (COND) in umho cm^{-1} at 25C in 67 study lakes in Minnesota. One estimate of D (Lake Lillian - 10.82) is omitted from the graph.

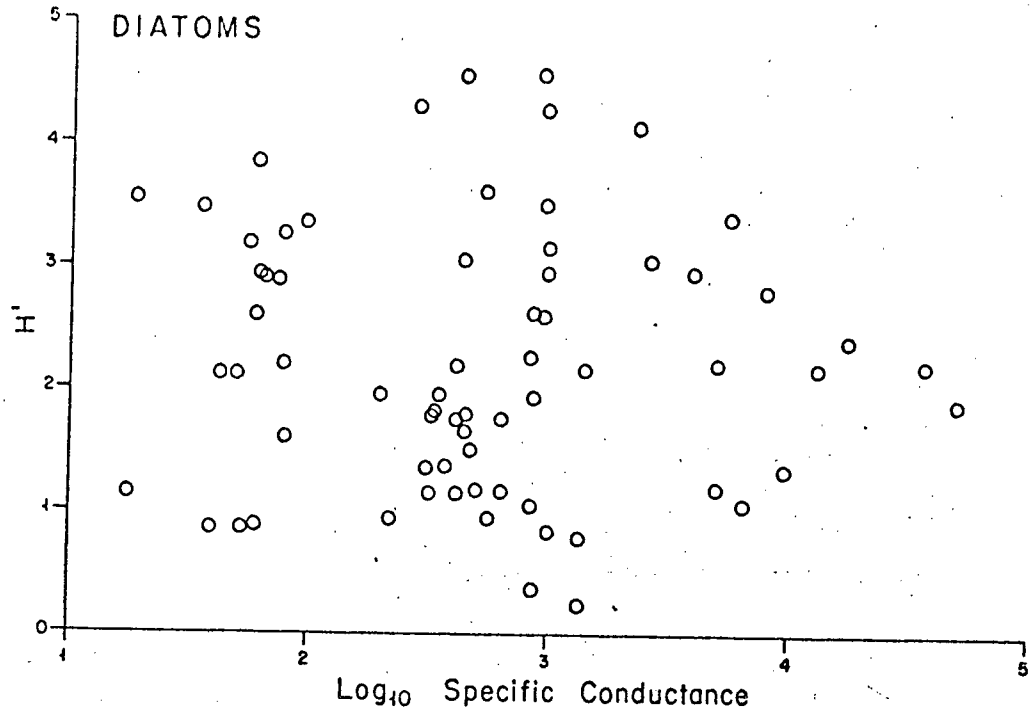

Fig. 36.

A plot of species diversity H (Shannon) in bits per cell in diatom communities versus $\log_{10}$ specific conductance in umho cm^{-1} at 25C in 68 study lakes in Minnesota.

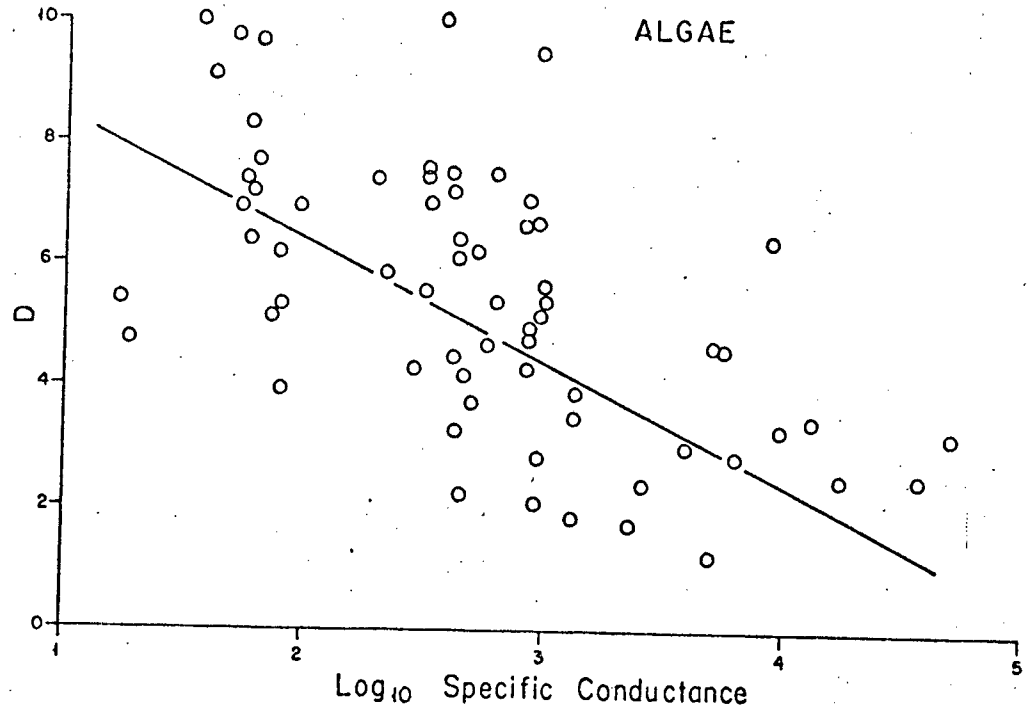

Fig. 37.

A regression of species diversity D (Margalef) in phytoplankton communities on $\log_{10}$ specific conductance (COND) in umho cm^{-1} at 25C for 68 study lakes in Minnesota. Two estimates of D (Lakes Big = 10.40 and Ball Club = 12.38) are omitted from the graph. The equation relating D to specific conductance is: $y = -1.598(\underline{\text{COND}}) + 9.60$.

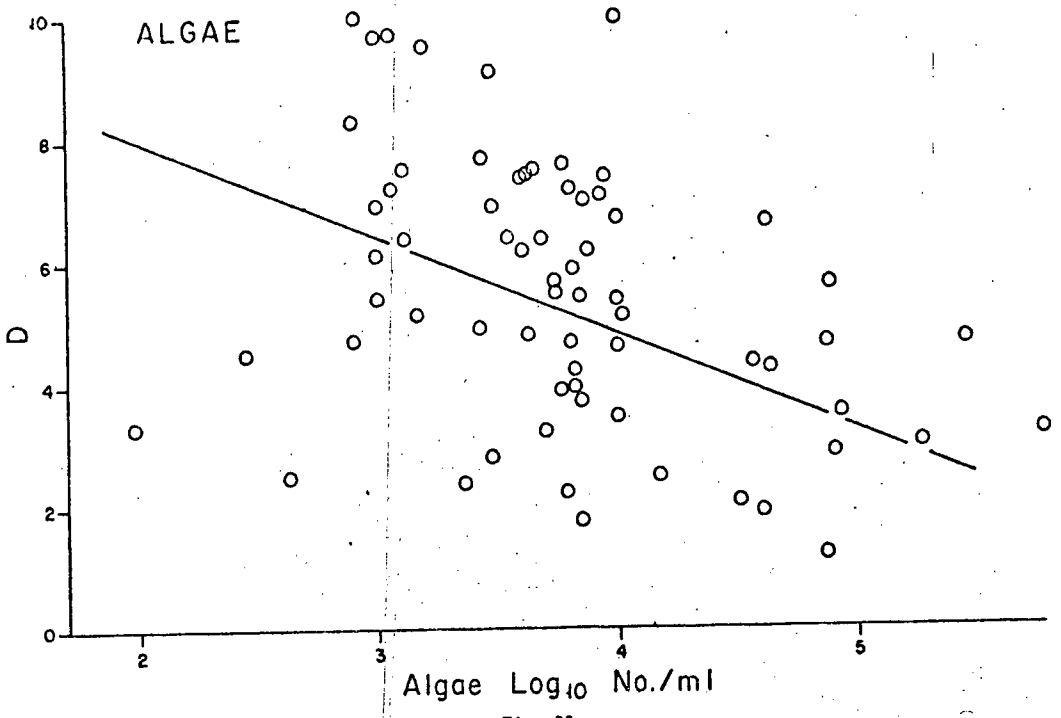

Fig. 38.

A regression of species diversity D (Margalef) in phytoplankton communities on standing crop of phytoplankton (Algae $\log_{10}$ No.ml) for 68 study lakes in Minnesota. Two estimates of D (Lakes Big = 10.40 and Ball Club = 12.38) are omitted from the graph. The equation relating D to the standing crop of phytoplankton is: $y = 1.476(\text{Algae } \log_{10} \text{ No./ml}) + 10.8$.

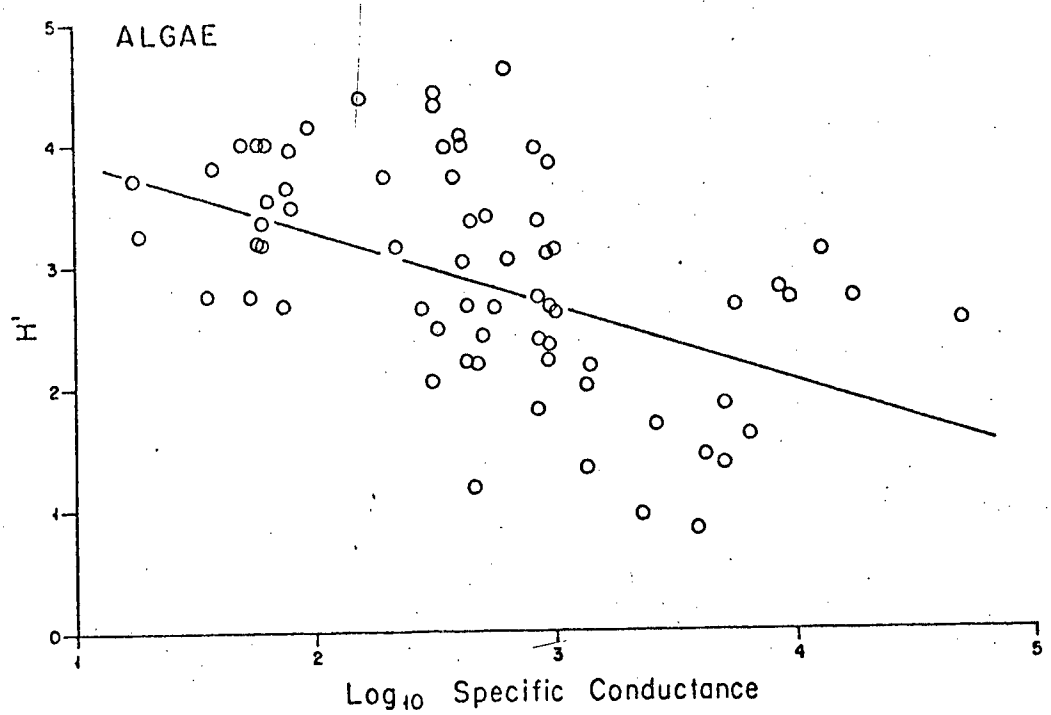

Fig. 39.

A regression of species diversity H (Shannon) in bits per individual in phytoplankton communities on $\log_{10}$ specific conductance (COND) for 68 study lakes in Minnesota. The equation relating H to specific conductance is: $y = -0.56$ (COND) + 4.37.

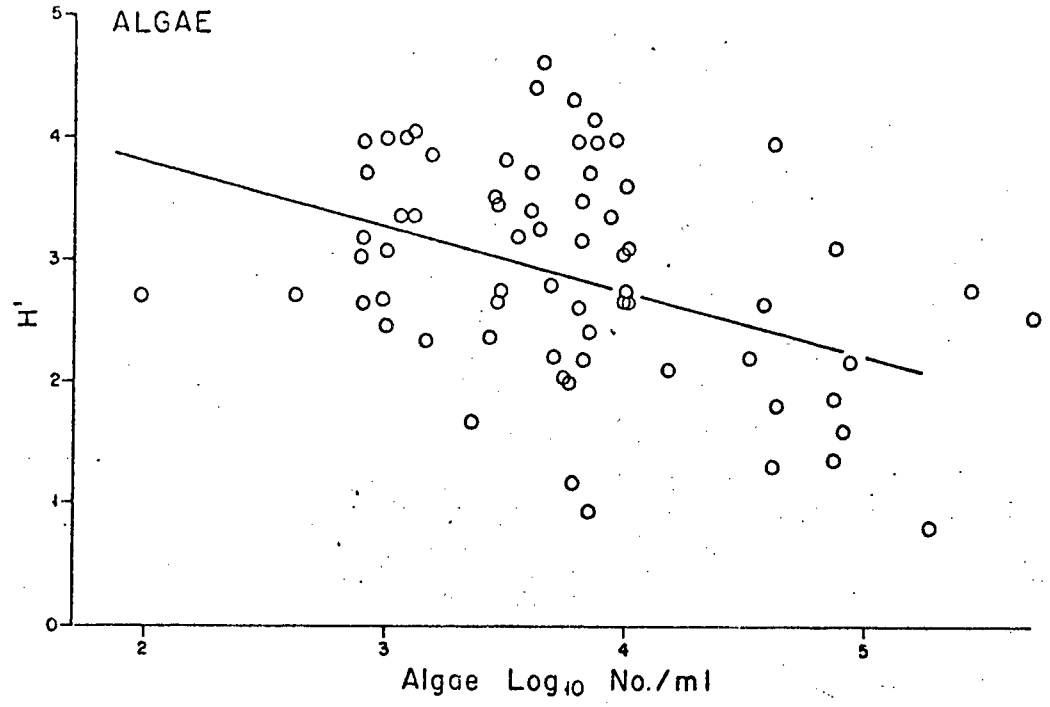

Fig. 40.

A regression of species diversity H (Shannon) in bits per individual in phytoplankton communities on standing crop of phytoplankton (Algae $\log_{10}$ No./ml) for 68 study lakes in Minnesota. The equation relating H to the standing crop of phytoplankton is: $y = -0.503$ (Algae $\log_{10}$ No./ml)$+ 4.766$.

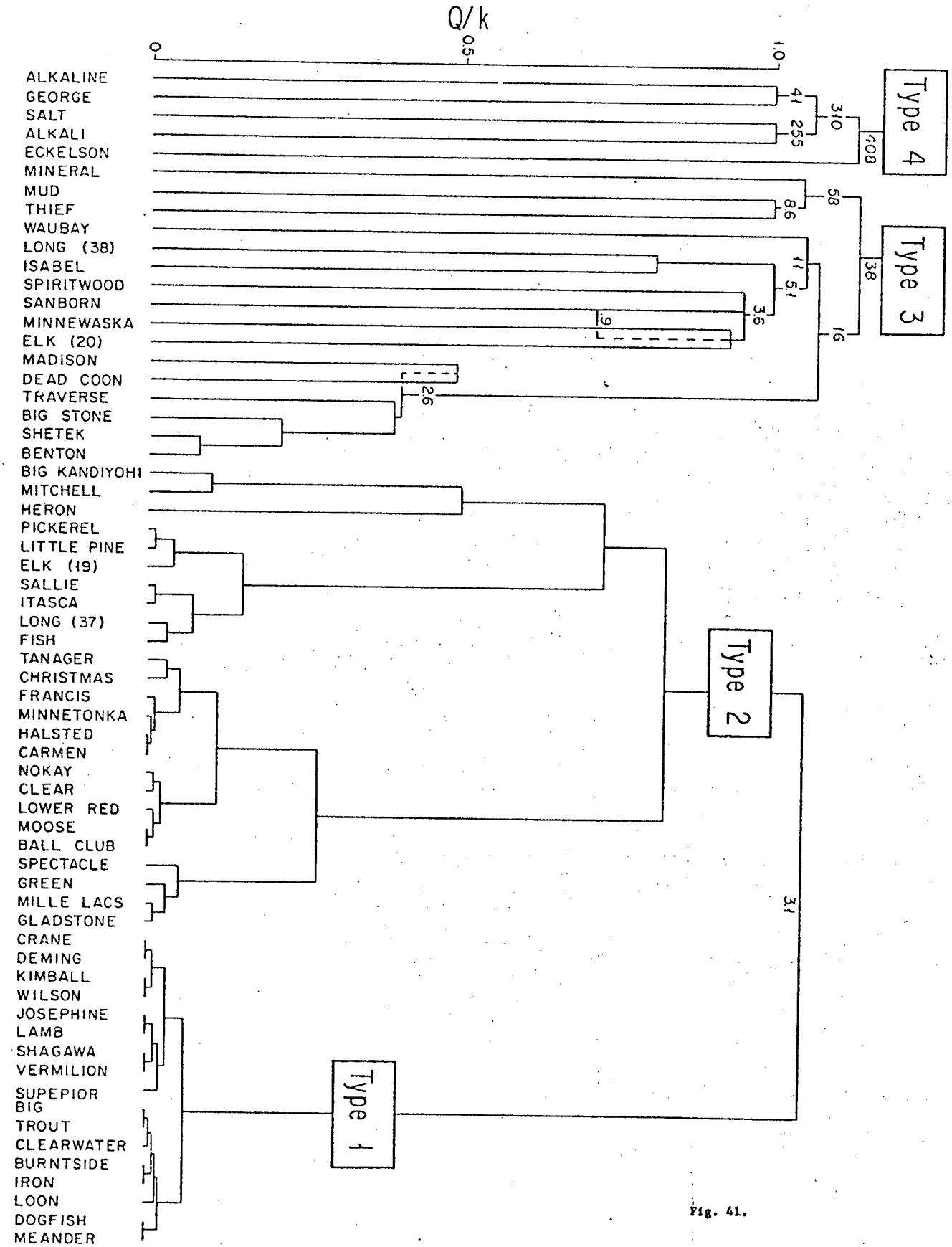

Fig. 41.

A dendrogram of the cluster analysis performed on chemical data (concentrations of major anions and cations) for 63 study lakes in Minnesota. See text for discussion and Table 42 (Run 3) for results.

Fig. 42.

