TAXONOMY AND ECOLOGY OF *APHANIZOMENON* IN FIVE MINNESOTA LAKES

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ABSTRACT

The ecology and taxonomy of five populations of Aphanizomenon were studied. The primary objective was to determine whether discrete species were present or whether the populations each consisted of a continuum of morphological variation. Ecological characters (eutrophy, depth of stratification, seasonal occurrence of the population, morphological characters (cell width, cell length, length to width ratio, cell shape, and presence of heterocysts and akinetes) and one physiological character were examined. Seasonal variation in filament density, heterocysts and akinetes were plotted. Computer programs were used to calculate morphological data as frequency polygons and scattergram plots. The acetylene reduction technique for nitrogen fixation was applied to lake populations and isolated colonies of Aphanizomenon.

The populations differed greatly in trophic conditions, stratification depth, and seasonal occurrence of the populations and yet the morphological characters showed no definite hiatuses in variation of cell size or cell shape that would indicate the presence of definite species. The means of morphological variation were different for each lake yet the ranges overlapped. There was a greater difference among lakes than within individual lakes. The cultures under similar environmental conditions had overlapping ranges of morphological variation yet discrete limits for each strain.

The cell characters that were the most useful were vegetative and end cell width for distinguishing between strains and population means. The populations are best described by Komarek's epithet Aphanizomenon flos-aquae Ralfs ex Bornet et Flahault. In addition, an indication of the range of variation present is recommended. Drouet's revision of the genus Aphanizomenon is not recommended mainly because it is based on the lack of published data.

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INTRODUCTION

Growths of Aphanizomenon flos-aquae, a blue-green algae are becoming an increasing problem in many bodies of water. The occurrence and dominance of this species may be increasing. Aphanizomenon flos-aquae was the only blue-green species to increase in the last few years with increasing eutrophy in pre-overturn months in Esthwaite water (Lund 1972). Aphanizomenon was known for decades in lakes of northern Germany but it was not discovered in Swiss Lakes until 1960, when it formed dense blooms in four lakes (Jaag 1972). A. flos-aquae has also increased in concentration in Lake Minnetonka for the last three decades (Wood 1938). Large colonies of this species often float to the surface of the lake and form obnoxious blooms. These blooms are not only esthetically unpleasing but may also be toxic to animals (Gorham 1964).

Information on the autecology of a blue-green species is needed, but first their taxonomy (identification, classification, and nomenclature) needs study. Traditionally morphological characters have been used to circumscribe species in natural populations. The taxonomy is difficult because natural populations in lakes may have filaments with morphological variations intermediate between characteristics of described taxa. These characters are cell size, shape, numbers of end cells heterocysts, akinetes, colonies, and filament shape, (Geitler 1932, Fig. 1).

End cells (differentiated vegetative cells) are at or adjacent to the end of the filament. They are distinguished from other vegetative cells by their reduced width, their increased length, or their cell contents. They either are hyaline or are more vacuolated than other vegetative cells, or have a string of protoplasm running the length of the cell. End cells have also been called terminal or hair cells.

A heterocyst is a differentiated vegetative cell that is usually rounded and larger than a vegetative cell, partially separated from neighboring cells by a constriction, and surrounded by a thick envelope, except at the polar nodules near the point of attachment to a vegetative cell (Fay 1973).

Akinetes are specialized vegetative cells that are distinguished by their large size, shape, modified pigmentation, large numbers of cytoplasmic granules and by an envelope that completely surrounds the cell and separates it from adjacent cells.

There is considerable disagreement on what is a species. Blue-green algae are procaryotes. They reproduce primarily by asexual means. Recombination does occur in culture (Bazin 1971). But whether it occurs in the natural environment and to what extent is unknown. With an asexually dividing population the term species is controversial. There are people who tend toward lumping species names (Drouet 1973) or tend toward splitting genera and species (Elenkin 1936).

More recent approaches in taxonomy include fatty acid composition (Kenyon 1970), DNA base ratios (Stanier et al. 1971), and ultrastructure (Lang and Whitton 1973). The most direct method for establishing species would ultimately be genetic. These approaches provide useful information but are not practical for field identification of blue-green algal species.

A field approach gives an idea as to limits of natural variation, and also the information can then be used on other natural populations. However, this approach does not relate cause and effect. The environment cannot be controlled. It is an indirect approach to distinctness of species. In clonal cultures, the environment can be varied and the limits of morphological variation recorded. This may not be variation present in the field. Both approaches have their advantages. Little work in fresh water has been done with blue-green algae that uses both field populations and populations in culture.

More criteria are needed to distinguish natural populations of flos-aquae. One approach might be the ability to fix nitrogen. The heterocyst is apparently the primary site of nitrogen fixation (Stewart et al. 1968; Ogawa and Carr 1969; Wolk 1970; Jewell and Kulasooriya 1970). Therefore, either the absolute or percent frequency of heterocysts may be positively correlated with nitrogen fixation.

Objectives

The first objective is to describe briefly the morphometry and water chemistry of lake habitats that supported Aphanizomenon populations.

The second objective is to describe aspects of the distribution and dynamics of the populations. What are the seasonal growth curves for these populations? What are the vertical and horizontal distributions of the populations? What is the seasonal variation in the percent and absolute concentration of cell types?

The third objective is to evaluate the use of acetylene reduction (nitrogen fixation) as a physiological character to distinguish among populations or strains of Aphanizomenon. Which lake populations fix nitrogen and how does this fixation correlate with heterocyst production?

The fourth objective is to quantify morphological characters of cell size and cell shape used previously to separate taxa in Aphanizomenon. The distribution of these characters for each lake population and seasonal variation for three of the lake populations are described. Are there discontinuities in the frequency distributions of the characters within the same lake population or among lake populations? Discontinuities in morphology may indicate distinct taxa either within or among lake populations. If there are discontinuities in distributions among lake populations, these populations may be composed of different species or ecotypes

of the same taxa. If there are no obvious discontinuities in or between lake populations there may be a continuum of variation with no distinct taxa. It is possible that characters that would separate different genotypes were not measured.

The fifth objective is to culture colonies to examine the range of variation possible under the same culture environment. This gives an indication of the relative reliability of taxonomic characters, and of how much phenotypic variation develops from a clonal culture (one genotype). Are there differences among cultures or is their morphology the same under the same environmental conditions? This also provides insight into the polymorphism in blue-green algae.

The last objective is to integrate the ecological and morphological information to draw conclusions on the taxonomy of these Aphanizomenon populations. Are there breaks in the variations present that delineate discrete taxa, and if so what characters distinguish the taxa? How polymorphic are these algae? What specific epithets can be used to describe the populations?

DESCRIPTION OF THE STUDY LAKES

Halsted Bay and Carman Bay are two of the fifteen basins of Lake Minnetonka located in the deciduous forest region of southern Minnesota; Spencer Pond, Elk Lake, and Squaw Lake are located in the coniferous-deciduous forest of north western Minnesota. These study lakes were chosen because they support populations of Aphanizomenon, each at different times seasonally or at different depths.

The study lakes share several features and yet differ in others. Surface deposits surrounding both lake areas are calcareous outwash or glacial till. The lakes are in regions where precipitation minus evaporation ranges from -3 to -4 inches (Bright 1968). The lakes are dimictic and are covered with ice during the winter. Break-up occurs generally in May for Squaw and Elk Lakes and in April for Lake Minnetonka. The lake volume decreases from Carman Bay, Elk Lake, Halsted Bay, Squaw Lake, to Spencer Pond (Table 1). Because of its small volume Spencer Pond has probably the highest ratio of mud surface area to lake volume. The calcium carbonate, calcium, and magnesium concentrations and the conductivity decrease in value from Elk Lake, Lake Minnetonka, and Squaw Lake to Spencer Pond (Table 2). Oxygen is depleted in the hypolimnetic waters of Halsted, Spencer, Squaw, and Elk Lakes during the summer, so these lakes are probably fairly productive. Halsted and Spencer both receive farmland drainage and have large inputs of

phosphorus and nitrogen.