The salinity ranges and mean salinity levels (vertical lines) occupied by each of the major lake types detected in cluster analysis on 63 study lakes in Minnesota: MAJOR SOLUTES (the concentration of 7 major ions); TSI (4 PHYSICAL-CHEMICAL Indicators), indicated as TSI (4 CHEMICAL) -- specific conductance, $\sum$calcium + magnesium, total alkalinity, and secchi-disc transparency); TSI (4 BIOLOGIC -- H diversity, standing crop of phytoplankton, compound phytoplankton quotient, and the number of net phytoplankton taxa); TSI (CHEMICAL + BIOLOGIC -- the 8 physical, chemical, and biologic indicators). See text for discussion and Table 42 (Run 3) and Table 44 (Runs 1, 7, and 8) for results.

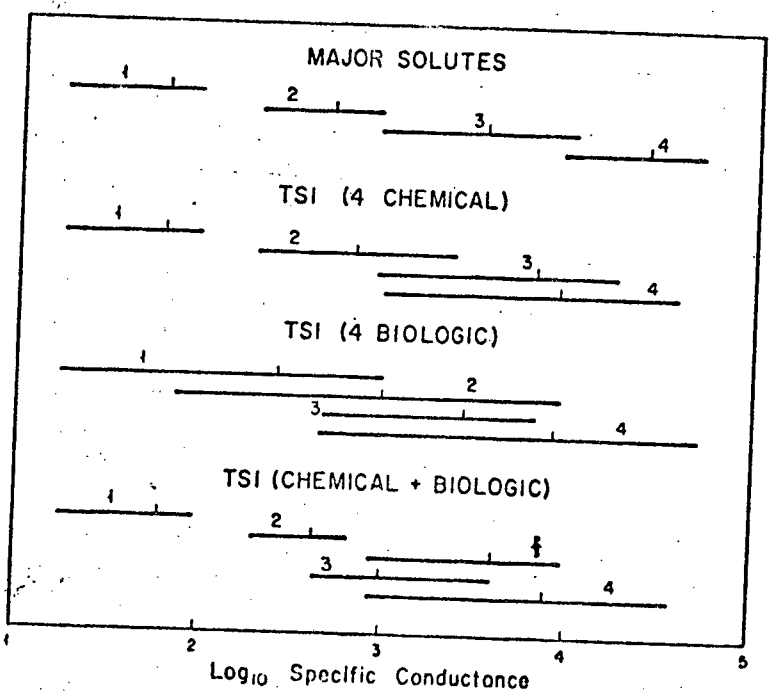

Fig. 43.

The salinity ranges and mean salinity levels (vertical lines) occupied by each of the major lake types detected in cluster analysis on suites of phytoplankton taxa in 68 study lakes in Minnesota: DIATOMS (25 species), DESMIDS (39 species), BLUE GREENS (29 species) and NET PHYTOPLANKTON (167 species). See text for discussion and Table 47 for results.

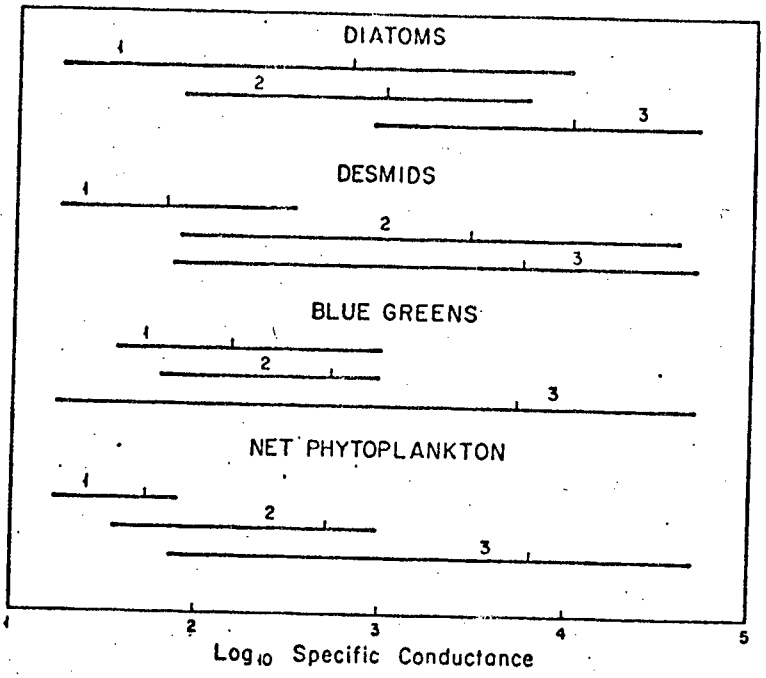

TABLE 1. The location of the lakes by State, County, and identification number. See text for discussion.

No.	Lake	State[1]	County[2]	Ident. No.[3]
1.	Albert	S	Kingsbury	" "
2.	Alkali[4]	M	Otter Tail	" "
3.	Alkaline	N	Kidder	- -
4.	Ball Club	M	Itasca	B0146
5.	Benton	M	Lincoln	41-43
6.	Big	M	St. Louis	69-50
7.	Big Kandiyohi	M	Kandiyohi	34-86
8.	Big Stone	M	Big Stone	6-152
9.	Burntside	M	St. Louis	69-118
10.	Carman Bay[5]	M	Hennepin	27-133
11.	Christmas	M	Hennepin	27-137
12.	Clear	M	Le Sueur	40-79
13.	Clearwater	M	Cook	16-139
14.	Crane	M	St. Louis	69-616
15.	Dead Coon	M	Lincoln	41-21
16.	Deming	M	Clearwater	C1605
17.	Dogfish	M	St. Louis	69-338
18.	Eckelson	N	Barnes	- -
19.	Elk	M	Clearwater	15-10
20.	Elk	M	Grant	26-47
21.	Fish	M	Cottonwood	32-18
22.	Frances[6]	M	Le Sueur	40-57
23.	George[7]	N	Kidder	- -
24.	Gladstone	M	Crow Wing	18-338
25.	Goose	M	Cass	11-298
26.	Green	M	Isanti	30-136
27.	Halsted Bay[5]	M	Hennepin	27-133
28.	Heron	M	Jackson	32-57
29.	Iron	M	Cook	16-328
30.	Isabel	N	Kidder	- -
31.	Itasca	M	Clearwater	15-16
32.	Josephine[8]	M	Clearwater	- -
33.	Kimball	M	Cook	16-45
34.	Lamb	M	St. Louis	69-341
35.	Lillian	M	Kandiyohi	34-72
36.	Little Pine	M	Otter Tail	56-142
37.	Long	M	Clearwater	15-50
38.	Long	N	Burleigh	- -
39.	Loon	M	Cook	16-448
40.	Lower Red Lake	M	Beltrami	4-35
41.	Madison	S	Lake	- -
42.	Meander	M	St. Louis	69-329
43.	Mille Lacs	M	Mille Lacs	48-2
44.	Mineral[4]	M	Otter Tail	- -
45.	Minnewaska	M	Pope	61-130
46.	Mitchell	S	Hanson	- -
47.	Moose	M	Itasca	C0607
48.	Mud	M	Marshall	45-2
49.	Nokay	M	Crow Wing	18-104
50.	Pickerel	S	Day	- -
51.	Sallie	M	Becker	3-359
52.	Salt[9]	M	Lac Qui Parle	220
53.	Sanborn	N	Barnes	- -
54.	School Grove	M	Lyon	42-2
55.	Shagawa	M	St. Louis	69-69
56.	Shetek	M	Murray	51-46
57.	Spectacle	M	Isanti	30-135
58.	Spiritwood	N	Stutsman	- -
59.	Stinking	N	Becker	C1604
60.	Superior[10]	M	Cook	16-1
61.	Tanager Bay[5]	M	Hennepin	27-141
62.	Thief	M	Marshall	45-1
63.	Traverse	M	Traverse	78-25
64.	Trout	M	Cook	16-49
65.	Upper Minnetonka[5]	M	Hennepin	27-133
66.	Vermilion	M	St. Louis	69-378
67.	Waubay	S	Day	- -
68.	Wilson	M	Lake	38-47

1 M (Minnesota), N(North Dakota), S (South Dakota).

2 Lakes in Minnesota are listed with county and identification number; those in North Dakota and South Dakota have a county listing only. Location of the lakes in these states may be found by reference to a state road map.

3 Identification number as listed in (1) An Inventory of Minnesota Lakes, Minnesota Department of Conservation, Division of Waters, Soils, Minerals. Bulletin No. 25, 1968. Identification numbers preceded by a letter have been taken from (2) Guide to Fun in Minnesota, Clarkson Map Co., Kaukauna, Wisconsin (available through State of Minnesota, Documents Section, 140 Centennial Building, St. Paul, Minnesota 55101).

4 Lakes Alkali and Mineral are located just off Route 59, two and three miles respectively, northwest of Ten Mile Lake.

5 Bays of the Lake Minnetonka complex, Hennepin County.

6 Listed as Lake Frances in publications cited in 3 above.

7 Called Salt Lake by local populace, located in Salt Lake Park.

8 Josephine is located in Itasca State Park, Clearwater County.

9 Salt Lake, situated on the Minnesota - South Dakota border, is approximately four miles southwest of Marietta, Minnesota. See (2) in Note 3.

10 Gorham's chemical analysis listed for Cook County. Algal samples taken at Silver Bay, Lake County (net plankton), and at approximately 15 miles due south of Silver Bay (quantitative sample).

Table 2. Precision of A/C_s (Stockner) estimation. Each of the three values for nine lakes is an independent ratio estimate from the same sample. Mean $\bar{x}$, standard deviation s, and coefficient of variation C.V. See text for sample sizes and discussion.

Lake	A/C_s Estimates			$\bar{x}$	s	C.V.
Trout	109.000	89.000	46.000	81.333	32.194	39.59
Burntside	14.300	12.700	11.900	12.960	1.000	7.72
Shagawa	1.170	1.300	1.690	1.387	0.271	19.54
Sallie	1.920	1.780	0.820	1.507	0.599	39.74
Itasca	0.730	0.680	0.420	0.610	0.166	27.28
Salt	2.510	3.340	2.480	2.777	0.662	23.85
Spiritwood	0.030	0.038	0.010	0.026	0.014	55.20
Pickerel	1.600	1.600	1.620	1.607	0.012	0.762
Elk [1]	27.600	16.200	4.280	16.027	11.661	72.76

[1] Itasca State Park, Clearwater County.

Table 3. Precision of A/C_t estimation. Each of the three values for nine lakes is an independent ratio estimate from the same sample. Mean $\bar{x}$, standard deviation s, and coefficient of variation C.V. See text for sample sizes and discussion.

Lake	A/C_t Estimates			$\bar{x}$	s	C.V.
Trout	0.750	3.000	0.600	1.450	1.344	92.72
Burntside	0.556	0.857	0.570	0.661	0.170	25.69
Shagawa	1.500	0.833	0.750	1.028	0.411	40.01
Sallie	1.800	1.800	3.500	2.367	0.982	41.47
Itasca	0.833	0.667	0.710	0.737	0.086	11.67
Salt	1.330	1.000	4.000	2.110	1.645	77.97
Spiritwood	2.330	1.667	1.670	1.889	0.382	20.22
Pickerel	1.000	0.800	1.000	0.933	0.116	12.38
Elk [1]	1.000	1.250	0.370	0.873	0.454	51.93

[1] Itasca State Park, Clearwater County.

Table 4. Precision of C/P (Nygaard) estimation. Each of the three values for nine lakes is an independent ratio estimate from the same sample. Mean $\bar{x}$, standard deviation s, and coefficient of variation C. V. See text for sample sizes and discussion.

Lake	C/P Estimates			$\bar{x}$	s	C.V.
Trout	0.571	0.125	1.000	0.565	0.437	77.39
Burntside	0.346	0.292	0.640	0.426	0.187	43.95
Shagawa	0.571	0.857	0.670	0.699	0.145	20.75
Sallie	0.192	0.200	0.140	0.177	0.033	18.36
Itasca	0.375	0.857	0.640	0.624	0.241	38.68
Salt	0.158	0.105	0.050	0.104	0.054	51.50
Spiritwood	0.150	0.158	0.180	0.163	0.014	8.91
Pickerel	0.750	0.556	0.500	0.602	0.131	21.79
Elk [1]	0.750	0.800	1.140	0.897	0.212	2.37

[1] Itasca State Park, Clearwater County.

Table 5. Precision of quantitative estimation. Both values for each of eight lakes are independent estimates of the number of individuals per ml. Mean $\bar{x}$, per cent deviation about mean $\bar{x} \pm \%$, and coefficient of variation C. V.

Lake	Estimates (No./ml)		$\bar{x}$	$\bar{x} \pm \%$	C.V.
Loon	2346	2145	2247 ± 101	4.5	6.3
Nokay	4004	5182	4592 ± 589	12.8	18.1
Vermilion	6359	5094	5726 ± 632	11.0	15.6
Shagawa	4290	5008	4649 ± 359	7.7	10.9
School Grove	1417	1302	1360 ± 57	4.2	5.9
Long [1]	3160	3198	3179 ± 19	0.6	0.8
Halsted [2]	4300	3936	4118 ± 182	4.4	6.2
Carman [2]	4625	4721	4673 ± 48	1.0	1.4

[1] Itasca State Park, Clearwater County.

[2] Bays in the Lake Minnetonka Complex, Hennepin County.

Table 6. A numerical comparison between estimates of H (Shannon) and D (Margalef) in three data sets. See text for discussion.

Data	No. Paired Observations	r	t-value
Hypothetical Population [1]	60	0.945	2.627**
Diatom Diversity [2]	68	0.893	5.267**
Algal Diversity [3]	68	0.730	33.3**

[1] H' = H max, range 2 (20 individuals) to 60 species (600 individuals)

[2] Minnesota lakes, 68 paired observations

[3] Minnesota lakes, 68 paired observations

** Significance at p = 0.01

Table 7. Diatoms. Precision of D (Margalef) diversity estimation. Each of the three values for the nine lakes is an independent estimate from the same sample. Mean $\bar{x}$, standard deviation s, and coefficient of variation C.V. See text for sample sizes and discussion.

Lake	D Diversity Estimates			$\bar{x}$	s	C.V.
Elk [1]	01965	1.287	1.303	1.185	0.192	16.17
Sallie	4.827	4.982	4.899	4.903	0.073	1.49
Salt	3.379	3.218	3.284	3.293	0.080	2.43
Itasca	3.379	1.931	2.682	2.664	0.724	27.17
Shagawa	1.609	1.931	1.881	1.807	0.141	7.81
Trout	1.609	1.287	1.416	1.437	0.162	11.26
Burntside	5.458	4.838	6.130	5.475	0.646	11.79
Pickerel	2.091	2.089	1.758	1.980	0.192	9.68
Spiritwood	3.540	3.379	2.993	3.304	0.281	8.50

[1] Itasca State Park, Clearwater County.

Table 8. Diatoms. Precision of H (Shannon) diversity estimation. Each of the three values for the nine lakes is an independent estimate from the same sample. Mean $\bar{x}$, standard deviation s, and coefficient of variation C.V. See text for sample sizes and discussion.

Lake	H Diversity Estimates			$\bar{x}$	s	C.V.
Elk [1]	0.514	0.381	0.472	0.456	0.066	14.55
Sallie	3.383	3.369	3.337	3.363	0.022	0.65
Salt	2.524	2.645	2.568	2.579	0.056	2.18
Itasca	2.478	2.243	2.436	2.386	0.125	5.25
Shagawa	1.995	2.074	2.082	2.050	0.047	2.31
Trout	0.680	0.520	0.658	0.619	0.087	14.01
Burntside	1.864	1.558	1.815	1.746	0.163	9.32
Pickerel	1.759	1.670	1.709	1.713	0.044	2.55
Spiritwood	1.413	1.403	1.343	1.386	0.037	2.67

[1] Itasca State Park, Clearwater County.

Table 9. Whole-water communities. Precision of D (Margalef) diversity estimation. Each of the three values for the nine lakes is an independent estimate from the same sample. Mean $\bar{x}$, standard deviation s, and coefficient of variation C.V. See text for sample sizes and discussion.

Lake	D Diversity Estimates			$\bar{x}$	s	C.V.
Loon	5.632	5.308	6.658	5.866	0.704	12.01
Pickerel	6.758	6.596	7.383	6.912	0.415	6.01
Minnewaska	6.112	5.958	6.658	6.243	0.299	4.80
Elk [1]	4.506	3.219	4.632	4.119	0.790	19.19
Itasca	6.276	6.758	7.093	6.709	0.410	6.11
Nokay	7.590	7.399	7.526	7.505	0.095	1.26
Minnetonka [2]	3.379	2.893	3.619	3.297	0.369	11.94
Shagawa	3.863	3.539	4.343	3.915	0.404	10.31
Vermilion	4.507	5.465	5.789	5.254	0.667	12.69

[1] Grant County

[2] Upper Minnetonka Bay, Hennepin County

Table 10. Whole-water communities. Precision of H (Shannon) diversity estimation. Each of the three values for the nine lakes is an independent estimate from the same sample. Mean $\bar{x}$, standard deviation s, and coefficient of variation C.V. See text for sample sizes and discussion.

Lake	H Diversity Estimates			$\bar{x}$	s	C.V.
Loon	3.256	3.074	3.224	3.185	0.095	2.99
Pickerel	4.644	4.509	4.634	4.596	0.073	1.59
Minnewaska	3.505	3.296	3.464	3.421	0.109	0.03
Elk [1]	2.948	2.712	2.865	2.842	0.119	4.21
Itasca	3.908	3.873	4.021	3.934	0.075	1.92
Nokay	4.347	4.202	4.301	4.283	0.068	1.58
Minnetonka [2]	2.264	2.427	2.392	2.361	0.085	3.61
Shagawa	3.471	3.458	3.507	3.479	0.024	0.69
Vermilion	3.800	3.802	3.851	3.818	0.025	0.67

[1] Grant County

[2] Upper Minnetonka Bay, Hennepin County

TABLE 11. Summary values (range, mean $\bar{x}$, median m, and standard deviation s) for the physical and chemical measurements made on the study lakes in Minnesota. All ion concentrations and statistics are based on meq/l.