The populations studied were late-summer, mid-summer, or perennial and were either epilimnetic or metalimnetic. I observed late-summer blooms of Aphanizomenon in Halsted Bay and perennial populations in Carman Bay during 1969. A bloom of this alga was observed in Spencer Pond during the summer of 1966 (Hill 1966). The occurrence is sporadic. Filaments were not found during 1970. Squaw and Elk Lakes support summer metalimnetic populations of Aphanizomenon (Baker and Brook 1971).

Halsted and Carman Bays

These bays are two of the fifteen basins of Lake Minnetonka, Hennepin County, east-central Minnesota (Fig. 2). Basins of Lake Minnetonka are ice-block depressions. Until 1974, six municipal sewage-treatment plants discharged wastes into the lake or its tributaries (Megard 1970). The present interceptor system diverts this sewage from the lake. The transparency of much of the lake has already increased substantially. Primary productivity levels of the various bays are at opposite ends of the range for lakes in central Minnesota: Halsted Bay is near the upper limit of algal productivity; and Carman Bay is the least productive body of water locally (Megard 1970).

Halsted Bay has an area of 220 ha. and a maximum depth of 9.5 m (Table 1). Its inflowing stream, rich in phosphorus, drains farmland on the western side of the

lake. The outlet drains eastward through a narrow channel into Priest Bay (Fig. 2). The hypsograph of the basin has a conical shape, with little volume at the greater depths (Fig. 3).

Halsted Bay has generally higher levels of nitrogen and phosphorus than Carman Bay during 1972 (Figs. 4, 5). Concentrations of dissolved orthophosphate were less than 15 ppb for Carman Bay and as great as 600 ppb in Halsted Bay during the spring, and 950 ppb in the hypolimnion during the summer. The nitrate-nitrogen concentrations were approximately 100-150 ppb in both bays during the spring. Nitrate concentrations decreased at all depths throughout the summer but increased to over 175 ppb during the fall in Halsted Bay. Carman Bay did not have a similar increase during the fall. The ammonia nitrogen concentrations during the spring were five times higher in Halsted Bay (500 ppb) than in Carman Bay (100 ppb). In both bays ammonia concentrations increased in the hypolimnion during the summer.

Aphanizomenon was first recorded in Lake Minnetonka by Crocker (1895) on the surface of the water and around the edges of the lake in quiet bays during the summer and early autumn (Tilden 1910). It was also recorded in the thirties in late summer in low concentrations (Wood 1938). The biomass of Aphanizomenon in Halsted Bay increased during each year of the study period. The sewage diversion program seems not to affect this bay, which receives nutrient input from surrounding farmland.

Spencer Pond, Squaw Lake, and Elk Lake

These lakes are located in Clearwater County, northwestern Minnesota (Fig. 6). Squaw and Elk Lakes are located inside Itasca State Park, and Spencer Pond is outside of the park three miles northeast of the University of Minnesota Lake Itasca Forestry and Biology Station. The landscape surrounding these lakes was formed during the late-Wisconsin glaciation when the Wadena Lobe stagnated in the region (Wright 1972). The lakes are probably ice-block depressions.

Spencer Pond is now separated from an adjacent Farm Pond by Minnesota State Highway #31, constructed in the 1950's. Spencer Pond had an area of 1.25 ha and a maximum depth of 2.5 m in 1969. The water level in 1971 and 1972 was lower than in 1969 because of decreased rainfall (Table 1). The only recorded evaporation measurement of the entire pond was in the 1930's. The Farm Pond has been periodically dry since that time. The hypsograph has a U-shape (Fig. 7) in contrast to the v-shape of the hypsograph for Halsted Bay (Fig. 3). The area surrounding both ponds is farmland, with a cattle feedlot adjacent to the Farm Pond. The Farm Pond drains into Spencer Pond during the spring via a culvert beneath the highway. Spencer Pond has no outlet.

The $CaCO_3$ concentrations in Spencer Pond were .4-.5 meq/L during the summer of 1969, low in comparison to many of the surrounding hard-water lakes, with concentrations of greater than 3.0 meq/L $CaCO_3$ (Table 2). This

lack of buffering capacity allows for rapid changes in pH. I observed changes in dominance of algae within several days.

Calcium and magnesium concentrations were .07-.57 meq/L and .09-.39 meq/L respectively, which was low in comparison with larger lakes in the area. The nitrogen and phosphorus concentrations in the spring are presumably high when the adjacent Farm Pond drains into Spencer Pond. On July 23, 1969, the orthophosphate concentration in the Farm Pond was 550 ppb, probably because of drainage from the surrounding feedlot. During the summer no drainage from the Farm Pond was observed, and the orthophosphate concentration on July 23, 1969, was 35-67 ppb in Spencer Pond.

Squaw and Elk Lakes are deeper lakes, 30 and 23 m respectively. They have higher alkalinity (2.9-3.5 meq/L $CaCO_3$) and conductivity (288-363 micromhos) (Table 2) (Bland 1971).

METHODS

1. PHYSICAL AND CHEMICAL MEASUREMENTS

Water temperatures were measured with a thermistor (Precision Scientific Co.). Oxygen concentrations were estimated with a submersible silver-lead galvanic cell (Precision Scientific Co.), which was calibrated daily with the Winkler oxygen technique. The Harvey, cadmium-reduction, and nesslerization methods were used respectively to determine phosphate (filtered sample), nitrate, and ammonia concentrations. Calcium and magnesium concentrations were determined titrimetrically with E.D.T.A. (Amer. Public Health Assoc. 1965).

2. FIELD COLLECTION AND MICROSCOPE ANALYSIS

Water samples were collected with a 3-liter Van Dorn sampler at the deep hole in all five bodies of water from OM to the bottom. A portion (1-4 oz) was preserved in amber glass bottles.

The algae in 5 or 10 ml of the preserved portion were sedimented in chambers and the filaments were counted with a Wild M40 inverted microscope at a magnification of 200x or 500x. Traverses of known width were made across the settling chamber (30 mm), and all the phytoplankton cells encountered were identified and recorded. If the portion of a filament within a transect was less than one-half the estimated length of the filament it was not counted. Sufficient transects were made (at right angles to the previous transect) to accumulate a count of at least 300 Aphanizomenon filaments and 500

total individuals of all species. The counting technique used was a modification of Utermohl's (Baker 1973).

The individual filaments of a colony were dispersed by the Lugol preservative. Fragmentation of each filament also occurred. Therefore, for Halsted Bay, where more seasonal information was recorded, the count was multiplied by the average number of cells/filament on each sampling date.

Variations in filament concentration in Halsted Bay, Carman Bay, and Spencer Pond have been expressed by either integrating the concentrations per ml at depth for each date and expressing them as numbers per m^2 or plotting the concentrations per ml for each date and depth and drawing lines of equal concentration (isopleths). Temperature, oxygen, and Secchi disc depth data are presented where available.

Filament concentrations in the water column of Squaw and Elk Lake were determined for several dates and were compared to the thermal and oxygen profiles on these dates.

A specific rate of change per day (S.R.C.) of cell or filament density was calculated from the numbers/m^2. This can have a positive value (increasing population) or a negative value (decreasing population). The formula used was:

$r = (1/w)(G/T)$ (Megard and Smith 1974)

r= specific growth rate
w= mean population size during an interval of T days
G= the change in population size
T= time in days

Sources of variation in sampling and counting exist; they are:

1. the settling chamber of the inverted microscope
2. the collection bottle - samples from the same collection bottle
3. the lake station - samples from several collection bottles
4. stations horizontally at the same depth - samples from different collection stations

The above sources of variation were estimated on two sets of samples, one from Halsted and one from Carman Bay (Table 3). The first two sources of variation may be distributed randomly. The next two would be expected to be distributed non-randomly because the distribution of the algae in the lake is not random. The horizontal variation may be influenced by wind in Halsted Bay (Baker and Baker 1976).