Parameter	Range	$\bar{x}$	m	s
Specific Conductance*	14-31,783	2036.	293.	5197.
Secchi Disc*	0.5-40.0	6.48	5.0	6.44
Calcium	0.100-17.8	2.22	1.35	2.98
Magnesium	0.054-204.	11.8	1.42	23.0
Sodium	0.022-328	17.0	0.278	59.9
Potassium	0.008-18.8	0.897	0.240	3.07
Sulfate	0.029-209.	14.1	0.204	40.1
Chloride	0.001-120	3.18	0.076	16.1
Total Alkalinity($CaCO_3$)	0.120-16.8	3.53	2.80	3.31
Calcium + Magnesium	0.160-208.	14.0	2.92	33.9
Water Temperature*	5.0-17.5	11.3	11.7	2.86

* Sixty-eight observations: Specific conductance, μmho cm^{-1} at 25C; Secchi disc, in feet; temperature of surface water, in C.

TABLE 12. The date of sampling, secchi-disc transparency (in feet), specific conductance (μmho cm^{-1} at 25C), and water temperature (in C), and the depth of the thermocline (in feet) in the 68 study lakes in Minnesota.

Lake No.	Date	Secchi	Specific Conductance	Temperature(C) Surface	Temperature(C) Hypolimnion	Thermocline
1	10-21-70	3.0	3160	10.5		--
2	10-19-70	2.0	8560	8.0		--
3	9-12-71	1.0	11467	15.0		--
4	9-27-70	11.0	198	13.8		--
5	10-22-70	2.0	889	10.1		--
6	9-27-70	11.0	20	12.3		--
7	10-31-70	2.5	697	5.0		--
8	10-20-70	0.5	1360	10.2		--
9	9-27-70	15.0	20	12.5		--
10	10-24-70	6.0	295	12.1		?
11	10-31-70	6.0	281	8.0		--
12	10-22-70	5.0	257	11.5		--
13	9-25-70	27.0	23	14.0	6.0	50
14	9-27-70	6.0	32	12.4		--
15	10-22-70	1.3	815	10.3		--
16	9-28-70	5.0	51	13.0	3.6	18
17	9-19-70	6.5	14	17.0		--
18	9-12-71	0.5	31783	15.0		--
19	9-28-70	13.0	210	13.9		--
20	10-19-70	4.5	725	8.8		--
21	10-22-70	2.3	402	11.0		--
22	10-22-70	8.0	193	11.9		--
23	9-12-71	4.0	23428	15.0		--
24	9-29-70	9.0	152	13.3		--
25	9-29-70	5.0	25	12.5		--
26	10-3-70	7.0	186	13.7		--
27	10-24-70	6.0	291	12.0		?
28	10-22-70	2.0	537	12.0		--
29	9-25-70	4.0	20	13.1		--
30	9-12-71	1.0	2429	15.0		--
31	9-28-70	7.0	237	15.3		--
32	10-16-70	5.0	53	7.0	4.8	28
33	9-25-70	12.0	19	14.0		--
34	9-19-71	6.5	37	16.0		--
35	10-31-70	2.0	833	5.0		--
36	10-19-70	4.0	271	6.5		--
37	10-16-70	14.0	270	9.9		--
38	9-11-71	1.0	1196	14.0		--
39	9-25-70	17.0	39	14.0	11.0	28
40	9-28-70	6.5	234	11.0		--
41	10-21-70	2.0	1174	10.2		--
42	9-18-71	13.0	15	17.5		--
43	10-3-70	7.0	183	9.0		--
44	10-19-70	2.0	3874	7.7		--
45	10-19-70	7.0	655	9.3		--
46	9-9-71	3.0	666	14.0		--
47	9-27-70	8.0	178	12.0		--
48	9-28-70	3.0	447	10.0		--
49	9-29-70	6.0	182	13.5		--
50	10-21-70	3.5	438	9.0		--
51	10-19-70	4.0	296	8.4		--
52	10-21-70	0.9	13767	9.0		--
53	10-20-70	1.0	768	6.0		--
54	10-31-70	2.0	1751	5.0		--
55	9-26-70	5.5	27	12.1		--
56	10-22-70	2.2	669	10.0		--
57	10-3-70	6.5	153	13.6		--
58	10-20-70	13.0	15711	9.0		--
59	10-19-70	1.5	970	7.5		--
60	9-26-70	*40.0	80	12.0		?
61	10-29-70	5.0	436	10.0		?
62	9-28-70	3.0	307	10.0		--
63	10-20-70	2.4	1008	10.0		--
64	9-25-70	21.0	18	14.0	6.0	33
65	10-24-70	7.0	319	12.2		?
66	9-27-70	7.0	53	9.5		--
67	10-21-70	2.0	3392	10.1		--
68	9-26-70	10.0	28	11.3		--

TABLE 13. A correlation matrix for the physical and chemical measurements, including standing crop of algae (individuals per ml), in the study lakes in Minnesota. Calcium (Ca), magnesium (Mg), sodium (Na), potassium (K), sulfate (SO_4), chloride (Cl), and total alkalinity ($CaCO_3$) are given in meq/l for 63 lakes. Specific conductance (COND) in umho cm^{-1} at 25C, secchi-disc transparency in feet, and standing crop of phytoplankton (Algae) are based on 68 lakes.

	Ca	Mg	Na	K	SO_4	CL	$CaCO_3$	COND	COND [1]	Σ Ca+Mg	Secchi	Secchi [2]	Algae	Algae [1]
Ca	1.000	.246	.330	.159	.549	.426	.430	.316	.521	.327	-.346	.432	.125	-.068
Mg		1.000	.587	.562	.848	.575	.660	.705	.590	.996	-.239	.421	.440	.236
Na			1.000	.952	.704	.769	.330	.962	.600	.601	-.214	.530	.558	.256
K				1.000	.535	.731	.317	.948	.572	.561	-.202	.520	.632	.342
SO_4					1.000	.634	.550	.733	.625	.875	-.255	.461	.311	.077
CL						1.000	.258	.774	.424	.597	-.177	.594	.765	.265
$CaCO_3$							1.000	.469	.790	.681	-.419	.404	.254	.216
COND								1.000	.676	.714	-.223	.547	.598	.253
COND [1]									1.000	.621	-.510	.624	.396	.308
Σ Ca+Mg										1.000	-.263	.448	.439	.224
Secchi											1.000	-.511	-.240	-.348
Secchi [2]												1.000	.605	.464
Algae													1.000	.672
Algae [1]														1.000

1 Log_{10} transformation of specific conductance and number of algae/ml.
2 1/Secchi disc value.
___ Non-significance at P=0.05, ___ significance at P=0.05 but not at P=0.01.

TABLE 14. A comparison between specific conductance estimates of the present study and those of previous investigations. The final estimate for each lake represents the mean of all determinations. All measurements are reported as μmho cm^{-1} at 25C.

Lake No.	No. Obs.	Present Study	Previous Studies			Previous Studies($\bar{x}$)	Final Value
1	1	3160					3160
2	2	8560	7392			7392	7976
3	1	11467					11467
4	2	198	248			248	223
5	2	889	945			945	908
6	4	20	24	29	24	26	24
7	4	697	823	717	700	747	734
8	2	1360	836			836	1185
9	2	20	33			33	27
10	1	295					295
11	2	281	265			265	273
12	2	257	285			285	266
13	4	23	41	47	45	44	39
14	2	32	55			55	44
15	4	815	1141	780	719	880	854
16	2	51	57			57	54
17	1	14					14
18	1	31783					31783
19	2	210	265			265	238
20	4	725	1131	1090	1059	1093	1001
21	4	402	371	334	360	355	374
22	2	193	232			232	206
23	1	23428					23428
24	4	152	162	159	150	157	156
25	2	25	21			21	23
26	3	186	206	247		227	213
27	1	291					291
28	2	537	1042			1042	705
29	4	20	36	33	39	36	32
30	1	2429					2429
31	2	237	283			283	260
32	2	53	70			70	62
33	3	19	52	56		54	42
34	1	37					37
35	1	833					833
36	2	271	310			310	291
37	1	270	273			273	272
38	1	1196					1196
39	3	39	37	41		39	39
40	2	234	282			282	258
41	2	1174	1627			1627	1701
42	1	15					15
43	4	183	202	182	202	195	192
44	2	3874	3421			3421	3648
45	2	655	809			809	732
46	1	666					666
47	2	178	253			253	216
48	2	447	1324			1324	886
49	2	182	238			238	210
50	3	438	422	435		429	433
51	2	296	360			360	328
52	4	13767	17303	14080	11600	14328	14188
53	2	768	5565			5565	3167
54	2	1751	1893			1893	1822
55	4	27	68	78	83	76	64
56	4	659	642	783	672	699	707
57	2	153	180			180	167
58	2	15711	2648			2648	9180
59	1	970					970
60	4	80	81	90	96	89	89
61	1	436					436
62	2	307	1456			1456	881
63	4	1008	1438	1165	1050	1218	1165
64	4	18	40	38	41	40	34
65	1	319					319
66	2	53	69			69	61
67	2	3392	5385			5385	4389
68	4	28	46	42	46	45	41

TABLE 15. The concentration of major solutes (in meq/l) in 63 study lakes. Calcium (Ca), magnesium (Mg), sodium (Na), potassium (K), sulfate (SO_4), chloride (Cl), and total alkalinity ($CaCO_3$).

Lake No.	Ca	Mg	Na	K	SO_4	Cl	$CaCO_3$
2	3.60	204.	26.4	0.570	188.	7.27	13.6
3	0.180	29.5	133.	8.70	35.0	0.068	4.50
4	1.72	0.944	0.131	0.035	0.138	0.017	2.63
5	4.75	4.85	0.696	0.410	7.26	0.423	2.95
6	0.212	0.127	0.026	0.010	0.080	0.018	0.260
7	2.52	4.96	1.24	0.345	4.67	0.490	3.80
8	4.15	3.54	1.58	0.229	5.59	0.373	3.48
9	0.185	0.054	0.046	0.017	0.092	0.002	0.214
10	1.35	1.32	0.440	0.150	0.200	0.560	2.51
11	1.20	1.63	0.196	0.097	0.177	0.076	2.84
12	1.80	1.13	0.151	0.144	0.492	0.072	2.60
13	0.200	0.144	0.041	0.015	0.124	0.005	0.293
14	0.358	0.174	0.061	0.017	0.156	0.019	0.432
15	6.36	7.04	0.991	0.380	10.3	0.340	3.76
16	0.344	0.173	0.030	0.029	0.070	0.024	0.470
17	0.100	0.058	0.026	0.008	0.029	0.076	0.169
18	6.15	146.	328.	18.8	135.	120.	9.00
19	1.65	1.38	0.313	0.045	0.068	0.019	3.25
20	1.37	10.3	1.25	0.767	6.34	0.180	6.67
21	1.08	2.44	0.393	0.200	0.787	0.115	3.19
22	1.25	1.08	0.100	0.148	0.180	0.048	2.35
23	0.170	62.5	272.	14.0	79.2	0.082	8.0
24	1.20	0.534	0.161	0.026	0.060	0.010	1.82
26	1.08	0.984	0.134	0.029	0.141	0.028	2.07
27	1.35	1.32	0.440	0.150	0.200	0.560	2.51
28	2.69	2.88	1.38	0.148	2.96	1.30	2.65
29	0.186	0.128	0.037	0.010	0.134	0.003	0.235
30	0.100	10.1	23.9	1.41	3.73	0.794	6.00
31	1.39	1.82	0.278	0.044	0.055	0.030	3.45
32	0.403	0.214	0.023	0.038	0.061	0.007	0.640
33	0.270	0.195	0.077	0.013	0.101	0.016	0.449
34	0.390	0.192	0.065	0.020	0.042	0.031	0.570
36	1.86	1.69	0.192	0.052	0.124	0.034	3.44
37	1.29	1.80	0.163	0.044	0.065	0.025	3.21
38	0.465	2.46	8.78	0.545	1.58	0.268	6.00
39	0.270	.120	0.040	0.008	0.140	0.	0.200
40	1.70	1.23	0.139	0.051	0.250	0.006	2.80
41	7.21	6.91	4.38	0.578	12.7	3.04	3.66
42	0.110	0.058	0.022	0.008	0.042	0.034	0.120
43	1.30	0.665	0.156	0.052	0.123	0.010	1.98
44	2.31	65.3	20.0	0.226	62.8	3.97	16.8
45	2.35	5.43	1.31	0.241	3.39	0.395	5.59
46	2.92	1.90	1.70	0.360	1.23	0.710	4.00
47	1.73	0.883	0.164	0.052	0.109	0.023	2.70
48	12.4	8.23	0.491	0.156	10.2	0.130	10.7
49	1.83	0.613	0.117	0.027	0.093	0.021	2.46
50	1.80	2.79	0.320	0.160	1.02	0.099	3.48
51	1.37	2.38	0.516	0.123	0.492	0.167	3.61
52	17.8	42.2	207.	3.81	209.	50.4	4.68
53	3.10	6.02	1.48	0.415	2.66	0.380	7.58
55	0.500	0.280	0.090	0.020	0.288	0.	0.440
56	4.69	3.90	0.895	0.219	5.62	0.689	3.37
57	0.956	0.760	0.143	0.039	0.096	0.042	1.75
58	3.00	20.8	10.0	1.25	22.7	3.19	8.08
60	0.556	0.228	0.051	0.014	0.092	0.022	0.746
61	1.45	1.42	0.475	0.158	0.224	0.614	2.75
62	7.97	4.73	0.257	0.124	3.73	0.098	9.49
63	4.67	4.70	1.44	0.250	6.65	0.130	4.12
64	0.198	0.135	0.042	0.012	0.126	0.005	0.274
65	1.35	1.32	0.435	0.148	0.204	0.564	2.51
66	0.477	0.140	0.071	0.014	0.186	0.	0.481
67	2.50	50.1	18.1	0.206	61.2	2.34	7.72
68	0.250	0.147	0.061	0.012	0.100	0.012	0.372

TABLE 16. A multiple correlation analysis for the physical, chemical, and biological measurement that are used as gradient parameters in 63 study lakes in Minnesota. Total alkalinity (ALK) and calcium and magnesium (Ca + Mg) in meq/l, specific conductance (COND) and $\log_{10}$ specific conductance (COND) in umho cm^{-1} at 25C, secchi-disc transparency (SD) in feet, and the standing crop of phytoplankton (SC) in individuals/ml were used alternatively as the dependent variable. The significance of partial correlation coefficients is indicated for each of the independent variables.

Dependent Variable	Independent Variable	Significance of Regression	R
COND	ALK, Ca+Mg**	**	.71
COND	ALK, Ca+Mg**, 1/SD**	**	.76
COND	ALK, Ca+Mg**, 1/SD, SC*	**	.79
COND	ALK**, 1/SD**	**	.86
COND	ALK**, Ca+Mg, 1/SD**	**	.86
COND	ALK**, Ca+Mg, 1/SD**, SC	**	.86
ALK	SD, COND**	**	.79
ALK	Ca+Mg**, SD, COND**	**	.83
ALK	Ca+Mg**, SD, COND**, SC	**	.84
Ca+Mg	ALK**, COND**	**	.82
Ca+Mg	ALK**, 1/SD**, COND	**	.82
Ca+Mg	ALK**, 1/SD, COND**, SC	**	.82
SD	ALK, COND**	**	.51
SD	ALK, Ca+Mg, COND**	**	.52
SD	ALK, Ca+Mg, COND*, SC	**	.56
1/SD	ALK, COND**	**	.65
1/SD	ALK*, Ca+Mg, COND**	**	.66
1/SD	ALK, Ca+Mg, COND**, SC**	**	.75

** Significance at P = 0.01.

TABLE 17. A list of symbols used for gradient parameters and phytoplankton and diatom variables. Underlined expressions in text and Tables represent a $\log_{10}$ transformation of a gradient parameter or an algal variable. The units of measurement or the method of expression are given for each parameter and variable.

Symbol	Parameter or Variable
COND	Specific conductance in umho cm^{-1} at 25C
ALK	Total alkalinity as $CaCO_3$ in meq/l
ΣCa + Mg	Summation of calcium and magnesium in meq/l
SD	Secchi-disc transparency in feet
GP	A gradient parameter (specific conductance, secchi disc, ΣCa + Mg, total alkalinity, or standing crop of phytoplankton) or any combination of these parameters in multiple regression and correlation analysis
S	Number of species in net phytoplankton analysis, diatom analysis, or whole-water phytoplankton analysis
CPQ	Nygaard's (1949) compound phytoplankton quotient
DESMID S	Number of desmid taxa
A_s	Relative abundance of Araphidineae
C_s	Relative abundance of Centrales
A/C_s	Stockner's (1967, 1971) diatom ratio (abundance of A_s/abundance of C_s)
C or C_t	Number of species of Centrales
P	Number of species of Pennales
C/P	Nygaard's (1949) diatom ratio (number of species of Centrales/number of species of Pennales)
A or A_t	Number of species of Araphidineae
A/C_t	Modified version of Stockner's ratio (number of species of Araphidineae/number of species of Centrales)
SC	Standing crop of phytoplankton (estimate of the average number of individuals/ml in the euphotic zone of the lakes)
NET SC	Standing crop of net phytoplankton (estimate of the average number of individuals/ml, 60 u or more in greatest dimension, in the euphotic zone of the lakes)
NANNO SC	Standing crop of nannoplankton (estimate of the average number of individuals/ml, 60 u or less in greatest dimension, in the euphotic zone of the lakes)
H	Shannon's (1963) index of species diversity in bits/cells (diatoms) and bits/individual (phytoplankton). See equation 3
D	Margalef's (1968) index of species diversity. See equation 1
J	Evenness component of H diversity ($H/\log_2 S$)
NET H	Species diversity (H Shannon) in communities of net phytoplankton
NANNO H	Species diversity (H Shannon) in communities of nannoplankton

TABLE 18. A summary (range, mean $\bar{x}$, median m, and standard deviation s) of net phytoplankton analysis in the 68 study lakes in Minnesota. Number of species (S), Nygaard's compound phytoplankton quotient (CPQ), and the number of desmids (DESMID S).