The Chi-square homogeneity test was applied to sources of variation #1 & 2. A lower value than expected was obtained for the error within a chamber. Therefore, the null hypothesis that the variation was random is accepted. However, when this same test was applied to the variation within a bottle #3 the Chi-square value was too great to accept the null hypothesis of random variation. (Table 3).

The coefficient of variation (the standard deviation expressed as a percent of the mean) was used to express all sources of variation. The value of the coefficient increases from one sampling source (#1-4, chamber-bottle-station-lake one depth) to the next.

Variations in cell types (vegetative, heterocysts, akinetes, and end-cells) are expressed as absolute

numbers per ml or as a percent of total cells. Seasonal variation of absolute numbers is presented for Halsted Bay, Carman Bay, and Spencer Pond. Seasonal variation of percent cell types is presented for Halsted Bay. The coefficient of variation for percent cell estimates is less than 21.9% (Table 4).

3. NITROGEN FIXATION

Aphanizomenon colonies isolated at the sampling site immediately after collection were re-suspended in 1 ml filtered lake water in a 7 ml serum bottle and returned to the collection depth. Total phytoplankton from .5 m, concentrated with a plankton net of 35 μ pore size, was re-suspended in a similar manner.

The methods used for acetylene reduction were those of Stewart et al. (1967) with modifications by Stewart et al. (1971). In most cases duplicates were run of each sample. Controls of Millipore-filtered lake water and net filtrate were run. Control samples were injected with Lugol's preservative to stop the reaction before incubation or were covered with black tape prior to incubation. After a 60-min. incubation (12:00 AM to 1:00 PM), Lugol's (.25 ml I_2KI) was added to stop the reaction and simultaneously preserve the algae. Triplicate samples of the gas phase were analyzed with a Beckman GC-M gas chromatograph fitted with a hydrogen flame-ionization detector. Coefficient of variation was 3% for the measurement of ethylene between bottle triplicates and 10% for the algal counts between triplicates.

The effectiveness of Lugol's in stopping the reduction reaction was compared to samples injected with 5N H_2SO_4. Lugol's solution stopped more quickly the acetylene reduction reaction. The gas phase in the Lugol's samples contained less ethylene than the gas phase over the H_2SO_4 treated samples. (Table 5).

The effects of adding phosphorus were tested by spiking some algal samples in the serum bottles with 500 ppb of K_2HPO_4 and incubating the samples for one hour prior to the acetylene reduction incubation.

4. ISOLATION AND CULTURE OF COLONIES

Colonies were isolated with a micropipette and either preserved in Lugol's for microscopic examination of the filaments or were cultured in modified Gorham's medium (Shapiro 1968). The cultures were placed in either a 65° or 85° F incubator at approximately 500 fc of constant light. The cultures were preserved or transferred approximately two months after inoculation when growth was apparent.

5. TAXONOMIC CHARACTERS

The quantitative characters measured are lengths and widths and length-to-width ratios of vegetative cells, heterocysts, akinetes, and end cells. The vegetative and end cell dimensions are averages per filament. The heterocysts and akinetes each were measured. The limit of resolution is .20 μm. The variation in these measurements was calculated for samples from a colony, culture, lake population (one date), and lake populations (all

dates) in Halsted Bay (Table 6).

The qualitative characters are cell shape (of vegetative cells, end cells, akinetes, and heterocysts) and end cell contents. (Fig. 8).

6. COMPUTER PROGRAMS

Two computer programs were used. 1) The initial transformations of raw data is performed by Phanny III, which prints a data summary table for each date, colony, or culture. This program also sends the filament data to tape for use by three S.P.S.S. programs. (Statistical Package for the Social Sciences).

2) The S.P.S.S. programs used are Codebook, which displays data as histograms, Scattergram, which displays data as two dimensional scatter plots, and Condescriptive, which computes statistics for the data.

The statistics used include the mean, mode, and range. Frequency polygons are graphed from the histogram print-out. The scattergram produces a two-dimensional array of two variables. On these graphs the areas of scatter are circumscribed by a line, and the mean and the standard deviation are marked. This technique of delineating area of scatter on a two-dimensional plot was used by Golubic (1973).

RESULTS

1. VARIATION OF FILAMENT CONCENTRATION IN THE FIVE STUDY LAKES

a. Halsted Bay

The Aphanizomenon population in Halsted Bay developed into a late summer-early fall bloom (Fig. 9). Filaments were not found from February to late April. The algae increased exponentially late in the spring, with no detectable lag phase of growth. The algal concentrations fluctuated (with approximately three to four maxima each year). The maximum concentrations increased successively from 1971, 1972, to 1974. The decrease of the fall population in 1971 (September-October) was exponential.

The specific daily rate of change was positive, and the maximum was during the spring for all three years, with a range of .16-.18 per day (Fig. 10). This is a doubling time of 3.7-4 days. The rates then fluctuated positively and negatively but with a decreasing positive value. The negative values were greatest during the winter of 1971 (-.24 per day) and after the 1974 initial increase in concentration (-.2 per day).

The maxima in algal concentration per m^2 corresponded to maxima in concentrations per ml in the epilimnetic waters during the summer, and in the fall to an increase in algal concentrations through the water column (Figs. 11-13). The exponential increase during the spring occurred in the epilimnetic water. The algae stratified during the summer, with maximum concentrations above 3 m.

The algae were mixed through the water column from August through September, when filament concentrations again increased. The algae stratified in mid-November of 1971, when they also decreased exponentially.

During all three years the algae increased in concentration in the epilimnetic water, when the lake began to stratify thermally (Fig. 11-13). The 50 filaments/ml isopleth at this time corresponded to the 18-20°C isopleths. The stratification pattern of the algae was similar to the thermal stratification. The highest concentrations of algae were located above the metalimnion during the summer, and in several instances during all three years the increases in algal concentrations occurred when temperatures increased. However, temperature measurements and algal sampling dates did not always coincide, so the patterns are difficult to compare. When the lake circulated during the fall of 1971 and 1972 the algae also were mixed, but in 1974 the algae were stratified above 4 m. When water temperatures decreased after the fall overturn the algal concentrations remained high and actually increased during all three years.

The transparency recorded by the Secchi disc depth was 4.5-5.5 m but decreased to 0.5-1.5 m (Fig. 11-13). The Secchi disc depth, however, decreased just prior to the increase of Aphanizomenon in the spring. The Secchi disc depth increased in the fall probably because of decreased concentrations of blue-greens other than Aphanizomenon.

Seasonal Variation of Phytoplankton Other Than Aphanizomenon

Aphanizomenon comprised 19-42% of the algal community biomass during the summer of 1974 (Fig. 14). During the early spring the algal community was dominated by other blue-green species (Anabaena flos-aquae, Anabaena spiroides var. crassa), later by a mixture of greens and diatoms (Schroederia setigera, Stephanodiscus niagarae), and then by a mixture of several blue-green species (Microcystis aeruginosa, Gomphosphaeria naegeliana, Anabaena spiroides var. crassa, and Anabaena flos-aquae). After the fall overturn blue-green species other than Aphanizomenon and diatom concentrations increased.

The seasonal variation of green algae, diatoms, and blue-green algae is typical. The green algae are high in concentration early in the summer. The diatoms have spring and fall maxima. The blue-green algae are dominant during the summer and late fall.

b. Carman Bay

During the study years the population of Aphanizomenon in this bay was perennial (Fig. 15). The maxima occurred in the spring and fall of 1971 and the fall of 1972. In 1971 the population concentrations were at a minimum during the summer. In 1972 the population was high in concentration during the winter, decreased to relatively low concentrations in the spring, but increased during the summer with a maximum in the fall.