Variable	Range	$\bar{x}$	m	s
S	4-79	39.2	38	20.2
CPQ	0.96-150	5.01	3.77	3.45
DESMID S	0-25	7.35	6.0	6.14

TABLE 19. A summary of net phytoplankton analysis for each of the 68 study lakes in Minnesota. Number of species (S), number of species in the numerator of the compound phytoplankton quotient (CPQ Numerator), number of desmids (DESMID S), Nygaard's compound phytoplankton quotient(CPQ), the number of bluegreen taxa, and the number of species of Chlorococcales.

Lake No.	S	CPQ Numerator	DESMID S	CPQ*	Bluegreen Taxa	Chlorococcales Taxa
1	34	25	3	8.33	7	8
2	21	9	0	9.00	4	2
3	10	9	0	9.00	4	3
4	68	38	14	2.70	16	21
5	13	10	0	10.0	2	2
6	78	31	25	1.24	9	18
7	20	14	3	4.67	6	7
8	16	11	2	5.50	2	4
9	78	26	24	1.08	11	8
10	41	26	5	5.20	12	10
11	38	24	6	4.00	12	10
12	38	29	5	5.80	12	14
13	55	27	10	2.70	11	10
14	59	31	10	3.10	12	10
15	14	13	1	13.0	3	2
16	37	24	5	4.80	10	6
17	37	14	7	2.00	7	2
18	15	13	1	13.0	6	4
19	69	36	11	3.27	15	13
20	31	17	6	2.83	8	7
21	39	26	6	4.33	12	10
22	56	34	10	3.40	16	11
23	4	3	0	3.00	2	1
24	48	33	5	6.60	10	16
25	72	39	16	2.44	10	21
26	40	27	7	3.86	9	12
27	32	23	3	7.67	9	8
28	36	30	2	15.0	5	16
29	55	18	17	1.06	9	3
30	15	10	1	10.0	8	2
31	50	35	6	5.83	11	17
32	20	11	2	5.50	6	3
33	77	38	15	2.53	16	15
34	54	23	16	1.44	9	8
35	29	20	3	6.67	4	7
36	47	29	8	3.63	10	16
37	25	15	1	15.0	6	4
38	9	7	0	7.00	2	0
39	60	22	23	0.960	14	7
40	50	25	13	1.92	8	12
41	19	13	0	13.0	4	1
42	51	18	16	1.13	4	6
43	70	41	14	2.93	11	23
44	46	18	2	9.00	6	4
45	60	38	12	3.17	14	18
46	17	11	1	11.0	3	2
47	58	36	5	7.20	14	16
48	45	28	8	3.50	7	12
49	65	39	10	3.90	16	19
50	39	20	10	2.00	8	8
51	46	28	9	3.11	12	12
52	8	5	2	2.50	2	2
53	13	10	3	3.33	2	5
54	10	8	1	8.00	2	0
55	32	17	6	2.83	7	6
56	31	23	4	5.75	4	11
57	36	32	7	4.57	11	16
58	15	9	2	4.50	3	3
59	35	22	6	3.67	4	10
60	31	15	5	3.00	3	1
61	39	24	8	3.00	10	9
62	44	28	8	3.50	7	12
63	7	5	2	2.50	2	2
64	57	30	12	2.50	15	10
65	32	20	5	4.00	9	8
66	79	42	21	2.00	14	18
67	25	19	4	4.75	8	6
68	63	29	18	1.61	14	10

*a zero term in the denominator of the compound phytoplankton quotient was arbitrarily assigned a value of 1.0.

TABLE 20. A correlation matrix for net phytoplankton indicators and gradient parameters in 63 study lakes in Minnesota. Phytoplankton variables are the number of species (S), Nygaard's compound phytoplankton quotient (CPQ), and the number of desmids (DESMID S). Gradient parameters are total alkalinity (ALK) and calcium + magnesium (ΣCa + Mg) in meq/l, specific conductance (COND) in umho cm^{-1}, secchi-disc transparancy (SC) in individuals/ml.

Parameter	Variable S	CPQ	DESMIDS
ALK	-.421	.342	-.487
COND[1]	-.442	.251	.338
	-.715	.499	-.708
ΣCa+Mg	-.348	.324	-.321
SD[2]	.409	-.326	.401
	-.575	.421	-.477
SC[1]	-.264	.469	-.261
	-.334	.445	-.324

1 Second row of coefficients is based on $\log_{10}$ transformation of the data.

2 Second row of coefficients is based on a reciprocal transformation of the data.

___ Non-significance at P = 0.05, ═══ significance at P = 0.05 but not at P = 0.01.

TABLE 21. A multiple correlation analysis between net phytoplankton indicators and combinations of gradient parameters in 63 study lakes in Minnesota. Phytoplankton variables are the number of species (S), Nygaard's compound phytoplankton quotient (CPQ), and the number of desmids (DESMID S). Gradient parameters are total alkalinity (ALK) and calcium + magnesium (ΣCa + Mg) in meq/l, $\log_{10}$ specific transparency (SD) in feet, and phytoplankton standing crop (SC) in individuals/ml.

Dependent Variable	Independent Variables	Significance of Regression	R
S	ALK**, 1/SD**	**	.61
S	ALK*, COND**	**	.74
S	COND**, SC	**	.72
S	1/SD, COND**	**	.73
S	ALK, Ca+Mg, 1/SD, COND**	**	.75
S	ALK, Ca+Mg, 1/SD, COND**, SC	**	.76
CPQ	ALK, 1/S**	**	.47
CPQ	ALK, COND**	**	.48
CPQ	ALK*, SC**	**	.53
CPQ	COND**, SC**	**	.57
CPQ	ALK, Ca+Mg, COND**	**	.49
CPQ	ALK, Ca+Mg, 1/SD, COND	**	.51
CPQ	ALK, Ca+Mg, 1/SD, COND, SC*	**	.58
DESMID S	1/S**, SC	**	.49
DESMID S	COND**, SC	**	.70
DESMID S	1/S, COND**, SC	**	.70
DESMID S	Ca+Mg, COND**	**	.70
DESMID S	ALK**, Ca+Mg, 1/S**	**	.58
DESMID S	ALK, Ca+Mg, 1/S, COND**, SC	**	.72

**Significance at P = 0.01.

TABLE 22. A summary of the most important diatom taxa in each of the 68 study lakes in Minnesota. Relative abundance is expressed as a per cent of the total count (N) in each sample. Key to generic abbreviations: S (Stephanodiscus), M (Melosira), F (Fragilaria), C (Cyclotella), A (Asterionella), Syn (Synedra), and T (Tabellaria).

No.	Lake	N	Species Abundance (%)
1.	Albert	742	S. hantzschii (52.0), S. astrea v. minutula (22.0), S. niagarae (10.2)
2.	Alkali	570	Chaetoceros muelleri (4.6), M. granulata (0.5), M. italica (0.2)
3.	Alkaline	572	Chaetoceros muelleri (60.7), M. italica (0.3), F. capucina (0.3)
4.	Ball Club	622	M. granulata (56.3), F. crotonensis (15.6), M. ambigua (15.9)
5.	Benton	681	S. niagarae (45.2), S. astrea v. minutula (14.9), C. stelligera (7.0)
6.	Big	555.5	A. formosa (87.3), T. flocculosa* (4.4), M. ambigua (3.4)
7.	Big Kandiyohi	526.5	S. niagarae (94.4), F. sp. (4.7)
8.	Big Stone	513	S. niagarae (97.5), M. granulata (0.4), M. ambigua (0.4)
9.	Burntside	542	A. formosa (49.4), T. flocculosa* (32.1), C. stelligera (2.2)
10.	Carman	541.5	M. ambigua (64.5), M. granulata (22.5), S. niagarae (6.6)
11.	Christmas	607.5	A. formosa (41.2), M. ambigua (5.3), F. pinnata (4.8)
12.	Clear	616	S. niagarae (64.3), M. granulata (33.0), F. crotonensis (1.6)
13.	Clearwater	507	A. formosa (45.2), T. flocculosa* (30.4), C. comta (6.0)
14.	Crane	548.5	M. granulata (40.7), A. formosa (18.8), M. ambigua (11.7)
15.	Dead Coon	588.5	C. pseudostelligera (47.8), S. niagarae (18.3), S. astrea v. minutula (5.9)
16.	Deming	597	F. crotonensis (54.1), C. sp. (5.0), T. flocculosa* (2.9)
17.	Dogfish	541	T. flocculosa* (81.2), A. formosa (9.6), C. stelligera (3.9)
18.	Eckelson	571.5	Chaetoceros muelleri (44.8), C. striata (1.8)
19.	Elk	595	F. crotonensis (79.0), S. astrea v. minutula (3.8), M. ambigua (7.1)
20.	Elk	515.5	F. crotonensis (79.0), Syn. acus v. angustissima (19.6), S. niagarae (1.1)
21.	Fish	560	S. niagarae (85.0), M. granulata (7.1), F. crotonensis (3.3)
22.	Frances	524	F. crotonensis (73.0), M. ambigua (16.8), A. formosa (4.8)
23.	George	512	Syn. pulchella v. lanceolata (11.5)
24.	Gladstone	540	F. crotonensis (51.9), A. formosa (26.7), Syn. acus v. angustissima (7.0)
25.	Goose	584.5	T. flocculosa* (29.9), F. crotonensis (12.0), Syn. rumpens v. familiaris (2.9)
26.	Green	579	F. capucina v. mesolepta (65.9), F. crotonensis (12.6), S. astrea v. minutula (8.9)
27.	Halsted	547	S. niagarae (69.8), Stephanodiscus astrea v. minutula (10.1), A. formosa (4.4)
28.	Heron	541.5	M. granulata v. angustissima (41.2), S. astrea v. minutula (29.5), M. ambigua (8.7)
29.	Iron	576	M. ambigua (26.8), F. crotonensis (27.1), T. flocculosa* (23.7)
30.	Isabel	504	Syn. acus (1.0), F. (capucina?)(0.6), F. capucina (0.3)
31.	Itasca	565.5	M. ambigua (43.1), F. crotonensis (24.7), M. granulata (21.6)
32.	Josephine	569	C. stelligera (63.4), F. flocculosa* (10.6), F. crotonensis (10.2)
33.	Kimball	606.5	A. formosa (35.3), M. ambigua (21.1), T. flocculosa* (17.4)
34.	Lamb	520	T. flocculosa* (26.7), C. stelligera (19.2), M. ambigua (18.3)
35	Lillian	775	F. sp. (19.2), s. astrea v. minutula (3.7), S. niagarae (2.9)
36.	Little Pine	544	M. ambigua (62.9), M. granulata (15,8), S. niagarae (14.5)
37.	Long	505	F. pinnata (8.3), C. Kützingiana (5.2), F. construens (5.0)
38.	Long	614	C. stelligera (5.0), S. sp. (4.4), C. striata (0.8)
39.	Loon	544	T. flocculosa* (81.8), A. formosa (12.1), F. crotonensis (5.3)
40.	Lower Red	553	M. ambigua (68.7), M. granulata (13.0), T. flocculosa* (5.4)
41.	Madison	756.5	S. niagarae (15.7), S. astrea v. minutula (13.4), S. hantzschii (11.6)
42.	Meander	530	A. formosa (34.9), M. ambigua (10.3), C. comta (10.3)
43.	Mille Lacs	529	M. ambigua (23.3), M. granulata (17.5), F. crotonensis (9.5)
44.	Mineral	860.5	F. crotonensis (12.4), Chaetoceros muelleri (10.2), M. granulata (3.5)
45.	Minnewaska	513.5	F. crotonensis (49.7), F. capucina v. mesolepta (38.1), M. ambigua (2.1)
46.	Mitchell	545	S. astrea v. minutula (59.4), M. granulata (15.2), S. niagarae (2.8)
47.	Moose	558.5	F. crotonensis (50.0), M. ambigua (35.8), M. granulata (5.4)
48.	Mud	681	M. ambigua (25.7), F. capucina v. mesolepta (22.6), A. formosa (16.2)
49.	Nokay	558.5	M. ambigua 970.7), M. granulata (24.9), T. flocculosa* (1.1)
50.	Pickerel	521	F. crotonensis (54.7), M. granulata (27.8), S. niagarae (9.5)
51.	Sallie	686.5	S. niagarae (31.8), F. construens v. binodis (15.8), M. granulata (6.4)
52.	Salt	598.5	Syn. sp. (19.7), S. niagarae (9.9), Syn. pulchella (3.5)
53.	Sanborn	542.5	S. astrea v. minutula (63.9), S. hantzschii (33.2), M. islandica v. helvetica (0.4)
54.	School Grove	623	Syn. ulna v. ramesi (49.9), F. capucina v. mesolepta (12.7), S. astrea v. minutula (2.8)
55.	Shagawa	574.5	F. crotonensis (60.7), M. ambigua (25.9), M. granulata (6.8)
56.	Shetek	583	M. italica v. tenuissima (83.4), M. granulata v. angustissima (7.4), S. acus (2.1)
57.	Spectacle	524.5	F. crotonensis (88.8), F. sp. (2.3), A. formosa (1.7)
58.	Spiritwood	571.5	S. niagarae (77.5), M. ambigua (0.7), S. sp. (0.3)
59.	Stinking	580.5	S. hantzschii (32.1), S. astrea v. minutula (19.0), M. granulata (16.5)
60.	Superior	647	C. ocellata (20.7), T. flocculosa* (19.4), F. crotonensis (17.6)
61.	Tanager	515.5	S. niagarae (81.3), M. granulata (6.6), M. ambigua (4.5)
62.	Thief	608.5	F. sp. (8.1), F. construens (6.7), F. pinnata (4.9)
63.	Traverse	506.5	S. niagarae (99.2), Syn. ulna v. impressa (0.2)
64.	Trout	575.5	T. flocculosa* (82.5), A. formosa (14.4), C. comta (1.4)
65.	Upper Minnetonka	553	M. ambigua (68.7), M. granulata (24.6), S. niagarae (5.8)
66.	Vermilion	628.5	M. ambigua (26.1), M. granulata v. angustissima (19.7), M. distans (12.9)
67.	Waubay	592	F. crotonensis (79.6), Chaetoceros muelleri (14.4), C. meneghiniana (0.1)
68.	Wilson	504.5	M. ambigua (26.6), A. formosa (25.6), M. islandica v. helvetica (5.7)

* Tabellaria flocculosa = T. flocculosa v. flocculosa

TABLE 23. A summary (range, mean $\bar{x}$, median m, and standard deviation s) of the computations of diatom ratios in the 68 study lakes in Minnesota. Stockner's ratio (A/C_s), Nygaard's ratio (C/P), and a modified version of Stockner's ratio (A/C_t).

Lake No.	A/C_s* Ratio	A/C_s* Value	A/C_t* Ratio	A/C_t* Value	C/P* Ratio	C/P* Value
1	0.90/92.9	0.010	4/8	0.500	8/22	0.364
2	0/5.40	0.010	0/4	0.250	4/16	0.250
3	0.30/61.0	0.005	1/2	0.500	2/21	0.095
4	23.9/76.0	0.314	7/6	1.17	6/9	0.667
5	1.80/77.3	0.023	8/6	1.33	6/34	0.176
6	91.7/7.40	12.4	2/4	0.500	4/8	0.500
7	4.70/94.4	0.050	1/1	1.00	1/6	0.167
8	0.20/98.7	0.002	1/4	0.250	4/4	1.00
9	86.9/7.30	11.9	4/7	0.571	7/11	0.636
10	6.30/93.8	0.067	3/4	0.750	4/3	1.333
11	52.2/7.5	6.96	7/2	3.50	2/24	0.083
12	2.10/97.5	0.022	3/3	1.00	3/6	0.500
13	82.9/9.00	9.21	10/7	1.43	7/26	0.269
14	24.2/73.0	0.332	6/11	0.545	11/13	0.846
15	1.10/80.6	0.014	2/9	0.222	9/15	0.600
16	62.2/12.8	4.86	4/9	0.444	9/24	0.375
17	92.1/5.60	16.4	3/4	0.750	4/13	0.308
18	0/46.6	0.010	0/2	0.500	2/11	0.182
19	80.5/18.8	4.282	3/8	0.375	8/7	1.14
20	98.6/1.40	70.4	2/2	1.00	2/2	1.00
21	3.70/95.2	0.039	3/4	0.750	4/7	0.571
22	80.0/19.6	4.08	4/6	0.667	6/6	1.00
23	11.5/0	100.	1/0	1.00	0/14	0.071
24	85.6/13.0	6.58	3/6	0.500	6/7	0.857
25	47.1/3.90	12.1	6/7	0.857	7/22	0.318
26	79.5/19.9	4.00	7/5	1.40	5/10	0.500
27	6.70/90.4	0.074	4/6	0.667	6/12	0.500
28	11.3/83.5	0.135	8/8	1.00	8/17	0.471
29	57.4/40.6	1.41	6/4	1.50	4/13	0.308
30	2.30/0	100.	4/0	4.00	0/26	0.038
31	29.2/69.7	0.419	5/7	0.714	7/11	0.636
32	24.6/66.5	0.370	7/3	2.33	3/24	0.125
33	67.4/26.0	2.59	7/7	1.00	7/21	0.333
34	35.0/54.2	0.646	4/6	0.667	6/12	0.500
35	24.2/10.6	2.28	12/8	1.50	8/65	0.123
36	6.80/93.2	0.073	5/3	1.667	3/6	0.500
37	49.4/11.5	4.30	13/5	2.600	5/57	0.088
38	0.90/11.2	0.080	2/6	0.333	6/20	0.300
39	99.2/0.700	142.	3/1	3.00	1/3	0.333
40	12.3/85.6	0.144	5/5	1.00	5/10	0.500
41	15.9/46.5	0.342	12/8	1.50	8/45	0.178
42	42.3/38.7	1.09	4/8	0.500	8/18	0.444
43	19.0/44.4	0.428	11/7	1.571	7/51	0.137
44	12.8/18.4	0.696	4/7	0.571	7/28	0.250
45	90.0/3.50	25.7	9/6	1.50	6/23	0.261
46	0.70/83.3	0.008	3/6	0.500	6/19	0.316
47	57.3/42.3	1.35	5/6	0.833	6/8	0.750
48	46.6/37.6	1.24	10/9	1.11	9.33	0.273
49	3.50/96.5	0.036	4/4	1.00	4/4	1.00
50	61.3/37.8	1.62	4/4	1.00	4/8	0.500
51	36.9/44.9	0.822	14/4	3.50	4/29	0.138
52	24.6/9.90	2.485	4/1	4.00	1/21	0.048
53	0/97.5	0.010	0.3	0.333	3/8	0.375
54	63.7/5.1	12.5	5/6	0.833	6/35	0.171
55	62.5/36.9	1.69	3/4	0.750	4/6	0.667
56	3.30/96.6	0.034	1/7	0.143	7/3	2.33
57	93.9/2.50	37.6	6/4	1.50	4/16	0.250
58	0.90/78.5	0.011	5/3	1.667	3/17	0.176
59	3.90/82.5	0.047	9/7	1.29	7/19	0.368
60	60.1/34.6	1.74	6/13	0.462	13/17	0.765
61	61.0/93.5	0.065	6/5	1.20	5/7	0.714
62	31.1/3.70	8.41	10/4	2.50	4/41	0.098
63	0.200/99.2	0.002	1/1	1.00	1/3	0.333
64	97.2/2.10	46.3	3/5	0.600	5/5	1.00
65	1.00/99.1	0.010	3/3	1.00	3/3	1.00
66	13.0/83.2	0.156	5/12	0.417	12/15	0.800
67	79.8/15.6	5.12	2/3	0.667	3/6	0.500
68	32.8/33.1	0.991	9/4	2.25	4/40	0.100

*A zero value in the numerator or denominator of a ratio has no meaning. For the A/C_s ratio, zero abundance of Araphidineae has been given a ratio value of 1/100 (A/C_s = 0.010); zero abundance of Centrales has been assigned a ratio value of 100/1 (A/C_s = 100). For the A/C_t and C/P ratios, a zero value in the numerator or denominator has been assigned arbitrarily an occurrence of 1.0 species in that group.

TABLE 24. A summary (range, mean $\bar{x}$, median m, and standard deviation s) of diatom ratio analysis and the number of taxa (S) and sample size (N) in 68 study lakes in Minnesota. Diatom ratios are Stockner's (A/C_s), Nygaard's (C/P), and a modified version of Stockner's ratio (A/C_t).

Variable	Range	$\bar{x}$	m	s
A/C_s	0.002-141.7	9.834	0.760	25.4
A/C_t	0.140-4.0	1.146	1.000	0.88
C/P	0.038-2.33	0.478	0.375	0.38
No. Taxa	4-73	22.3	19.0	14.2
No. Individuals	504-860.5	577.9	563	67.7

TABLE 25. A correlation matrix for diatom ratios and gradient parameters in 63 study lakes in Minnesota. Diatom ratios are Stockner's (A/C_s), Nygaard's (C/P), and a modified version of Stockner's ratio (A/C_t). Gradient parameters are total alkalinity (ALK) and calcium + magnesium (ΣCa + Mg) in meq/l, specific conductance (COND) in umho cm^{-1} at 25C, secchi-disc transparency (SD) in feet, and phytoplankton standing crop in individuals/ml.

Parameter	Variable		
	A/C_s	A/C_t	C/P
ALK	.023	-.015	-.236
COND[1]	.159	.011	-.270*
	.021	.058	-.223
ΣCa + Mg	.003	-.095	-.222
SD[2]	.142	-.020	.150
	-.064	-.038	-.131
SC[1]	.048	-.030	-.129
	.095	-.218	-.022

[1] Second row of coefficients is based on $\log_{10}$ transformation of the data

[2] Second row of coefficients is based on a reciprocal transformation of the data

* Significance at P = 0.05, ** significance at P = 0.01

TABLE 26. A multiple correlation analysis between diatom and combinations of gradient parameters in 63 study lakes in Minnesota. Diatom ratios are Stockner's (A/C_s), Nygaard's (C/P), and a modified version of Stockner's ratio (A/C_t). Gradient parameters are total alkalinity (ALK) and calcium + magnesium (ΣCa + Mg) in meq/l, specific conductance (COND) and $\log_{10}$ specific conductance (COND) in umho cm^{-1} at 25C, secchi-disc transparency (SD) in feet, and $\log_{10}$ phytoplankton standing crop (SC) in individuals/ml.

Dependent Variable	Independent Variables	Significance of Regression	R
A/C_s	SD, COND	NS	.24
A/C_s	SD, SC	NS	.22
A/C_s	ALK, Ca+Mg, COND	NS	.23
A/C_s	ALK, Ca+Mg, SD, SC	NS	.24
A/C_s	ALK, Ca+Mg, SD, COND, SC	NS	.32
C/P	SD, SC	NS	.13
C/P	SD, COND	NS	.29
C/P	COND*, SC	NS	.29
C/P	ALK, Ca+Mg, SD, COND	NS	.31
C/P	ALK, Ca+Mg, SD, SC	NS	.26
C/P	ALK, Ca+Mg, SD, COND, SC	NS	.32
A/C_t	1/SD, SC	NS	.23
A/C_t	1/SD, COND	NS	.13
A/C_t	COND, SC*	NS	.26
A/C_t	ALK, Ca+Mg, 1/SD, COND	NS	.22
A/C_t	ALK, Ca+Mg, COND, SC	NS	.26
A/C_t	ALK, Ca+Mg, 1/SD, COND, SC	NS	.32

NS = Non-significance at P = 0.05

TABLE 27. A summary (range, mean $\bar{x}$, median m, and standard deviation s) of diatom ratio component analysis in 63 study lakes in Minnesota. The components are relative abundance of Araphidineae (A_s), relative abundance of Centrales (C_s), number of species of Araphidineae (A_t), number of species of Centrales (C), and the number of species of Pennales (P).

Variable	Range	$\bar{x}$	s
A_s	0.200-99.2	38.9	33.7
C_s	0.700-99.1	47.3	35.8
A_t	1-14	5.29	3.16
C	1-13	5.48	2.58
P	2-65	17.3	13.8

TABLE 28. A correlation matrix for the components of the diatom ratios and gradient parameters in 63 study lakes in Minnesota. The components are relative abundance of Araphidineae (A_s), relative abundance of Centrales (C_s), number of species of Araphidineae (A_t), number of species of Centrales (C), and the number of species of Pennales (P). Gradient parameters are total alkalinity (ALK) and calcium + magnesium (ΣCa + Mg) in meq/l, secchi-disc transparency (SD) in feet, specific conductance (COND) in umho cm^{-1} at 25C, and phytoplankton standing crop (SC) in individuals/ml.

Parameter	Variable A_s	C_s	A_t	C_t	P
ALK	-.348**	-.107	-.133	-.215	.154
COND[1]	-.283*	-.122	-.297*	-.364**	-.055
	-.522**	.098	-.234	-.388**	.064
ΣCa+Mg	-.259*	-.188	-.274*	-.225	.022
SD[2]	.490**	-.277*	.212	.374**	.015
	-.467**	.150	-.345**	-.272*	-.027
SC[1]	-.241	.010	-.162	-.138	-.015
	-.254*	.025	-.257*	-.000	.014

[1] Second row of coefficients is based on $\log_{10}$ transformation of the data
[2] Second row of coefficients is based on a reciprocal transformation of the data
* Significance at P = 0.05, ** significance at P = 0.01

TABLE 29. A summary of the most important phytoplankton species in each of 68 study lakes in Minnesota. Standing crop of phytoplankton (SC) is given as individuals per ml. The percentage contribution of each species to SC in the lakes is given in parentheses. An underlined percentage value indicates that the taxon is a nannoplankter (<60 u in greatest dimension). (* after SC and taxon indicates a state of "bloom"). Z in parentheses after a lake indicates a zooplankton "bloom".

No.	Lake	SC	Species Abundance (%)
1.	Albert	54,453*	Stephanodiscus astrea v. minutula + S. hantzschii (48.3), Oscillatoria agardhii (33.2)*, Ankistrodesmus falcatus (3.9)
2.	Alkali	3,070	Ochromonas sp. (47.5), Ochromonas sp. (18.8), Amphora pusilla (5.0)
3.	Alkaline	9,959	Cryptomonas sp. (23.1), Ochromonas sp. (19.3), Chromulina sp. (17.3), Botryococcus braunii (10.1)
4.	Ball Club	651	Chroomonas acuta (28.0), Ochromonas sp. (13.3), Chromulina sp. (11.8), Melosira granulata (5.9)
5.	Benton (Z)	1,960*	Aphanizomenon flos-aquae (25.7)*, Ochromonas sp. (25.4), Cyclotella stelligera + Stephanodiscus astrea v. minutula (15.6)
6.	Big	2,092	Ochromonas sp. (17.0), Chromulina sp. (13.8), O. sp. (13.3), Chroomonas acuta (10.6)
7.	Big Kandiyohi	1,865	Chroomonas acuta (51.8), Stephanodisucs niagarae (13.6), Cryptomonas sp. (13.3), Cryptomonas sp. (6.2)
8.	Big Stone	3,870	Stephanodiscus niagarae (42.7), Aphanizomenon flos-aquae (41.5), Chroomonas acuta (4.5)
9.	Burntside	1,992	Ochromonas sp. (22.6), Chromulina sp. (19.7), O. sp. (19.2), Chroomonas acuta (13.0)
10.	Carman	4,673	Aphanizomenon flos-aquae (61.4), Chroococcus dispersus (10.5), Oscillatoria agardhii (8.4), Ochromonas sp. (7.3)
11.	Christmas	922	Chroomonas acuta (56.0), Aphanizomenon flos-aquae (7.3), Katablepharis ovalis (7.3), Asterionella formosa (3.1)
12.	Clear	614	Stephanodiscus astrea v. minutula (27.5), Stephanodiscus niagarae (27.2), Chroomonas sp. (9.4), Microcystis aeruginosa (8.4)
13.	Clearwater	644	Chroomonas acuta (29.0), Ochromonas sp. (26.0), Ochromonas sp. (19.3), Katablepharis ovalis (3.0)
14.	Crane	1,890	Chroomonas acuta (33.7), Ochromonas sp. (12.9), O. sp. (12.7), Katablepharis ovalis (4.6)
15.	Dead Coon	21,153*	Aphanizomenon flos-aquae (35.9)*, Cyclotella pseudostelligera + Stephanodiscus astrea v. minutula (29.7), Ankistrodesmus falcatus (23.4)
16.	Deming	10,194	Lyngbya limnetica (34.7), Ochromonas sp. (16.4), Anabaena sp. (14.5), Chromulina sp. (13.6)
17.	Dogfish	5,050	Ochromonas sp. (21.1), Chromulina sp. (19.6), C. sp. (14.3), Merismopedia glauca (6.7)
18.	Eckelson	403,893*	Chaetoceros muelleri (59.4)*, Rhabdoderma irregulare (12.3), Nitzschia acicularis (6.8)
19.	Elk	672	Ochromonas sp. (28.5), Ochromonas sp. (19.9), Anabaena sp. (13.9), Dinobryon divergens (6.4)
20.	Elk	4,381	Chroomonas acuta (29.6), Comphosphaeria lacustris (22.8), Ochromonas sp. (21.7)
21.	Fish	622	Stephanodiscus niagarae (47.2), Microcystis aeruginosa (13.0), Chlamydomonas sp. (6.1), Chroomonas acuta (3.8)
22.	Francis	3,553	Chroomonas acuta (63.6), Tetraedron lunula (14.0), Cyclotella stelligera (7.5)
23.	George	12,583	Nitzschia frustulum (50.5), Nitzschia fonticola (29.9), Botryococcus braunii (5.3)
24.	Gladstone	2,525	Ochromonas sp. (18.6), O. sp. (17.5), Chroomonas acuta (15.2)
25.	Goose	9,533	Lyngbya limnetica (46.0), Ochromonas sp. (16.0), Chromulina sp. (14.8)
26.	Green	2,711	Stephanodiscus astrea v. minutula (15.9), Melosira granulata (9.9), Coelastrum microporum (8.5)
27.	Halsted	4,118	Aphanizomenon flos-aquae (81.1), Stephanodiscus niagarae (9.0), Oscillatoria agardhii (3.0)
28.	Heron	189,588*	Stephanodiscus astrea v. minutula (38.6)*, S. hantzschii (25.7)*, Synedra nanna (11.2), Oscillatoria agardhii (8.6), Chroomonas acuta (8.5)
29.	Iron	1,085	Anabaena planktonica (26.5), Chromulina sp. (12.4), Chroomonas acuta (7.1)
30.	Isabel	149,256	Lyngbya contorta (90.8), Lyngbya limnetica (1.8), Ochromonas sp. (1.5)
31.	Itasca	4,343	Chroomonas acuta (18.1), Chroomonas sp. (14.6), Ochromonas sp. (13.6), O. sp. (13.1)
32.	Josephine	9,507	Ochromonas sp. (17.3), Oscillatoria redecki (13.9), Anabaena sp. (13.7) Chroomonas acuta (9.7)

33.	Kimball	1,010	Ochromonas sp. (16.2), Katablepharis ovalis (14.3), O. sp. (13.3), Chroomonas acuta (11.4)
34.	Lamb	8,076	Chromulina sp. (20.4), Ochromonas sp. (19.2), Chroomonas sp. (8.5), Katablepharis ovalis (4.7)
35.	Lillian	9,921	Ankistrodesmus falcatus (44.0), Ochromonas sp. (0.7), Cryptomonas sp. (8.6), Chroomonas acuta (7.9)
36.	Little Pine	1,158	Stephanodiscus niagarae (34.5), Melosira ambigua (18.4), M. granulata (11.2), Aphanizomenon flos-aquae (7.5)
37.	Long	3,179	Lyngbya limnetica (54.5), Chroomonas acuta (16.3), Ochromonas sp. (15.2)
38.	Long	70,988	Lyngbya contorta (37.7), Aphanizomenon flos-aquae (32.0), Ankistrodesmis falcatus (6.6)
39.	Loon	2,246	Chromulina sp. (30.3), Ochromonas sp. (24.8), Chroomonas acuta (16.2), Tabellaria flocculosa v. flocculosa (5.7)
40.	Lower Red	1,157	Ochromonas sp. (16.6), Ochromonas sp. (15.8), Chroomonas acuta (10.8), Nitzschia palea (6.6)
41.	Madison	5,077*	Aphanizomenon flos-aquae (85.1)*, Anabaena sp. (8.5), Chroomonas acuta (2.5)
42.	Meander	2,694	Chromulina sp. (23.8), Ochromonas sp. (15.3), O. sp. (13.6)
43.	Mille Lacs	23,798	Chroomonas acuta (53.5), Chroomonas (10.9), Chlamydomonas sp. (8.9), Katablepharis ovalis (4.9)
44.	Mineral	9,657	Anabaena sp. (50.5), Selanastrum muticum (15.4), Tetraedron trigonum (10.2)
45.	Minnewaska	7,383	Chroomonas acuta (46.6), Lyngbya limnetica (11.3), Ochromonas sp. (4.8)
46.	Mitchell	26,489	Anabaena sp. (19.0), Stephanodiscus astrea v. minutula (18.4), Chroomonas sp. (16.8)
47.	Moose	987	Chroomonas acuta (37.4), Chromulina sp. (22.3), Ochromonas sp. (17.5)
48.	Mud	1,287	Chroomonas acuta (28.3), Aphanizomenon flos-aquae (13.9), Ochromonas sp. (11.2)
49.	Nokay	3,941	Aphanizomenon flos-aquae (18.0), Ochromonas sp. (12.9), Ochromonas sp. (12.5), Chroomonas acuta (8.0)
50.	Pickerel	2,902	Chroomonas acuta (8.4), Mallomonas sp. (8.0), Aphanizomenon flos-aquae (7.0)
51.	Sallie	2,585	Chroomonas acuta (27.0), Stephanodiscus niagarae (26.9), Stephanodiscus astrea v. minutula (12.6)
52.	Salt (Z)	266	Ochromonas sp. (32.4), O. sp. (28.8), Navicula lanceolata (10.8)
53.	Sanborn	53,955	Stephanodiscus hantzschii (61.2), Stephanodiscus astrea v. minutula (32.5), Didymocystis sp. (2.9)
54.	School Grove	1,714	Chroomonas acuta (67.0), Chroomonas sp. (19.0), Schroederia setigera (5.0)
55.	Shagawa	4,649	Katablepharis ovalis (21.9), Cryptomonas sp. (15.1), Chroomonas acuta (11.8)
56.	Shetek	27,158*	Oscillatoria agardhii (70.2)*, Stephanodiscus hantzschii (7.8), Stephanodiscus astrea v. minutula (7.0)
57.	Spectacle	4,516	Ochromonas sp. (24.7), Chromulina sp. (20.0), C. sp. (16.2), Chroomonas acuta (14.9), Katablepharis ovalis (8.1)
58.	Spiritwood (Z)	89	Coelosphaerium sp. (35.0), Chroomonas sp. (18.9), Chroomonas sp. (18.0), Oscillatoria limosa (7.9)
59.	Stinking	57,480	Stephanodiscus hantzschii (34.4), Stephanodiscus astrea v. minutula (26.1), Oscillatoria agardhii (9.6)
60.	Superior	5,296	Synechococcus elongatus (20.7), Chromulina spp. + Ochromonas spp. (10.3), Chroomonas acuta (7.2), Dinobryon sociale (5.8)
61.	Tanager	997	Aphanizomenon flos-aquae (25.9), Stephanodiscus niagarae (32.9), Anabaena spiroides v. crassa (9.7)
62.	Thief	1,220	Chroomonas sp. (47.1), Chroomonas acuta (22.8), Cocconeis placentula (3.1)
63.	Traverse	25,480	Aphanizomenon flos-aquae (74.5), Anabaena sp. (12.5), Stephanodiscus niagarae (9.2)
64.	Trout	2,058	Ochromonas sp. (43.3), Chromulina sp. (28.1), Chroomonas acuta (5.7), Katablepharis ovalis (3.6)
65.	Upper Minnetonka	4,908	Oscillatoria agardhii (48.7), Aphanizomenon flos-aquae (20.9), Ochromonas sp. (11.9)
66.	Vermilion	5,736	Ochromonas sp. (18.6), O. sp. (10.0), Melosira distans (10.0), Chroomonas acuta (9.7)
67.	Waubay	62,615*	Anabaena sp. (66.5)*, Fragilaria crotonensis (18.8), Ankistrodesmus falcatus (9.6)
68.	Wilson	1,069	Chroomonas acuta (24.7), Katablepharis ovalis (23.3), Ochromonas sp. (12.1)

TABLE 30. A summary (range, mean $\bar{x}$, median m, and standard deviation s) of quantitative phytoplankton indicators in 68 study lakes in Minnesota. The phytoplankton variables are the standing crop of phytoplankton (SC), the standing crop of net phytoplankton (NET SC), and the standing crop of nannoplankton (NANNO SC). NET SC and NANNO SC are also expressed as a per cent of SC. All computations are based on individuals/ml.