The specific rate of change was highest during the spring (.05 per day 1971) and fall (.12 per day for 1971,

and .09 per day for 1972) when the concentrations were highest (Fig. 16). The rate fluctuated up and down, with no other definite patterns.

The early spring and fall populations were mixed through the water column except for the 1971 spring maximum when the algae were stratified above 4.5 m (Figs. 17 and 18). The summer populations in 1971 and 1972 were stratified above 5-7 m.

The algal isopleths and the thermal isopleths had a more complex pattern in this bay than in Halsted Bay because Carman Bay is a small unprotected part of a larger Upper Lake (Figs. 17 and 18). The 1971 spring population increased when water temperatures were 12° to 20° C. During the spring of 1971 and both summers the algae were stratified above the 18-20° C isopleths.

The Secchi disc depth decreased during the spring of 1971 during the increase of Aphanizomenon filaments, but the same decrease occurred in 1972 when Aphanizomenon was low in concentrations. Also, the concentrations of Aphanizomenon were relatively low during the summer when the Secchi disc depth was low. And it is probable organisms other than Aphanizomenon were influencing the Secchi disc depth.

c. Spencer Pond

This small pond supported summer populations of Aphanizomenon (Fig. 19). These blooms were of short duration compared to the other study lakes. The phase of exponential increase was soon followed by an exponential

decrease in concentration. The maxima lasted from two to four weeks. These maxima occurred at different times of the summer for each study year (1969-early July, 1971-early August, 1972-early June). The occurrence of this alga is sporadic. Aphanizomenon was not found during the summer of 1970.

The positive specific rate of change was maximal prior to the maximal algal concentrations per m^2 (.12 per day 1969, .13 per day 1971, .12 per day 1972) (Fig. 20). The rate then fluctuated positively and negatively.

Aphanizomenon was stratified in the pond during 1969 even though the pond was only 2.5 m deep. The highest concentrations were above 1.5 m. The thermocline in Spencer Pond was shallow (1.5-2.0 m) during late July and August of 1969 (Fig. 21).

In 1969 algal concentrations of 50 filaments/ml corresponded to water temperatures of 14-16° C at the beginning of the bloom (Fig. 21). The highest rates of increase occurred in water with temperatures from 14-22° C. After the algal maxima the water was still thermally stratified but the algae were in approximately equal concentrations with depth.

The oxygen gradient was sharper than the thermal gradient in 1969. Oxygen concentrations increased simultaneously with the Aphanizomenon bloom. Oxygen was absent below 2 m during July. The gradient was even steeper after the Aphanizomenon bloom when Anabaena flos-aquae increased above 2 m.

d. Squaw Lake

In Squaw Lake the maximal concentrations of Aphanizomenon occurred in the metalimnion during the summer of 1969 (Fig. 22). The maximum shifted in location down from 6 m on June 24 through the metalimnion to 9 m, the base of the metalimnion, on August 16. There were few filaments above and below this population stratum.

There was a decrease of water temperature from 10° on June 24 to 6° C on August 16 at the algal maximum. There was a similar change in oxygen concentration at the algal maximum from 4.5 ppm O_2 on June 24 to 3 ppm O_2 on August 16.

e. Elk Lake

Aphanizomenon in Elk Lake formed a metalimnetic maximum during the summer of 1969 (Fig. 23). Earlier, on May 17 the algae were less stratified, and high concentrations occurred also in the epilimnion. On succeeding sampling dates the algae were sharply stratified around 9 m. In contrast to Squaw Lake, this populations' maximum remained at the same depth during the summer.

The water temperature at 9 m increased from 7°C on May 17 to 11°C on August 26. The oxygen concentration decreased at this depth from 10.4 ppm on May 17 to 2.37 ppm O_2 on August 26. There was a slight maximum of oxygen above the region of algal stratification on June 17, June 7, and July 23.

2. SEASONAL VARIATION IN CELL TYPES

In Halsted Bay both the areal concentration of

heterocysts (numbers per m^2) (Fig. 24) and the heterocysts as percent of total cells (Fig. 25) were maximal during the summer months for all three study years. The maxima occurred in July of 1971 and in August of 1972 and 1974, prior to fall mixing and the maximal areal concentration of filaments each year. Although the heterocyst concentration varied seasonally there was one obvious heterocyst maximum each year, which increased in value successively from 1971, 1972, to 1974 (3019, 4620, 8160 heterocysts per m^2 respectively).

The akinetes in Halsted Bay, although present in low concentrations during the summer, did not reach maximal areal concentration or percent concentration until after isothermal conditions in October (Figs. 24, 25). This was prior to the exponential decrease in biomass per m^2. The maximal concentration of akinetes increased successively from 1971, 1972, to 1974 (650, 1382, 2736 akinetes per m^2 respectively).

The areal concentrations of end-cells (Fig. 24) had qualitative changes similar to the areal concentration of total cells. They both increased in concentration successively each year, with maxima occurring during the fall. End-cell concentrations increased early in the summer of 1974, corresponding to an increase in total cell concentrations.

The seasonal changes in percent end-cells in Halsted Bay increased to a maximum in late June or early July for all three years (Fig. 25).

Heterocyst concentrations in Carman Bay were low compared to those in Halsted Bay, with only one significant maximum during the spring of 1971 (2889 heterocysts per m^2) (Fig. 26). There were no other obvious maxima.

Akinete concentrations were low during the summer but increased during the fall, as in Halsted Bay (Fig. 26). In 1972 the akinete concentrations were maximum during October (298 akinetes per m^2). The 1971 akinete maximum was not evident.

In the Spencer Pond population the heterocysts per m^2 were maximum in concentration when the filament concentrations were maximal (Fig. 27). The greatest concentration of heterocysts sampled occurred in 1971 (2073 heterocysts per m^2).

The maximal concentration of akinetes occurred also at the time of maximal filament concentration in 1971 and 1972 (Fig. 27). For 1969, however, the akinetes were maximal in concentration prior to the maximal filament and heterocyst concentrations. The akinete concentrations sampled in 1971 and 1972 were comparatively lower than 1969 (36, 41, 242 akinetes per m^2 respectively). Low concentrations of heterocysts and no akinetes were found in the Squaw and Elk Lake populations.

3. NITROGEN FIXATION

Because of the various problems encountered, research on nitrogen fixation was confined primarily to a study of seasonal variation in acetylene reduction by the phytoplankton community in Halsted Bay. Information on

reduction by Aphanizomenon colonies was drawn from both data on isolated colonies and reduction by the total phytoplankton community (Aphanizomenon was approximately 40% of the total biomass).

Spencer Pond colonies had relatively high rates of fixation (2.0 μmoles/1000 heterocysts/hr. on June 8, 1972; 2700 filaments per ml the highest biomass sampled that year). This was the highest specific rate of fixation for all three lakes tested.

The net plankton from Carman Bay on June 7, August 25, and October 4 of 1972 showed no measurable fixation. On August 15 the rate of reduction was .7 μmoles/1000 heterocysts/hr. Aphanizomenon flos-aquae, Anabaena flos-aquae, and Anabaena spiroides were present.

In Halsted Bay a maximum of acetylene reduction by net plankton occurred in early spring, with a decrease through the summer (Fig. 28). The dominant blue-green algae present were Aphanizomenon flos-aquae, Anabaena flos-aquae, and Anabaena spiroides. The concentration of algae in the sample bottles was 20-56 times the concentration in the lake. The range in acetylene reduction was .2-1.4 μmoles ethylene/1000 heterocysts/hr. and .2-.5 μmoles ethylene/10^6 μm^3 algae/hr. Aphanizomenon was the dominant blue-green alga (50-98% of the biomass of the three blue-green species with heterocysts) except for June 7, when fixation was maximal and Anabaena flos-aquae was the dominant (1.4 μmoles/1000 heterocysts/hr. and .5 μmoles/10^6 μm^3 blue green algae/hr.