Variable	Range	$\bar{x}$	m	s
SC	89-402,893	20,105.	3,906.	56407.
SC[1]	1.949-5.606	3.650	3.592	0.687
NET SC	8-305,794	11,887.	9725.	41,502
NET SC[1]	0.889-5.485	3.001	2.988	0.970
NANNO SC	75-129,522	8,218.	1872	20,881.
NANNO SC[1]	1.874-5.112	3.330	3.272	0.655
% NET SC	0.0-97.4	37.9	31.0	30.24
% NANNO SC	2.6-100.	62.1	69.0	30.25

[1] Statistics based on logarithmic values.

TABLE 31. A correlation matrix for quantitative phytoplankton indicators and gradient parameters in 63 study lakes in Minnesota. Phytoplankton variables are the standing crop of phytoplankton (SC), the standing crop of net phytoplankton (NET SC), the standing crop of nannoplankton (NANNO SC), and the per cent of NET SC and NANNO SC. All computations are based on individuals/ml. Gradient parameters are total alkalinity (ALK) and calcium + magnesium (ΣCa + Mg), specific conductance (COND) in umho cm^{-1} at 25C, secchi-disc transparency (SD) in feet, and phytoplankton standing crop (SC) in individuals/ml.

	Variable							
Parameter	SC	SC[1]	NET SC	NET SC[1]	NANNO SC	NANNO SC[1]	%NET SC	%NANNO SC
ALK	.254	.216	.274	.161	.143	.098	1.97	-.197
COND[1]	.598	.253	.633	.212	.359	1.56	.170	-.170
	.396	.308	.395	.287	.284	.116	.314	-.313
ΣCa+Mg	.439	.224	.467	.134	.259	.176	.070	-.070
SD[2]	-.240	-.348	-.215	-.308	-.220	-.212	-.249	.249
	.605	.464	.606	.380	.430	.320	.288	-.288
SC[1]	1.000	.672	.954	.569	.805	.566	.250	-.250
		1.000	.592	.828	.637	.825	.360	-.360

[1] Second row of coefficients is based on $\log_{10}$ transformation of the data.
[2] Second row of coefficients is based on a reciprocal transformation of the data.
___ Non-significance at P=0.05, ___ significance at P=0.05 but not at P=0.01.

TABLE 32. A multiple correlation analysis between the standing crop of phytoplankton (SC) and $\log_{10}$ standing crop of phytoplankton (SC) based on individuals/ml and combinations of gradient parameters in 63 study lakes in Minnesota. Gradient parameters are total alkalinity (ALK) and calcium + magnesium (ΣCa + Mg) in meq/l, specific conductance (COND) and $\log_{10}$ specific conductance (COND) in umho cm^{-1} at 25C, secchi-disc transparency (SD) in feet, and phytoplankton standing crop (SC) in individuals/ml.

Dependent Variable	Independent Variables	Significance of Regression	R
SC	ALK, Ca+Mg**	**	.44
SC	1/S, COND**	**	.69
SC	Ca+Mg, COND**	**	.60
SC	ALK, Ca+Mg, 1/S**	**	.65
SC	Ca+Mg, 1/S**, COND**	**	.69
SC	ALK, Ca+Mg, 1/S*, COND**	**	.69
SC	1/S**, COND	**	.47
SC	ALK,1/S**, COND	**	.48
SC	ALK, Ca+Mg, COND	NS	.32
SC	ALK, Ca+Mg, 1/S**	**	.48
SC	ALK, Ca+Mg, 1/S**, COND	**	.48

NS = Non-significance at P = 0.05

** Significance at P = 0.01

TABLE 33. A multiple correlation analysis between the standing crop of net phytoplankton (NET SC) and nannoplankton (NANNO SC) in individuals/ml and combinations of gradient parameters in 63 study lakes in Minnesota. The gradient parameters are total alkalinity (ALK) and calcium + magnesium (ΣCa + Mg) in meq/l, specific conductance (COND) and $\log_{10}$ specific conductance (COND) in umho cm^{-1} at 25C, and secchi-disc transparency (SD) in feet.

Dependent Variable	Independent Variables	Significance of Regression	R
NET SC	ALK, Ca+Mg**	**	.47
NET SC	ALK, COND**	**	.63
NET SC	Ca+Mg, COND**	**	.63
NET SC	1/SD**, COND**	**	.71
NET SC	ALK, Ca+Mg, 1/SD**	**	.66
NET SC	ALK, Ca+Mg, 1/SD**, COND**	**	.71
NET SC	ALK, Ca+Mg	NS	.16
NET SC	ALK, 1/SD	**	.40
NET SC	ALK, COND*	*	.33
NET SC	ALK, Ca+Mg, COND	NS	.33
NET SC	ALK, 1/SD, COND	*	.41
NET SC	ALK, Ca+Mg, 1/SD*, COND	*	.42
NANNO SC	ALK, Ca+Mg	NS	.26
NANNO SC	ALK, COND**	*	.38
NANNO SC	ALK, 1/SD**	**	.43
NANNO SC	1/S, COND	**	.46
NANNO SC	ALK, Ca+Mg, 1/SD*, COND	**	.47
NANNO SC	ALK, COND	NS	.17
NANNO SC	ALK, 1/SD*	*	.32
NANNO SC	Ca+Mg, COND	NS	.19
NANNO SC	1/SD*, COND	*	.32
NANNO SC	LAK, Ca+Mg, 1/SD*	NS	.33
NANNO SC	ALK, 1/S*, COND	NS	.32
NANNO SC	ALK, Ca+Mg, 1/SD*, COND	NS	.33

NS = Non-significance, * significance at P = 0.05, ** significance at P = 0.01.

TABLE 34. A summary (range, mean $\bar{x}$, median m, and standard deviation s) of species diversity in diatom communities in 68 study lakes in Minnesota. Community properties are Margelef's index (D), Shannon's index (H), in bits cell, the evenness component of H diversity (J), and the number of species (S).

Variable	Range	$\bar{x}$	m	s
D	0.476-10.8	3.367	2.994	2.205
H	0.079-4.566	2.207	2.149	1.084
J	0.040-0.777	0.500	0.510	0.169
S	4-73	22.3	19.0	14.2

TABLE 35. A correlation matrix for diatom species diveristy and gradient parameters in 63 study lakes in Minnesota. Community properties are Margalef's index (D), Shannon's index (H) in bits per cell, the evenness component of diversity (J), and the number of species (S). Gradient parameters are total alkalinity (ALK) and calcium + magnesium (ΣCa + Mg) in meq/l, specific conductance (COND) in umho cm^{-1} at 25C, secchi disc transparency (SD) in feet, and phytoplankton standing crop (SC) in individuals/ml.

Parameter	Variable D	H	J	S
ALK	.072	.105	.105	.099
COND[1]	-.094	-.029	.019	-.089
	-.001	-.042	-.079	.025
ΣCa+Mg	-.037	.073	.120	-.026
SD[2]	.032	.045	.067	.017
	-.055	-.087	-.143	-.042
SC[1]	-.049	.033	.032	-.048
	.051	.069	.065	.051

[1] Second row of coefficients is based on $\log_{10}$ transformation of the data

[2] Second row of coefficients is based on a reciprocal transformation of the data

* Significance at P = 0.05, ** significance at P = 0.01

TABLE 36. A multiple correlation analysis between species diversity indices in diatom communities and combinations of gradient parameters in 63 study lakes in Minnesota. Community properties are Margalef's index (D), Shannon's index (H) in bits/cell, the evenness component of diversity (J), and the number of species (S). The gradient parameters are total alkalinity (ALK), and calcium + magnesium (Ca + Mg) in meq/l, specific conductance (COND) and $\log_{10}$ specific conductance (COND) in umho cm^{-1} at 25C, secchi disc transparency (SD) in feet, and $\log_{10}$ phytoplankton standing crop (SC) in individuals/ml.

Dependent Variable	Independent Variables	Significance of Regression	R
H	1/SD, SC	NS	.15
H	COND, SC	NS	.07
H	ALK, Ca+Mg, 1/SD, COND	NS	.26
H	ALK, Ca+Mg, 1/SD, SC	NS	.23
H	ALK, Ca+Mg, 1/SD, COND, SC	NS	.27
D	1/SD, SC	NS	.12
D	COND, SC	NS	.10
D	ALK, Ca+Mg, 1/SD, COND	NS	.18
D	ALK, Ca+Mg, 1/SD, SC	NS	.19
D	ALK, Ca+Mg, 1/SD, COND, SC	NS	.19
J	1/SD, SC	NS	.21
J	COND, SC	NS	.09
J	ALK, Ca+Mg, 1/SD, COND	NS	.31
J	ALK, Ca+Mg, COND*, SC	NS	.29
J	ALK, Ca+Mg, 1/SD, COND, SC	NS	.33
S	1/SD, COND	NS	.09
S	ALK, Ca+Mg, COND	NS	.18
S	ALK, Ca+Mg, 1/SD, COND	NS	.20
S	ALK, Ca+Mg, COND, SC	NS	.18
S	ALK, Ca+Mg, 1/SD, COND, SC	NS	.21

NS = Non-significance at P = 0.05

TABLE 37. A summary (range, mean $\bar{x}$, median m, and standard deviation s)of species diversity in phytoplankton communities and in communities of net phytoplankton and nannoplankton. Community properties are Margalef's index (D), Shannon's (H) in bits/individual, the evenness component of diversity (J), and the number of species (S). Net phytoplankton diversity and nannoplankton diversity are indicated as NET H and NET S and NANNO H and NANNO S, respectively.

Variable	Range	$\bar{x}$	m	s
D	1.241-12.38	5.558	5.380	2.349
H	0.805-4.622	2.915	2.908	0.879
J	0.178-0.811	0.580	0.587	0.141
NET H	0.0-4.274	2.252	2.389	1.097
NANNO H	1.147-3.769	2.562	2.541	0.627
S	10-70	34.3	35.5	13.159
NET SC	1-35	17.1	18.0	8.176
NANNO SC	4-37	17.2	17.5	6.691

TABLE 38. A correlation matrix for species diversity in phytoplankton communities and in communities of net phytoplankton and nannoplankton in 63 study lakes in Minnesota. Community properties are Margalef's index (D), Shannon's index (H) in bits/individual, the evenness component of H diversity (J), and the number of species (S). Shannon's index H and the number of species (S) for net phytoplankton and nannoplankton communities are indicated as NET H and NET S and NANNO H and NANNO S, respectively.

	Variable							
PARAMETER	D	H	J	NET H	NANNO H	NET S	NANNO S	S
ALK	-.281*	-.340**	-.240	-.373**	-.258**	-.334**	-.326**	-.379**
COND[1]	-.345**	-.206	-.009	-.238	-.158	-.349**	-.354**	-.397**
	-.562**	-.500**	-.280*	-.519**	-.422**	-.531**	-.605**	-.638**
Ca+Mg	-.200	-.181	-.069	-.181	-.104	-.273*	-.226	-.289*
SD[2]	.421**	.346**	.249*	.480**	.109	.346**	.293*	.364**
	-.475**	-.407**	-.407**	-.506**	-.054	-.476**	-.322**	-.459**
SC[1]	-.253	-.243*	-.228	-.246*	-.135	-.166	-.148	-.179
	-.371	-.370**	-.444**	-.424**	-.126	-.195	-.005	-.124

[1] Second row of coefficients is based on $\log_{10}$ transformation of the data

[2] Second row of coefficients is based on a reciprocal transformation of the data

* Significance at P = 0.05, ** significance at P = 0.01

TABLE 39. A multiple correlation analysis between species diversity in phytoplankton communities and combinations of gradient parameters in 63 study lakes in Minnesota. The indices are Margalef's index (D) and Shannon's index (H). The gradient parameters are total alkalinity (ALK) and calcium + magnesium (Ca + Mg) in meq/l, $\log_{10}$ specific conductance (COND) in umho cm^{-1} at 25C, secchi-disc transparency (SD) in feet, and $\log_{10}$ phytoplankton standing crop (SC) in individuals/ml.

Dependent Variable	Independent Variables	Significance of Regression	R
D	ALK, 1/SD**	**	.49
D	ALK*, COND**	**	.59
D	Ca+Mg, 1/SD**	**	.49
D	1/SD, COND**	**	.57
D	ALK*, 1/SD, COND**	**	.61
D	1/SD, COND**, SC*	**	.62
D	ALK*, 1/SD, COND**, SC*	**	.65
D	ALK, Ca+Mg, 1/SD, COND**, SC*	**	.66
H	ALK, 1/SD**	**	.52
H	1/SD, COND**	**	.52
H	1/SD*, SC	**	.47
H	COND**, SC*	**	.56
H	ALK*, Ca+Mg, 1/SD*	**	.48
H	ALK*, Ca+Mg, COND**	**	.53
H	ALK, 1/SD, COND*, SC	**	.56
H	ALK, Ca+Mg, 1/SD, COND*, SC	**	.59

** Significance at P = 0.01

TABLE 40. A multiple correlation analysis between species diversity in phytoplankton communities and combinations of gradient parameters in 63 study lakes in Minnesota. The indices are species number (S) and the evenness component of H diversity (J). The gradient parameters are total alkalinity and calcium + magnesium (ΣCa + Mg) in meq/l, $\log_{10}$ specific conductance (COND) in umho cm^{-1} at 25C, secchi-disc transparency (SD) in feet, and phytoplankton standing crop (SC) and $\log_{10}$ phytoplankton standing (SC) in individuals/ml.

Dependent Variable	Independent Variables	Significance of Regression	R
S	ALK, 1/SD**	**	.53
S	ALK*, COND**	**	.68
S	1/SD, COND**	**	.65
S	1/SD**, SC	**	.50
S	ALK, Ca+Mg, COND**	**	.68
S	1/SD, COND**, SC	**	.67
S	ALK, 1/SD, COND**, SC	**	.70
S	ALK, Ca+Mg, 1/SD, COND**, SC	**	.70
J	ALK, 1/SD	NS	.31
J	1/SD, COND	NS	.30
J	COND, SC**	**	.47
J	1/SD, SC**	**	.45
J	ALK, 1/SD, COND	NS	.31
J	ALK, Ca+Mg, 1/SD, COND	NS	.36
J	ALK, 1/SD, COND, SC**	**	.47
J	ALK, Ca+Mg, 1/SD*, COND, SC**	**	.50

NS = Non-significance at P = 0.05, ** significance at P = 0.01

TABLE 41. A multiple correlation analysis between species diversity in communities of net phytoplankton and nannoplankton in 63 study lakes in Minnesota. Community properties are Shannon's index (H) and the number of species (S). Net phytoplankton diversity and nannoplankton diversity are indicated as NET H and NET S and NANNO H and NANNO S, respectively. The gradient parameters are total alkalinity (ALK) and calcium + magnesium (ΣCa + Mg) in meq/l, $\log_{10}$ specific conductance (COND) in umho cm^{-1} at 25C, secchi-disc transparency (SD) in feet, and standing crop of phytoplankton (SC) and $\log_{10}$ standing crop of phytoplankton (SC) in individuals/ml.