Acetylene reduction by isolated Aphanizomenon colonies in Halsted Bay was high on June 16 but then fluctuated in the July samples. On July 29 when 150 rafts were isolated there was no appreciable reduction. Because the results are variable and too many colonies are needed for measurable fixation this method was discontinued.

Because Aphanizomenon was a high percentage of the biomass in Halsted Bay, it is reasonable that fixation by this alga had a maximum early in the summer, with a decrease through July and August. The few times that colonies were isolated also indicate this. The reduction was highest when the percentage of Aphanizomenon heterocysts was highest, but not when the absolute number of heterocysts was the highest.

The decrease in efficiency in acetylene reduction during the summer may be caused by a phosphorus deficiency, because an increase in reduction occurred with added phosphorus at 20 ppb, but a reduction occurred at 40 ppb on August 25.

When algae were incubated with acetylene in the dark (black-taped bottle) no appreciable fixation occurred.

Lugol's solution stopped the acetylene reduction reaction, although the gas phase in the Lugol's samples contained less ethylene than the gas phase over the H_2SO_4 treated samples (Table 5).

The membrane-filtered samples, net-filtered samples, and samples injected with Lugol's before incubation

showed negligible fixation. Bacteria apparently were not reducing acetylene.

4. QUANTITATIVE MORPHOLOGICAL VARIATION

a. Frequency Polygons of Quantitative Characters for each Study Lake

Cell Width

The distributions for cell width of the vegetative cell (vc), end-cell (ec), and heterocyst (h) are unimodal and overlapping for all the study lake populations (Fig. 29). The total range for vegetative, end-cell and heterocyst widths is 1.25-5.75 μm, 1.25-5.75 μm and 2.25-6.75 μm respectively. The mode for the vegetative cell width is either 3.25 or 3.75 μm for the Halsted, Carman, Squaw, and Elk populations but is 5.25 μm for the Spencer Pond population. The highest mean width for vegetative cells, end-cells, and heterocysts was for the Spencer population (vc 4.9, ec 4.3, h 5.8 μm), Carman and Elk Lake populations had the lowest means (vc 3.5, ec 3.0; vc 3.3, ec 2.9 μm respectively).

The three distributions in akinete width are overlapping (Fig. 29). The distributions in the Halsted and Carman populations are skewed at the greater widths. The range in width for all three populations is 3.0-11.0 μm. The mean for the akinete cell width is highest for the Spencer population (7.0 μm) and lowest for the Carman Bay population (5.6 μm).

Cell Length

The distributions of vegetative, end-cell, and

heterocyst lengths are all unimodal and overlapping. The range for the vegetative, end-cell, and heterocyst lengths for all the populations is 2-10 μm, 1-25 μm, and 7-17 μm respectively (Fig. 30).

The means of vegetative, end-cell, and heterocyst length are highest for the Spencer Pond population (5.9 μm, 11.3, and 10.3 μm respectively). The frequency polygons for heterocysts are bimodal for the Carman Bay population (Fig. 30). However, there are only 57 observations for Carman Bay. The range in length is 5.5-15.5 μm for all the lake populations. The mean is highest for the Spencer population (11.4 μm) and lowest for the Carman Bay population (8.3 μm).

The akinete length distributions are skewed, as are the akinete widths at the greater lengths in Carman and Halsted Bay populations (Fig. 30). In the Spencer Pond population the distribution is skewed to the narrower widths. The Spencer Pond population has a higher mean akinete length (42 μm) (H.B. 27 μm; C.B. 32 μm).

Length-to-width-Ratios

The frequency distributions were unimodal for length/width ratios of vegetative cell, end-cells, and heterocysts except for the Carman Bay heterocyst ratio, which is bimodal (Fig. 31).

The Spencer population has the lowest mean vcl/vcw (1.3), and the Elk Lake population has the highest (1.8). The Squaw Lake population has the lowest mean aecl/we (2.2) and the Elk Lake population the highest (3.5).

The distribution of length to width for the akinetes is even for the Carman, Halsted, and Spencer populations. The range is 1.5-10. The mean is highest for the Spencer population (5.9). Carman and Halsted populations both have a mean ratio of 5.2.

b. Scattergrams of Cell Length and Width for each Study Lake and for each cell type

The length and width values in these diagrams are two different scales. An example is given where the x and y scales are equal for a line of slope equal to one. (Fig. 32).

For all the populations the range of cell size increased from vegetative cell, heterocyst and end cell to akinete. The means for the width of the end cell, vegetative cell, heterocyst, and akinete increase successively (Figs. 32-35. The commonly used taxa for Aphanizomenon populations are listed (Table 7).

The range for each cell type is compared to these published ranges of the common taxa (Figs. 36-39). There is no published range for the end cells. The range for each population of cell types overlapped. Each range overlapped with several previously described taxa.

c. Scattergrams of Seasonal Variation of Cell Size in Halsted Bay, Carman Bay and Spencer Pond

Halsted Bay population data on cell lengths and widths are divided into a lag phase, an exponential phase, a stationary-before-overturn phase, a stationary-after-overturn phase, and a winter-declining phase.

Carman Bay population data are divided into spring, summer, fall, and winter phases. The Spencer Pond population is divided into exponential, high-biomass, and declining phases.

The means and standard deviations in Halsted and Carman Bays for the vegetative-cell and end-cell lengths and widths did not vary in an obvious pattern, except for a small increase in cell width and length through the season in Carman Bay (.25-1.0 μm respectively). However, the vegetative mean width and length in Spencer Pond filaments increased by .5 μm and 1.5 μm and end-cells by 2.5 μm and 1.5 μm (Figs. 40, 41).

The heterocyst sample size differed for each phase, so the data are variable (Fig. 42). Akinetes were present only during certain phases, so there are no seasonal data.

d. Scattergrams of Colony and Culture Variation for Halsted Bay and Carman Bay

A colony has a smaller range and standard deviation in vegetative and end cell dimension that a culture grown from a single colony (Table 6). The range of each colony or culture from the Halsted Bay population overlaps but is distinctive (Figs. 43, 44). The scattergrams for each culture or colony are less in range than the range for the entire lake (Fig. 33). In some cultures the range of variation extends beyond the range in variation of cell dimensions from lake filaments.

There is greater variation in heterocyst length and width than in vegetative cells or end-cells in single

colonies from Halsted Bay. In one colony the range of variation was the same as that found in one culture. Cultures had heterocysts with overlapping size ranges, except for one culture with a distinctly separate range (Fig. 45).

The range of akinete lengths and widths in Halsted Bay colonies is greater in colonies of many filaments (max. 40000 filaments/colony) but narrower in colonies with relatively few filaments (max. 200 filaments/colony). The variation of length and width found in some of the isolated colonies is greater than the variation in dimensions of akinetes measured in the lake samples. The colonies with many filaments have akinetes of various lengths. Unless these large colonies are not of the same genotype, this variation indicates that akinete length is not a reliable taxonomic character to distinguish among strains (Fig. 46).

The Halsted Bay cultures collectively had a range in widths of vegetative cells, end cells, and heterocysts equal to that found in the lake, but the range in lengths is not so great. It may be that the culture environment did not bring out all the phenotypic length variation possible, or there may be genetic limits to the variation in length as well as width.

In the Carman Bay cultures the range of vegetative cell dimensions of filaments from colonies is narrower than it is in the filaments from the lake population

(Fig. 47). The narrow (2.0-2.5 μm) filaments found in the lake were not found in the colonies or cultures sampled. Filaments of narrow width may also be filaments that do not form colonies, but their cell size and shape intergrade with filaments that do form colonies.