Dependent Variable	Independent Variables	Significance of Regression	R
NET H	ALK**, Ca+Mg	**	.39
NET H	ALK, 1/SD**	**	.60
NET H	ALK, COND**	**	.57
NET H	Ca+Mg, 1/SD**	**	.53
NET H	1/SD**, SC	**	.56
NET H	ALK, Ca+Mg*, 1/SD, COND*	**	.65
NET H	ALK, 1/SD, COND*, SC	**	.63
NET H	ALK, Ca+Mg, 1/SD, COND*, SC	**	.67
NANNO H	ALK*, Ca+Mg	NS	.28
NANNO H	ALK, SC	NS	.27
NANNO H	ALK, COND**	**	.41
NANNO H	ALK*, Ca+Mg, 1/SD*	NS	.28
NANNO H	ALK, Ca+Mg, COND**	**	.44
NANNO H	ALK*, Ca+Mg, SC	NS	.30
NANNO H	ALK, Ca+Mg, 1/SD*, COND**	**	.51
NANNO H	ALK, Ca+Mg, 1/SD*, COND**, SC	**	.53

NS = Non-significance at P = 0.05, ** significance at P = 0.01

Table 42. The results of four cluster analyses based on the concentrations of major solutes (calcium, magnesium, sodium, potassium, bicarbonate alkalinity, sulfate, and chloride) for 63 study lakes in Minnesota. The analyses are based on ion concentrations expressed as raw data (meq/l) or as standardized variables. Absolute (ABS) and Standard (STAND) distance are two independent agglomeration measures of the similarity among lakes. The cluster analyses are: Run 1 (meq/l, absolute distance), Run 2 (meq/l, standard distance), Run 3 (standardized variables, absolute distance), and Run 4 (standardized variables, standard distance). The numbers opposite the lakes in each analysis designate the major cluster to which each lake is assigned (Types 1, 2, 3, and 4). Single residuals are indicated as R and multiple residuals as Rn. FINAL indicates the lake type to which each lake is assigned. See text for discussion.

		Meq/l		Standardized		
	Run	1	2	3	4	FINAL
		Distance Measure				
Lake	No.	ABS	STAND	ABS	STAND	
Alkali	2	4	3	4	3	4
Alkaline	3	4	4	4	R1	4
Ball Club	4	2	2	2	2	2
Benton	5	3	3	3	4	3
Big	6	1	1	1	1	1
Big Kandiyohi	7	3	2-3	2	2	3
Big Stone	8	3	3	3	4	3
Burntside	9	1	1	1	1	1
Carman	10	2	2	2	2	2
Christmas	11	2	2	2	2	2
Clear	12	2	1	2	2	2
Clearwater	13	1	1	1	1	1
Crane	14	1	1	1	1	1
Dead Coon	15	3	3	3	4	3
Deming	16	1	1	1	1	1
Dogfish	17	1	2	1	1	1
Eckelson	18	4	4	4	R2	4
Elk	19	2	2	2	2	2
Elk	20	3	2-3	3	3	3
Fish	21	2	2-3	2	2	2
Frances	22	2	2	2	2	2
George	23	4	4	4	R1	4
Gladstone	24	2	2	2	2	2
Green	26	2	2	2	2	2
Halsted	27	2	2	2	2	2
Heron	28	2	4	2	2	2
Iron	29	1	1	1	1	1
Isabel	30	3	4	3	3	3
Itasca	31	2	2	2	2	2
Josephine	32	1	2	1	1	1
Kimball	33	1	1	1	1	1
Lamb	34	1	2	1	1	1
Little Pine	36	2	2	2	2	2
Long	37	2	2	2	2	2
Long	38	3	4	3	3	3
Loon	39	1	1	1	1	1
Lower Red	40	2	2	2	2	2
Madison	41	3	3	3	4	3
Meander	42	1	R1	1	1	1
Mille Lacs	43	2	2	2	2	2
Mineral	44	R1	3	3	3	3
Minnewaska	45	3	2-3	3	3	3
Mitchell	46	2	1	2	2	2
Moose	47	2	2	2	2	2
Mud	48	3	1	3	4	3
Nokay	49	2	2	2	2	2
Pickerel	50	2	2-3	2	2	2
Sallie	51	2	2-3	2	2	2
Salt	52	4	4	4	4	4
Sanborn	53	3	2-3	3	3	3
Shagawa	55	1	1	1	1	1
Shetek	56	3	3	3	4	3
Spectacle	57	2	2	2	2	2
Spiritwood	58	3	3	3	3	3
Superior	60	1	2	1	1	1
Tanager	61	2	2	2	2	2
Thief	62	3	1	3	4	3
Traverse	63	3	3	3	4	3
Trout	64	1	1	1	1	1
Upper Minnetonka	65	2	2	2	2	2
Vermilion	66	1	1	1	1	1
Waubay	67	R1	3	3	3	3
Wilson	68	1	1	1	1	1

Table 43. The mean concentrations of the seven major anions and cations in meq/l that were used to classify the 63 study lakes in Minnesota, and the results of an analysis of variance based on the four lake types. Symbols: calcium (Ca), magnesium (Mg), sodium (Na), potassium (K), sulfate (SO_4), chloride (Cl), and total alkalinity ($CaCO_3$).

Lake Types	1	2	3	4	
No. Lakes	17	24	17	5	F-test
Ca	.295	1.56	4.11	5.58	10.2**
Mg	.151	1.455	12.9	96.8	29.3**
Na	.048	.360	5.69	193	58.4**
K	.020	.103	.458	9.18	33.3**
SO_4	.110	.395	13.6	129	54.1**
Cl	.016	.215	1.01	35.6	10.5**
$CaCO_3$	.374	2.77	6.46	7.96	31.9**

**Significance at P = 0.01

Table 44. The results of eight cluster analyses based on selected combinations of eight trophic-state indicators (TSI) for 63 study lakes in Minnesota. The analyses are based on standardized variables. The physical, chemical, and biological TSI are secchi-disc transparency in feet (SD), specific conductance in umho cm^{-1} at 25C, total alkalinity (ALK) and calcium + magnesium ($\sum$ Ca + Mg in meq/l, number of net phytoplankton species (S), compound phytoplankton quotient (CPQ), standing crop of phytoplankton (SC) in individuals/ml, and Shannon's index of diversity (H) in bits/individual for whole-water phytoplankton communities. The analyses are: Run 1 (COND, ALK, $\sum$Ca + Mg, 1/SD); Run 2 (COND, ALK, $\sum$Ca + Mg, 1/SD, SC, 1/H); Run 3 (COND, ALK, $\sum$Ca + Mg, 1/SD, CPQ, SC); Run 4 (COND, ALK, $\sum$Ca + Mg, 1/SD, SC, 1/H); Run 5 (COND, ALK, $\sum$Ca + Mg, 1/SD, 1/S, CPQ); Run 6 (COND, ALK, $\sum$Ca + Mg, 1/SD, CPQ, 1/H, SC); Run 7 (All 8 TSI); Run 8 (1/S, CPQ, SC, 1/H). The numbers opposite the lakes in each analysis designate the cluster to which each lake is assigned (Types 1, 2, 3, and 4). Single residuals are indicated as R and multiple residuals as Rn. See text for discussion.

Lake	Run No.	1(4)	2(4)	3(4)	4(4)	5(5)	6(5)	7(5)	8(4)
Alkali	2	R1	R1	R1	R1	R1	R1	R1	2
Alkaline	3	3	R2	3	4	4	4	4	4
Ball Club	4	2	2	2	2	2	2	2	1
Benton	5	2	3	3	2	3	3	3	4
Big	6	1	1	1	1	1	1	1	1
Big Kandiyohi	7	3	3	2	2	2	2/3	4	2
Big Stone	8	3	R2	3	4	4	4	4	2
Burntside	9	1	1	1	1	1	1	1	1
Carman	10	2	2	2	2	2	2	2	2
Christmas	11	2	2	2	2	2	2	2	2
Clear	12	2	2	2	2	2	2	2	2
Clearwater	13	1	1	1	1	1	1	1	1
Crane	14	1	1	1	1	1	1	1	1
Dead Coon	15	3	3	3	4	3	3	3	4
Deming	16	1	1	1	1	2	1	1	2
Dogfish	17	1	1	1	1	1	1	1	1
Eckelson	18	R1	R1	R1	R1	R1	R1	R1	4
Elk	19	2	2	2	2	2	2	2	1
Elk	20	2	2	2	2	2/3	2/3	2/3	2
Fish	21	2	2	2	2	2	2	2	2
Frances	22	2	2	2	2	2	2	2	2
George	23	4	R3	4	3	4	4	4	R2
Gladstone	24	2	2	2	2	2	2	2	2
Green	26	2	2	2	2	2	2	2	2
Halsted	27	2	2	2	R2	2	3	3	3
Heron	28	2	2	3	4	3	3	3	4
Iron	29	1	1	1	1	1	1	1	1
Isabel	30	3	3	3	R2	4	3	3	3
Itasca	31	2	2	2	2	2	2	2	2
Josephine	32	1	1	1	1	2	1	1	2
Kimball	33	1	1	1	1	1	1	1	1
Lamb	34	1	1	1	1	1	1	1	1
Little Pine	36	2	2	2	2	2	2	2	1
Long	37	2	2	3	2	3	3	3	4
Long	38	3	3	3	4	4	4	4	3
Loon	39	1	1	1	1	1	1	1	1
Lower Red	40	2	2	2	2	2	2	2	1
Madison	41	2	3	3	R2	3	3	3	3
Meander	42	1	1	1	1	1	1	1	1
Mille Lacs	43	2	2	2	2	2	2	2	2
Mineral	44	4	4	4	3	R1	R1	R1	2
Minnewaska	45	2	2	2	2	2/3	2/3	2/3	1
Mitchell	46	2	3	3	4	3	3	3	4
Moose	47	2	2	2	2	2	2	2	2
Mud	48	4	4	4	3	2/3	2/3	2/3	1
Nokay	49	2	2	2	2	2	2	2	2
Pickerel	50	2	2	2	2	2	2	2	1
Sallie	51	2	2	2	2	2	2	2	1
Salt	52	3	R2	3	4	4	4	4	R1
Sanborn	53	3	3	3	4	4	4	4	3
Shagawa	55	1	1	1	1	1	1	1	1
Shetek	56	2	2	2	4	2	4	4	3
Spectacle	57	2	2	2	2	2	2	2	2
Spiritwood	58	4	4	4	3	2/3	2/3	2/3	R1
Superior	60	1	1	1	1	1	1	1	1
Tanager	61	2	2	2	2	2	2	2	1
Thief	62	4	4	4	3	2/3	2/3	2/3	2
Traverse	63	2	3	2	R2	4	4	4	3
Trout	64	1	1	1	1	1	1	1	1
Upper Minnetonka	65	2	2	2	2	2	2	2	2
Vermilion	66	1	1	1	1	1	1	1	1
Waubay	67	4	4	4	3	2/3	4	4	3
Wilson	68	1	1	1	1	1	1	1	1

Table 45. The mean values of the trophic-state indicators (TSI) that were used to classify the 63 study lakes in Minnesota, and the results of an analysis of variance based on the lake groupings detected in three cluster analyses. Numbers in parentheses indicate the number of lakes in each type. Symbols: specific conductance (COND) in umho cm^{-1} at 25C, total alkalinity (ALK) and calcium + magnesium ($\sum$Ca + Mg) in meq/l, secchi-disc transparency (SD) in feet, standing crop of phytoplankton (SC) in individuals/ml, compound phytoplankton quotient (CPQ), Shannon's index of diversity (H) for whole-water phytoplankton communities in bits/individual, and number of species of net phytoplankton (S). The analyses are Run 1 (ALK, $\sum$Ca + Mg, SD, COND), Run 8 (SC, CPQ, H, S), Run 7 (ALK, $\sum$Ca + Mg, SD, COND, SC, CPQ, H, S).

			Run 1		
Lake Type	1(17)	2(30)	3(8)	4(6)	F-test
ALK	0.374	3.10	4.98	10.1	81.0**
$\sum$Ca + Mg	0.446	4.45	17.6	23.7	27.7**
SD	12.4	5.89	1.15	4.50	8.88**
COND	42.4	450	4,402	7,068	10.8**

			Run 8		
Lake Type	1(24)	2(21)	3(8)	4(7)	F
SC	2,662	4,851	49,831	93,746	6.880**
CPQ	2.312	5.068	6.750	12.3	54.3**
H	3.630	2.888	1.388	2.765	32.2**
S	55.4	40.3	18.9	18.6	22.7**

			Run 7			
Lake Type	1(17)	2(20)	2/3(5)	3(8)	4(10)	F-test
ALK	0.374	2.71	8.11	3.59	5.33	67.3**
$\sum$Ca + Mg	0.446	2.80	15.3	7.93	25.0	15.5**
SD	12.4	6.6	6.1	3.9	1.8	4.87**
COND	42.2	267	2,536	978	6,163	9.00**
SC	3,840	3,411	2,872	50,102	26,874	4.26**
CPQ	2.32	4.06	3.5	11.8	4.8	7.38**
H	3.531	3.289	2.968	2.079	2.049	10.6**
S	54.3	48.5	39.0	21.4	14.3	18.9**

**Significance at P = 0.05

Table 46. The mean values of specific conductance in umho cm^{-1} at 25C as $\log_{10}$ estimates for the lake types identified in four cluster analyses, and the results of Scheffe's (1959) multiple comparison test (P = 0.05). ALL COMBS signifies statistical differences among all mean values except for those indicated. Numbers in parentheses indicate the number of lakes in each type. The analyses are: MAJOR SOLUTES (the 7 major anions and cations); TSI (4 PHYSICAL-CHEMICAL indicators), indicated as TSI (4 CHEMICAL); TSI (4 BIOLOGIC indicators); and TSI (CHEMICAL + BIOLOGIC indicators). The composition of the lake types for each analyses and the specific classificatory variables can be identified in Table 42 (MAJOR SOLUTES, FINAL) and Table 44 (Run 1, TSI 4 CHEMICAL; Run 8, TSI 4 BIOLOGIC; Run 7, TSI CHEMICAL + BIOLOGIC). See text for discussion.

Analyses	Major Lake Types					Significant Mean Differences (P=0.05)
MAJOR SOLUTES	1(17)	2(24)	3(17)	4(5)		
	1.625	2.481	3.310	4.250		ALL COMBS
TSI (4 CHEMICAL) Run No. 1	1(17)	2(30)	3(8)	4(6)		
	1.625	2.653	3.644	3.849		ALL COMBS, except 3-4
TSI (4 BIOLOGIC) Run No. 8	1(24)	2(21)	3(8)	4(7)		
	2.266	2.949	3.274	3.824		ALL COMBS, except 2-3, 3-4
TSI (CHEMICAL & BIOLOGICAL) Run No. 7	1(17)	2(20)	2/3(5)	3(8)	4(10)	
	1.625	2.428	3.404	2.990	3.790	ALL COMBS, except 2-3, 2/3-3, 2/3-4

Table 47. The results of four cluster analyses based on selected suites of phytoplankton taxa for 68 study lakes in Minnesota. The analyses are based on presence/absence data. Run 1 DESMIDS (39 species), Run 2 NET PHYTOPLANKTON (167 species), DIATOMS (25 species), and Run 4 BLUE GREENS (29 species). The numbers opposite the lakes in each analysis designate the cluster to which each lake is assigned (Types 1, 2, 3). The species used as variables are given in Table 57. See text for discussion.

	Run No.	DESMIDS	Total NET PHYTO-PLANKTON	DIATOMS	BLUE GREENS
Albert	1	2	3	2	3
Alkali	2	3	3	3	3
Alkaline	3	3	3	3	3
Ball Club	4	2	2	1	2
Benton	5	3	3	2	3
Big	6	1	1	1	1
Big Kandiyohi	7	3	2	3	3
Big Stone	8	3	3	2	3
Burntside	9	1	1	1	1
Carman	10	2	2	2	2
Christmas	11	2	2	1	3
Clear	12	2	2	2	2
Clearwater	13	1	1	1	1
Crane	14	1	1	1	2
Dead Coon	15	3	3	2	3
Deming	16	2	3	1	3
Dogfish	17	1	1	1	3
Eckelson	18	2	3	3	3
Elk	19	2	2	2	2
Elk	20	2	3	3	1
Fish	21	2	2	2	2
Frances	22	2	2	1	2
George	23	3	3	3	3
Gladstone	24	2	2	1	1
Goose	25	1	2	1	1
Green	26	2	2	2	3
Halsted	27	2	2	2	2
Heron	28	2	3	2	3
Iron	29	1	1	1	1
Isabel	30	3	3	3	3
Itasca	31	2	2	1	2
Josephine	32	3	3	1	3
Kimball	33	1	1	1	1
Lamb	34	1	1	1	1
Lillian	35	2	3	2	2
Little Pine	36	2	2	1	3
Long	37	3	3	1	3
Long	38	3	3	2	3
Loon	39	1	1	1	3
Lower Red	40	2	2	1	3
Madison	41	3	3	2	3
Meander	42	1	1	1	3
Mille Lacs	43	2	2	1	3
Mineral	44	3	3	2	3
Minnewaska	45	2	2	2	2
Mitchell	46	3	3	2	3
Moose	47	1	2	1	2
Mud	48	2	2	1	3
Nokay	49	2	2	1	2
Pickerel	50	2	2	2	2
Sallie	51	2	2	2	2
Salt	52	2	3	3	3
Sanborn	53	3	3	2	3
School Grove	54	3	3	2	3
Shagawa	55	3	2	2	1
Shetek	56	2	3	2	3
Spectacle	57	2	2	1	1
Spiritwood	58	3	3	1	3
Stinking	59	2	3	2	3
Superior	60	3	3	1	3
Tanager	61	2	2	2	2
Thief	62	2	2	2	3
Traverse	63	3	3	3	3
Trout	64	1	1	1	1
Upper Minnetonka	65	2	2	2	2
Vermilion	66	1	1	1	3
Waubay	67	2	3	3	3
Wilson	68	1	1	1	1

Table 48. The mean values of specific conductance in umho cm^{-1} at 25C as log_{10} estimates for the lake types identified in four cluster analyses, and the results of Scheffe's (1959) multiple comparison test (P = 0.10). ALL COMBS signifies statistical differences among all mean values except for those indicated. Numbers in parentheses indicate the number of lakes in each type. The analyses are: DESMIDS, NET PHYTOPLANKTON, DIATOMS, and BLUE GREENS. The composition of the lake types for each analyses can be identified in Table 47.