5. QUALITATIVE MORPHOLOGICAL VARIATION

Cell shapes range from cylindrical to barrel for vegetative cells, heterocysts, and akinetes in each lake population. The distributions all have only one mode, with no obvious discontinuities in cell shapes (Table 8). However, the cell shape was judged subjectively, and therefore it is not a very reliable taxonomic character.

There were discontinuities in end-cell shapes (Fig. 8). A conical end-cell is typical of A. elenkinii (Hill 1966). A. flos-aquae and its varieties have cylindrical end-cells (Komarek 1958). No filaments were found with end-cells grading between conical (or ovoid) and cylindrical shapes. The filaments with conical or ovoid end-cells are in low numbers in Halsted, Carman, and Spencer populations. The highest concentration was found in the fall population in Carman Bay, when 14 filaments were measured. In addition to end-cell shape, these filaments can also be distinguished by their high vegetative and end-cell length-to-width ratio (Fig. 48).

Komarek (1958) distinguished forms of Aphanizomenon by their end-cell contents. Filaments with string-like protoplasm in the end-cells were classified as form

flos-aquae (Fig. 8).

Filaments with end-cells (contents with a string of protoplasm along the length) occur in Halsted Bay, Carman Bay, and Spencer Pond populations but not in the metal-imnetic populations in Squaw and Elk Lakes. However, filaments with string end cells were seen in a metal-imnetic population in Cassidy Lake (Table 9). Spencer Pond filaments have a greater proportion of these end cells than the other populations. This character may be restricted to a certain size filament and may possibly be a distinguishing character between strains or forms. The range in width of the vegetative cell for these filaments was more narrow than for the entire population. The more narrow filaments did not have string end cells.

6. UNUSUAL MORPHOLOGICAL VARIATIONS

Filaments were observed that did not fit Morren's (1838) description of Aphanizomenon. These were filaments with multiple heterocysts and akinetes, filaments with no distinctive end cells, and filaments with vegetative and end cells that were typical of Aphanizomenon (cylindrical to barrel-shaped) but with spherical cells (either vegetative, heterocyst, or an akinete) (Fig. 49).

Filaments were observed with up to three akinetes, three heterocysts, two heterocysts and one akinete, or two akinetes and one heterocyst. When more than one heterocyst or one akinete was present, the other heterocysts or akinetes were often less developed. Filaments with

both a heterocyst and an akinete were rare. Of all the filaments counted only one filament in 20,000 had both a heterocyst and an akinete.

Filaments with Aphanizomenon-shaped vegetative cells but no heterocysts, akinetes, or distinguishable end cells were found in all of the lake populations. These filaments may result from fragmentation of longer filaments.

A combination of cell shapes on one filament were seen. Spherical cells (all cell types) are a typical Anabaena characteristic. However, filaments were observed in Halsted Bay, Carman Bay, and Spencer Pond populations with cylindrical vegetative and end cells on one end of the filament and spherical vegetative and end cells on the other end (Fig. 49). A few filaments were seen with cylindrical vegetative and end cells but with a spherical heterocyst or akinete. These forms are rare.

DISCUSSION

The purpose of this investigation is to describe the habitats and morphological characters of natural populations of Aphanizomenon flos-aquae, and to compare the natural morphological variation with the variation in culture. Cultures often produce aberrant forms not found in the field populations. This field approach then produces a base of information to which variation in cultures can then be compared.

Ecology, nitrogen fixation, and the morphological variations of the populations are discussed. Information concerning the ecology is then related to the morphological variations in field and culture samples to aid in the discussion of the taxonomy of these populations.

1. ECOLOGY

Variation of Filament Density

Aphanizomenon grows in diverse habitats. It is found in flowing and standing water in temperate belts of the northern hemisphere but seldom in the tropics (Komarek 1958). It has often been recorded as a bloom-forming blue-green alga in lakes (Eberly 1967), and filaments are often present in large concentrations in productive lakes (Lake Minnetonka) during the summer (Hutchinson 1967). Jarnefelt (1952) collected filaments of Aphanizomenon in all of the lake types he sampled (eutrophic, dyseutrophic, oligotrophic, oligohumos, mesohumos, and polyhumus) and found them to be especially prevalent in the dyseutrophic habitat. It has also been

found in small oligotrophic lakes in northern Saskatchewan (Koshinsky 1965) and hard-water lakes in Wisconsin (Prescott 1962). Unlike most bloom-forming algae, Aphanizomenon has also been reported during the winter under the ice (Fjerdingstad 1966; Komarek 1958). It also forms deep-water strata in lakes (Eberly 1967 and the present study). Other habitats where Aphanizomenon species have been recorded include ponds with high inputs of organic matter (Fogg et al. 1973) and the present study; rivers, especially in areas of low flow (Pascher 1925; Baker 1974); and salt water (Fjerdingstad 1966).

The populations in this study are from diverse habitats, and the seasonal concentration curves are all unique. There are spring, summer, and fall maxima; epilimnetic and metalimnetic populations, high concentrations and low concentrations of phosphorus and nitrogen, and varying surface areas (1.3-202ha).

The Aphanizomenon population in Carman Bay had two maxima in 1971, one in the spring and one in the fall, with a summer minimum probably resulting from lower nutrient input into this bay. The population was present during the winter but did not increase, so its persistence may reflect low loss rates rather than positive rates of increase. Aphanizomenon in Spencer Pond was dominant for a relatively short period of time. The metalimnetic populations in Squaw and Elk Lakes were low in concentration compared to the other lakes, perhaps because of insufficient nutrients in the epilimnion, where higher

temperature and light should otherwise foster rapid increase (Baker 1973).

The biomass curve for the Aphanizomenon population in Halsted Bay was similar for all three years studied. The phases of change were similar to those reported for micro-organisms in a batch culture. There was no lag phase, but there was an exponential increase, a stationary phase, and an exponential decrease. During the winter the alga was not present in detectable concentrations.

In the spring the population increased exponentially for several weeks. That this increase occurred throughout the lake and not just at the main sampling station was verified for the initial increase in 1974 by sampling at nine different sampling stations (Baker and Baker 1976).

A stationary population has equal rates of gain and loss, that is, zero specific growth or rate of increase. The word "stationary" is not usually used with natural algal populations, although it is appropriate to apply it to the Aphanizomenon population in Halsted Bay during the summer for the following reasons. The biomass fluctuated after the period of exponential increase, but the fluctuations are small relative to the magnitude of the exponential increase in concentration. These fluctuations could be called oscillations around a carrying capacity (maximum "stable" amount of biomass supported by a particular habitat), and they may be real increases and decreases in algal concentrations throughout the lake. Alternatively, they may be brought about by a redistribution

of the algae by wind. The high biomass lasted for approximately three and one-half months each year. The specific rate of increase was not zero but fluctuated positively and negatively with an approximate average of zero. Other evidence to support the hypothesis of a stationary population is the relative constancy of the photosynthetic rate, concentration of phosphorus, and of carbon (all per unit chlorophyll) (Megard 1975).

In a population of Aphanizomenon flos-aquae, Healey and Hendzel (1976) also found no lag phase but an exponentially growing population (Lake 154) and a stable phase. They did not define "growing", however.

Aphanizomenon was 30-40% of the total algal community in Halsted Bay. The community was probably maintained during late summer by low specific rates of production and loss. Thus the algae had relatively small nutrient demands (Megard 1975).

The decline of the Aphanizomenon population in Halsted Bay in the fall was exponential, perhaps as an interaction of both decreasing growth rates and increasing loss rates. One source of loss is associated with the hypolimnion. When algae from several depths were collected at meter intervals and were incubated (millipore-enclosed plastic tubing) in the hypolimnion, their decay occurred within 10 days.