Analyses	Major Lake Types			Significant Mean Differences (P=0.10)
DESMIDS	1(15)	2(33)	3(20)	
	1.661	3.299	3.556	1-2, 1-3
NET PHYTOPLANKTON	1(13)	2(27)	3(28)	
	1.538	2.521	3.663	ALL COMBS
DIATOMS	1(31)	2(27)	3(10)	
	2.638	2.990	3.994	1-3, 2-3
BLUE GREENS	1(13)	2(17)	3(38)	
	2.113	2.525	3.538	ALL COMBS

Table 49. The mean values of specific conductance in umho cm^{-1} at 25C as log_{10} estimates for the major types identified in four cluster analyses, and the results of Scheffe's (1959) multiple comparison test at P = 0.01 and P = 0.05. The major types are 1, 2, 3, and 4. The lake groupings are based on MAJOR SOLUTES (A); TSI 4 Physical-Chemical, indicated as 4 CHEMICAL (B); TSI 4 BIOLOGIC (C); and TSI CHEMICAL + BIOLOGIC (D). The composition and size of the types are given in Tables 42 and 43 (MAJOR SOLUTES) and in Tables 44 and 45 (TSI).

Major Types	MAJOR SOLUTES	TSI (4 CHEMICAL)	TSI (4 BIOLOGIC)	TSI (CHEMICAL + BIOLOGIC)	Significant Mean Differences
	A	B	C	D	
1	1.625	1.625	2.266	1.625	P = 0.05 A-C, B-C, C-D
2	2.481	2.653	2.949	2.428	P = 0.05 None P = 0.10 A-C, C-D
3	3.310	3.644	3.274	2.990	P = 0.10 None
4	4.250	3.849	3.824	3.790	P = 0.10 None

Table 50. The mean values of specific conductance in umho cm^{-1} at 25C as log_{10} estimates for the major types identified in four cluster analyses, and the results of Scheffe's (1959) multiple comparison test at P = 0.01 and P = 0.05. The major types are 1, 2, and 3. The lake groupings are based on DESMIDS (A), NET PHYTOPLANKTON (B), DIATOMS (C), and BLUE GREENS (D). The composition and size of the lake types for each analyses can be identified in Tables 47 and 48. See text for discussion.

Major Types	DESMIDS	NET PHYTOPLANKTON	DIATOMS	BLUE GREENS	Significant Mean Differences
	A	B	C	D	
1	1.661	1.538	2.638	2.113	P = 0.10 None
2	3.299	2.521	2.989	2.526	P = 0.10 None
3	3.556	3.663	3.994	3.538	P = 0.05 None P = 0.10 A-C, C-D, B-C

Table 51. Analysis of variance of net phytoplankton indicators among the four MAJOR SOLUTE lake types in Minnesota. Number of net plankton species (S), compound phytoplankton quotient (CPQ), and the number of desmids (DESMID S).

Variable	Lake Types 1	2	3	4	F	Significant Mean Differences*
S	55.3	45.0	25.3	11.6	19.8**	All Combs
CPQ	2.33	5.41	6.32	7.30	6.82**	All Combs except 2-3, 3-4
DESMID S	13.8	7.1	3.5	1.4	19.6**	All Combs

*Significance at P=0.01, **Significance at P=0.05.

Table 52. Analysis of variance of net phytoplankton indicators among three chemical lake types in Minnesota. Number of net plankton species (S), compound phytoplankton quotient (CPQ), and the number of desmids (DESMID S). The location and composition of the types are similar to those of the present study. The number of lakes in each group is given in parentheses. Mean specific conductance values (COND) in umho cm^{-2} at 25C are given for each type.

Variable	Lake Types 1(22)	2(26)	3(7)	F	Significant Mean Differences*
S	30.7	27.1	20.3	3.66*	1-3, 2-3
CPQ	2.54	6.78	10.1	11.9**	All Combs
DESMID S	8.00	3.4	2.3	14.1**	1-2, 1-3
COND	60	265	1028	218**	All Combs

*Significance at P=0.05, ** Significance at P=0.01.

Table 53. Analysis of variance of diatom ratios and their components among the four MAJOR SOLUTE lake types in Minnesota. Relative abundance of Araphidineae (A_s) and Centrales (C_s); Stockner's Ratio (A/C_s); number of species of Araphidineae (A_t) and Centrales (C); modified A/C_t ratio; number of species of Pennales (P); Nygaard's Ratio (C/P).

Variable	Lake Types 1	2	3	4	F	Significant Mean Differences*
A_s	59.9	36.0	23.0	7.38	6.55**	All Combs
C_s	29.8	59.1	50.1	24.5	3.23**	All Combs except 1-4, 2-3
A/C_s	14.8	3.06	10.8	20.5	1.09	None
A_t	5.11	5.67	5.00	1.60	2.35	None
C_t	6.44	5.04	5.19	2.00	4.37**	All Combs except 1-2, 1-3, 2-3
A/C_t	1.03	1.24	1.11	1.25	0.23	None
P	16.2	14.0	21.7	16.6	1.27	None
C/P	0.48	0.59	0.43	0.13	2.28	None

*Significance at P=0.05, **Significance at P=0.01.

Table 57. A species inventory of 272 planktonic taxa and a summary of their distribution in 68 Minnesota lakes. All of these species were identified in the analysis of net plankton samples and are designated as planktonic forms (Chapter 2). The total number of occurrences (TN) of each taxon and its distribution within the MAJOR SOLUTE lake groupings are tabulated. The number of lakes in each group is: Type 1 (18N), Type 2 (24N), Type 2 (21N), and Type 4 (5N). See Chapters 5 and 6 for discussions concerning the composition and characterization of the groups. Species, varieties, and forms were weighted equally in the computation of the number of taxa per lake and in the calculation of the compound phytoplankton quotient (Chapter 4). The taxa utilized as variables in lake classification (Chapter 5) and in calculations on the indicator value of species (Chapter 6) consist of the species and their closely related forms that are bracketed in the table. Taxa occurring in fewer than three lakes were not used as classificatory variables and were not considered in indicator computations. Parentheses indicate that the identification is not certain.

	TN	Lake Types			
		1	2	3	4
CHLOROPHYTA					
VOLVOCALES					
Asterococcus limneticus	9	7	2	0	0
Elakatothrix gelatinosa	4	2	2	0	0
Eudorina elegans	24	11	11	2	0
Gemellicystis neglecta	6	4	2	0	0
Gonium pectorale	3	1	2	0	0
Paulschultzia pseudovolvox	17	9	7	1	0
TETRASPORALES					
Sphaerocystis schroeteri	21	9	5	7	0
CHLOROCOCCALES					
Actinastrum hantzschii [v. elongatum, v. fluviatile]	7	0	4	3	0
Ankistrodesmus falcatus [v. mirabilis]	24	5	12	7	0
A. spiralis	11	1	6	4	0
Botryococcus braunii	56	16	21	15	4
B. sudeticus	2				
Closteriopsis longissima	1				
Coelastrum cambricum	4	1	2	1	0
C. microporum	33	8	15	10	0
C. reticulatum	10	2	6	2	0
Crucigenia irregularis	7	3	3	1	0
C. lauterbornii	1				
C. rectangularis	16	7	5	4	0
C. regularis	5	3	2	0	0
C. tetrapedia	1				
Dictyosphaerium ehrenbergianum	17	4	6	5	2
D. pulchellum	44	13	19	10	2
Kirchneriella contorta	5	2	3	0	0
K. elongatum	2				
K. lunaris (v. irregularis)	4	3	1	0	0
K. obesa [v. major]	15	6	7	2	0
K. subsolitaria	1				
Nephrocytium agardhianum	11	2	7	1	1
N. limneticum	5	2	3	0	0
N. obesum	2				
Oocystis asterefera	4	4	0	0	0
O. borgei	29	6	13	7	3
O. elliptica	6	1	5	0	0
O. lacustris	23	5	14	4	0
O. parva	15	5	6	3	1
Pediastrum araneosum	1				
P. boryanum	49	11	21	16	1
P. duplex	43	10	21	11	1
P. simplex [v. duodenarium]	20	2	12	6	0
P. tetras	7	2	2	3	0
Planktosphaeria gelatinosa	13	4	6	3	0
Quadrigula chodatii	5	3	2	0	0
Q. closterioides	12	5	6	1	0
Q. lacustris	6	2	4	0	0
Schroderia setigera	3	0	2	1	0
Selenastrum bibraianum	2				
[illegible]cile	2				
[illegible]utum	1				
[illegible]stii	5	1	3	1	0
Tetrallantos lagerheimii	2				
Tetraedron caudatum v. longispinum	1				
T. gracile	4	1	2	1	0
T. hastatum	3	0	2	1	0
T. limneticum [v. gracile]	16	5	7	4	0
T. minimum	6	1	2	1	2
T. muticum	3	1	1	1	0
T. planctonicum	5	3	2	0	0
T. regulare [v. bifurcatum, v. incus, v. torsum]	5	2	2	1	0
T. trigonum [v. gracile]	11	3	5	3	0
Westella botryoides	9	3	5	1	0
W. linearis	4	2	2	0	0
DESMIDIALES					
Closterium aciculare [v. subpronum]	17	0	12	3	2
C. acutum v. variabile	14	0	12	2	0
Cosmarium botrytis	7	4	3	0	0
C. contractum [v. ellipsoideum]	12	9	3	0	0
C. depressum [v. achoridum]	25	15	10	0	0
Hyalotheca dissiliens	4	4	0	0	0
Spondylosium planum	12	11	1	0	0
Staurastrum anatinum	22	9	9	2	2
S. arctiscon	4	4	0	0	0
S. avicula	7	5	2	0	0
S. brachiatum [v. robustum]*	3	2	1	0	0
S. brevispinum	5	3	2	0	0
S. bullardhi*	9	1	5	2	1
S. chaetoceras	30	3	18	7	2
S. cingulum [fo. annulatum, v. inflatum, v. obesum]	31	7	11	12	1
S. contortum*	17	2	9	5	1
S. denticulatum	3	3	0	0	0
S. gracile	17	5	7	4	1
S. leptocladum [v. denticulatum, v. insigne, v. sinuatum]*	11	3	8	0	0
S. longipes	12	9	3	0	0
S. lunatum [v. planctonicum]	4	2	1	1	0
S. longiradiatum	5	3	2	0	0
S. pentacerum [v. tetraforme]*	8	8	0	0	0
S. pingue	35	6	19	9	1
S. planctonicum	20	7	12	1	0
S. pseudopelagicum [v. tumidum]	3	0	1	2	0
S. sebaldi [v. ornatum]	8	1	4	3	0
Staurodesmus crassus [v. productus]	4	4	0	0	0
S. cuspidatus [v. canadense]	16	11	4	1	0
S. curvatus [v. elongatus, v. inflatus]	14	12	1	1	0
S. dejectus [(dejectus)]	3	3	0	0	0
S. extensus [v. joshuae]	5	5	0	0	0
S. glabrus	5	5	0	0	0
S. leptodermis	5	3	2	0	0
S. megacanthus [v. scroteri]	10	9	1	0	0
S. subtriangulus [v. inflatus]	9	8	1	0	0
S. triangularis	3	3	0	0	0
Xanthidium antilopeum [v. canadense, v. polymazum]	6	6	0	0	0
X. subhastiferum [v. johnsonii, v. toweri]	7	7	0	0	0
Cosmarium abbreviatum	1				
C. humile	2				
Euastrum elegans [v. ornatum]	2				
E. verrucosum	1				
Micrasterias radiata	2				
Staurastrum boreale	2				
S. brasiliense [v. lundellie]	1				
S. excavatum	2				
S. lacustre*	2				
S. leptacanthum*	2				
S. longispinum	2				
S. manfeldtii	1				
Staurodesmus controversus	2				
S. convergens [v. lapporti]	2				
S. corniculatus [v. pelagicum]	1				
Staurastrum pendulum v. pinguiforme	2				
Staurastrum ophiura	1				
CYANOPHYTA					
Aphanizomenon flos-aquae	38	9	18	10	1
Anabaena affinis	7	1	6	0	0
A. circinalis	25	13	12	0	0
A. flos-aquae	34	12	18	4	0
A. macrospora v. robusta	4	2	2	0	0
A. planctonica	21	11	9	1	0
A. spiroides v. crassa	26	3	20	2	1
Aphanocapsa clathrata	1				
A. elachista [v. conferta, v. planctonica]	17	12	5	0	0
Aphanothece nidulans	13	8	5	0	0
A. stagnina	2				
Chroococcus dispersus	26	5	16	5	0
C. limneticus	38	14	18	6	0
[v. distans, v. elegans]					
C. prescottii	10	4	5	1	0
Coelosphaerium dubium	2				
C. kuetzingianum	23	12	9	2	0
C. naegelianum	38	17	14	6	1
C. pallidum	4	3	0	1	0

Dactylococcopsis fascicularis	5	0	4	1	0
D. raphidioides	2				
D. smithii	1				
Gomphosphaeria aponica	19	6	7	3	3
G. compacta	9	3	4	1	1
G. lacustris	32	8	17	5	2
Lyngbya birgei	23	6	14	3	0
L. contorta	8	0	1	5	2
L. lagerheimii	2				
L. limnetica	19	5	9	4	1
Merismopedia glauca	8	0	2	5	1
M. punctata	3	3	0	0	0
M. tenuissima	14	4	3	5	2
Microcystis aeruginosa	51	14	19	15	3
M. incerta	5	1	1	3	0
Oscillatoria aghardhii	20	1	11	6	2
O. limnetica	1				
O. redechii	2				
O. rubescens	2				
Rhabdoderma lineare	6	5	1	0	0
Rhaphidiopsis curvata	2				
CHRYSOPHYTA					
CHRYSOPHYCEAE					
Chrysocapsa planctonica	12	11	1	0	0
Chrysosphaerella longispina	10	9	1	0	0
Dinobryon bavaricum [v. vanhoeffenii]	17	14	3	0	0
D. cylindricum	18	10	5	3	0
D. divergens [v. schauinslandii]	23	14	7	2	0
D. pediforme	4	4	0	0	0
D. sertularia [v. protuberans]	9	7	2	0	0
D. sociale [v. americanum, v. stipitatum]	24	9	10	4	1
Hyalobryon borgei v. radiosum	3	2	1	0	0
Mallomonas acaroides	4	2	2	0	0
M. caudata	15	7	7	1	0
M. elongata	25	9	9	7	0
M. fastigata	3	1	2	0	0
M. tonsurata [v. alpina]	24	6	13	5	0
Stichogloea doederleinii	18	14	4	0	0
Synura adamsonii	2				
Synura sphagnicola	5	5	0	0	0
S. uvella	13	11	1	1	0
DIATOMS					
Melosira ambigua	37	13	15	8	1
M. distans	7	7	0	0	0
M. granulata	46	9	21	13	3
M. granulata v. angustissima [fo. spiralis, (M. italica v. tenuissima)]	11	4	2	4	1
M. islandica subspec. helvetica	7	3	1	2	1
M. italica [subspec. subarctica]	14	5	0	5	4
Cyclotella comta	17	11	4	2	0
C. glomerata	2				
C. kützingiana	14	7	6	1	0
C. ocellata	2				
C. stelligera [v. tenuis]	22	11	7	4	0
C. striata	12	0	1	9	2
C. meneghiniana	13	0	2	11	0
Stephanodiscus astrea v. minutula	37	10	11	16	0
S. hantzschii	22	3	10	9	0
S. niagarae	49	9	21	18	1
Rhizoselenia eriensis	11	3	4	4	0
R. longiseta	11	6	4	1	0
Chaetoceros muelleri	5	0	0	2	3
Tabellaria flocculosa v. flocculosa	29	17	9	3	0
Fragilaria capucina	18	1	10	7	0
F. capucina v. mesolepta	17	1	10	6	0
F. crotonensis	45	14	19	12	0
Asterionella formosa	40	17	18	5	0
Synedra acus [v. angustissima]	26	4	9	12	1
Nitzschia acicularis	15	1	6	7	1
N. longissima [βreversa]	3	0	2	1	0
PYRROPHYTA					
Ceratium hirundinella	45	16	20	6	3
P. cinctum	2				
P. limbatum	2				
Peridinium willie	28	14	12	2	0
P. wisconsinense	7	6	1	0	0
P. inconspicuum	6	3	3	0	0
P. volzii	2				
EUGLENOPHYTA					
Phacus helikoides	2				
P. longicauda	1				
P. orbicularis	4	0	1	3	0
P. nordstedtii	9	1	1	6	1
Trachelomonas hispida	4	0	4	0	0
T. volvocina	6	3	3	0	0

Table 58. A summary of frequency (FR) and preference (PR) of selected planktonic diatoms among Minnesota lake groupings. The lake types are the same as those given in Table 57. TN is the total number of occurrences. See text for discussion.

		Lake Types							
		1		2		3		4	
Taxon	TN	FR	PR	FR	PR	FR	PR	FR	PR
Asterionella formosa	40	.95	.43	.75	.45	.24	.13	0	0
Cyclotella comta	17	.61	.65	.17	.24	.09	.11	0	0
Fragilaria capucina	18	.06	.06	.42	.56	.33	.39	0	0
Fragilaria capucina v. mesolepta	17	.06	.06	.42	.59	.29	.35	0	0
Fragilaria crotensis	45	.78	.31	.79	.42	.57	.27	0	0
Melosira ambigua	37	.72	.35	.63	.41	.38	.21	.20	.03
Melosira granulata	46	.50	.20	.88	.46	.62	.28	.60	.07
Stephanodiscus astrea v. minutula	37	.56	.27	.46	.30	.76	.43	0	0
Stephanodiscus hantzschii	22	.16	.14	.25	.45	.43	.41	0	0
Stephanodiscus niagarae	49	.50	.18	.88	.43	.86	.37	.20	.02