The maximum specific rate of change for each population ranged between .12 to .18, or a doubling time of 3 to 4 days. This is comparable to the doubling time of

110 hours (4.6 days) for a strain of Aphanizomenon flos-aquae grown in ASM culture medium at 15 and 20° C and 860 lux from Klamath Lake (O'Flaherty and Phinney 1970).

For populations in Halsted Bay, Carman Bay, and Spencer Pond the filaments increased throughout the epilimnion when the water was thermally stratified. However, during the fall overturn the increases occurred through the entire column in Halsted Bay and Carman Bay. There was evidently enough wind at the deep hole at all these sites to keep the filaments from accumulating at the surface. However, in protected shore areas and early morning calm hours the algae accumulated at the surface in Halsted Bay and Spencer Pond. Reynolds (1967, 1971) also found that surface scums in Shropshire Meres resulted from concentration of Aphanizomenon filaments previously distributed in a water layer several meters deep rather than from growth at the surface.

The position of the alga in the water column may result from interaction of gas vacuoles and wind currents. Gas vacuoles of blue-green algae have been shown to regulate buoyancy (Walsby 1973). During periods of calm the algae may rise to the surface as a result of increased formation of gas vacuoles. Collapse in gas vacuoles may cause the algae to sink. Although in Halsted Bay, Carman Bay, and Spencer Pond the wind-driven currents may keep the algae in suspension through the epilimnion regardless of gas-vacuole formation.

The populations were evidently able to regulate their

position in the water column or were regulated by thermal mixing patterns. In Halsted Bay and Carman Bay, when the thermocline descended during the late summer, the algae also descended. The descent probably indicated that the algae are primarily controlled by the thermal mixing patterns. This has also been reported by Haynes (1971), although he felt temperature was not the only controlling factor.

Thermal stratification is not necessary for positive specific rates of change in Aphanizomenon populations, however. In Halsted Bay the population concentration per ml was maximum before overturn. In contrast, areal concentrations per m^2 were at a maximum after overturn. The Carman Bay fall populations in 1971 and 1972 were at a maximum (both areal and volumetric concentrations) after overturn. In Spencer Pond the population was present only when the water was thermally stratified.

Also, Lund (1972) reported the two largest Aphanizomenon maxima in Esthwaite Lake occurred a week before overturn, but in 1966 the concentrations (per m^2) increased after overturn. This is in contrast to Ahlgren (1970), who hypothesized that the decrease of Aphanizomenon and increase of Oscillatoria in Lake Norrviken was a result of mixing that carried Aphanizomenon from the trophogenic layer. Oscillatoria then became dominant because of its lower light optimum.

Blue-green algae "grow" best when nutrients are lowest in concentration (Fogg et al. 1973). This is

paradoxical, because blue-green algae are characteristic of water receiving high nutrient inputs, yet the maximum in algal biomass occurs when the dissolved nutrient concentrations are low (Pearsall 1932). This may be a result of blue-green algae having a high affinity for phosphorus and ability to outcompete other algae when nutrients are low (Shapiro 1972).

In contrast the specific rates of change (S.R.C.) in the Halsted Bay population (1972) were highest when the phosphorus concentrations were high (30 ppb PO_4-P). Later in the summer when the biomass was at its maximum, the positive specific rates of increase were less and the dissolved nutrients were low (2-15 ppb PO_4-P). That the late-summer algal community became phosphorus-limited has been shown by other studies (Megard 1970). The highest S.R.C. for all three years occurred early in the summer (.15-.18 per day). Later in the summer, when the biomass was maximal, the S.R.C. only reached .06-.09 per day for all three years.

Aphanizomenon was therefore increasing in concentration and "growing" the fastest early in the summer, when biomass was still low and phosphorus was probably not yet limiting. Nitrogen was probably already limiting, as indicated by the high acetylene reduction by isolated Aphanizomenon colonies and concentrated plankton samples early in the summer of 1972. Megard's (1970) study showed the same relations. Later in the summer the population was limited by phosphorus and nitrogen. Hesley and

Hendzel (1967) also found nitrogen can be limiting even though a nitrogen-fixer is present because nitrogen fixation needs a certain level of phosphorus.

May and June were months of high S.R.C. for all the study populations for at least one year. This may be because of increasing light or temperature or both. It is paradoxical that blue-greens develop when light is high, yet light requirements in culture are comparatively low.

Temperature was measured in this study, and circulation patterns were inferred from the temperature profiles. These two factors will be discussed briefly.

The temperature range in which Aphanizomenon blooms is 20-25^{0}C; "maximum abundance" occurs at 25^{0} C (Gentile and Maloney 1968) or 20-24^{0} C (Lin 1972); "peak production" occurs at 23^{0} C (Hammer 1964); "maximum growth rate in culture" occurs at 26^{0} C (Gentile and Maloney 1968). An Aphanizomenon population in Kezar Lake increased in concentration when water temperatures were 13^{0} C, and the algal bloom occurred at temperatures ranging from 17 to 25^{0} C (Haynes 1975).

In this study the range of temperature tolerance was broad for populations in Halsted and Carman Bay but was narrower for the populations in Spencer Pond, Squaw Lake, and Elk Lake (Table 10). The populations in these study lakes may be comprised of many different strains, with narrower temperature limits than those of the entire population.

Maximal specific rates of increase occurred when temperatures were 12-18° C for the Halsted Bay and Spencer Pond populations, but 10-24° C for the Carman Bay population. The range for the temperature tolerance of Aphanizomenon was broad for the Halsted and Carman Bay populations (4-28° C), and narrow for the 1969 populations in Spencer Pond (10-28° C), Squaw Lake (6-10° C), and Elk Lake (7-11° C). The temperature range during the periods of maximal biomass was broad for Halsted Bay (8-26° C) and Carman Bay (8-20° C) and narrow for Spencer Pond (22-26° C).

The temperature optimum (temperature when increase rate is maximum) of these populations was low. It would be expected to correspond more closely to the periods of high specific increase rates rather than maximal biomass. The temperature range for the maximal specific rates of increase in this study was lower than during periods of maximal biomass.

Seasonal Variation of Aphanizomenon Cell Types

Lemmermann (1910) reported seasonal variation in the presence of specialized cells (heterocysts and akinetes) on Aphanizomenon filaments from a perennial population. The Aphanizomenon populations in Halsted Bay and Spencer Pond were not perennial but the cell types also varied seasonally, (Table 11). The filaments present in December through February had no akinetes or heterocysts. The Aphanizomenon population in Carman Bay was perennial, as was Lemmermann's population. However, these filaments

were usually without heterocysts or akinetes. No akinetes were found in the Elk or Squaw Lake Aphanizomenon populations for the months sampled (April through August). Heterocysts were present in Squaw Lake on all the sampling dates. Elk Lake had heterocysts present only in July and August (Table 11).

Frequency of occurrence of cell types may differ among lake populations. For example, the Spencer Pond population had the greatest frequency of heterocysts, and the Squaw and Elk Lake populations had no akinetes. The presence or absence and concentration of end-cells, heterocysts, and akinetes may depend on the environment. The lack of a cell type does not indicate lack of capability to produce this cell type under certain environmental conditions. The variability of occurrence of these cells makes use of characters in the taxonomy of these organisms questionable.

The possible functions of each of the cell types and how these functions may relate to seasonal variation of presence and percent concentration is discussed briefly below.

END CELLS

End cells were present on filaments in all the study lakes, but the percent of end cells varied seasonally between populations and within a population.

The function of end cells is unknown, but their presence has been shown to be related to nitrogen concentrations. When ammonium was supplied to a culture of

Gloeotrichia the filaments lost their whip-like form and became uniform in width along their length. Also, forms lacking long terminal hairs (end cells) usually have higher nitrogen content than do forms with hairs present (Fogg et al. 1973).

It seems reasonable that the percent end cells was higher during the summer months in Halsted and Carman Bay populations, if their formation is a function of low supplies of nitrogen. Concentrations of dissolved nitrogen are lower during the summer than in the winter (Megard 1970), the algal community has been shown to be nitrogen (ammonia)-limited in early July (Megard 1970), and the acetylene reduction tests were negative during the early winter months (November) but positive during the summer months, with a maximum in early summer.

High percent end cells with high specific rate of change values in the Halsted Bay population may indicate the alga is growing too fast to keep up with its needs for nitrogen. Also if the intercalary heterocyst is the site of nitrogen fixation and the end cells are located farthest from the heterocyst, perhaps the end cells are the last cells to receive the combined nitrogen from the heterocyst.

A number of functions for end cells could be hypothesized. Aphanizomenon filaments can reproduce by fragmentation of the filament, and perhaps the end cells aid in some way in the process of fragmentation. Short filaments with end cells on one end and a few vegetative

cells were often seen. Also, occasionally filaments with end cells in the middle of the filament were seen. Perhaps the filament breaks at these end cells. Or perhaps end cells function as cells of excretion or absorption of nutrients.

HETEROCYSTS

Heterocysts occurred during the spring, summer, or fall. Maximal concentrations per m^2 correspond usually to high filament concentrations. However, high filament concentration is not an indicator of high heterocyst concentration.

The primary function of the heterocyst is nitrogen fixation, but other functions have been reported. A scenescent and degenerate heterocyst may bring about breakage of the filament and therefore function in fragmentation. Heterocysts have been known to germinate. Also, they may function in control of spore formation. These and other functions have been reviewed by Fay (1973).

In Halsted Bay, as with the percent end cells, the maximum percent heterocysts corresponded usually to periods of the high specific rates of increase and not to periods of highest biomass per m^2. That heterocysts are most abundant during the active growth phase of a culture was also shown by Fogg (1949) and Fay (1969b). In Halsted Bay the highest percent heterocysts but not necessarily the highest absolute concentrations of heterocysts were usually at times of highest specific rates of increase.

The formation of a heterocyst is a function of low

levels of combined nitrogen in culture (Ogawa and Carr 1969, Fogg 1942). However, in lake studies the relationships between heterocyst abundance and nitrogen concentrations are not so evident. Horne and Fogg (1970) found no significant negative correlation of the rate of fixation with nitrate concentration in Esthwaite Water, a mesotrophic lake in the English Lake District. In the present study, although there is a gradient in heterocyst maximal percentage in the study lakes (Spencer, Halsted, Elk, Carman, Squaw highest to lowest respectively) there are not enough nutrient data to relate this gradient to available nitrogen.

The highest percentage of heterocysts and the highest absolute concentration of heterocysts per m^2 occurred during the summer months in Halsted Bay, when the water was low in combined nitrogen in the epilimnion. Percent and absolute concentrations of heterocysts decreased with overturn. In previous years this was when dissolved nutrient concentrations increased (Megard 1970). However, filaments with heterocysts were present in April and May when levels of combined nitrogen were high.

AKINETES

The akinete tides an algal population over an unfavorable period of growth; it usually forms at the end of the vegetative period (Komarek 1958). In culture akinetes form at the termination of the exponential phase of growth, and their formation can be prevented by maintaining steady-state growth conditions (Fay 1969a).

In the Halsted Bay population the akinetes were maximum in both percent and absolute concentration late in the "stationary phase" and much later than the exponential phase of increase. They were not, however, found from November through January when the alga was decreasing exponentially.

A limited supply of phosphorus has been suggested as the most important single factor controlling sporulation (Wolk 1965b, Gentile and Maloney 1969). But in Halsted Bay, however, spores were present only sporadically from July through September, when phosphorus was limiting, and they reached a maximum in concentration in October and December after overturn when nutrients increased. In previous years dissolved phosphorus was limiting during the summer (Megard 1970).

Low temperatures were previously thought to be a factor controlling the development of spores. Akinetes were only recorded during the colder months (Lemmermann 1910). However, Rose (1934) found spores both in the winter and the summer. In the Spencer Pond population spores were found only in the summer months when the alga was present. Also, in the Halsted Bay and Carman Bay populations spores occurred infrequently during the summer months from June through September.

The factors that induce akinete formation are complex and factors that directly influence formation are not obvious from field data.

Heterocysts have been implicated as possibly controlling

spore formation (Fritsch 1951). In the present study one out of every 20,000 filaments had a heterocyst and an akinete. If heterocysts do control spore formation, one would expect a high percent of filaments with heterocysts and akinetes. It is possible, however, that a filament with a heterocyst and an akinete could fragment, leaving filaments with either a heterocyst or akinete.

Nitrogen Fixation

Williams and Burris (1952) reported that Aphanizomenon flos-aquae does not fix nitrogen to a measurable extent. More recently nitrogen fixation has been reported in several studies (Stewart et al. 1968; Vanderhoef et al. 1975; Duong 1972; Brezonik 1973; Horne 1971), although this species may be relatively inefficient (Duong 1972).

The Aphanizomenon populations in this study reduced acetylene and presumably fixed nitrogen in Halsted Bay and Spencer Pond. The Carman Bay tests were run on the entire concentrated phytoplankton, and Aphanizomenon presumably contributed to the reduction. The maximal reduction rates measured decreased in value from Spencer Pond to Halsted Bay to Carman Bay. This was also the sequence for maximal percent heterocysts on Aphanizomenon filaments. However, more data are needed to draw conclusions on relationships between reduction and percent heterocysts.

In the Halsted Bay algal community and presumably also in the Aphanizomenon population, reduction was highest in early summer, with a decrease in reduction through

the summer. These results indicate that reduction was maximal when heterocyst frequency rather than the absolute number of heterocysts was high. Burns and Mitchell (1974) found a negative correlation between heterocyst frequency and levels of nitrate and total inorganic nitrogen. The number of heterocysts per ml was not significantly related to levels of inorganic nitrogen in the water. Duong (1972) found a negative correlation between acetylene reduction and filament density. Also in Halsted Bay fixation was highest (spring) when blue-green algal biomass was low, and the fixation decreased when the blue-green algal biomass increased. The algae may need more nitrogen when the specific increase rates are the highest, or phosphorus may not be limiting.

The nitrogen fixation in Halsted Bay occurred when levels of combined nitrogen decreased in the epilmnion. High nitrogren fixation at times of low combined nitrogen has been reported in many studies (Duong 1972; Horne 1971).

Since this study was completed, several diurnal studies have been reported. Duong (1972) found the highest rates of fixation with Aphanizomenon at sunrise. He concluded that the algae were quickly light-saturated. Vanderhoef et al. (1974) found 80% of fixation in a bloom of Aphanizomenon occurring between 800 and 1200 CDT. Therefore, the estimates in this study for nitrogen fixation may be conservative, but they are comparable because the samples were all incubated near solar noon.

Measuring the nitrogen fixation of an individual

species proved difficult in this study. As the bloom progressed, more colonies were needed to show a measurable and reliable reduction response -- more than feasible to isolate in a short time. This variable fixation rate among isolated colonies may indicate there are differences among colonies in rates of fixation, and/or the resolution of the technique is low.

Nitrogen fixation as a physiological process may be useful in distinguishing strains in culture. Some heterocystous blue-green species in other genera have strains that are non-nitrogen fixing (Fogg et al. 1973; Wilcox et al. 1975). But its use with field populations is questionable. Fixation depends not only on the strains present but also on the environmental conditions. All three Aphanizomenon populations probably fixed nitrogen but to different degrees.

2. MORPHOLOGY

LAKE POPULATIONS

There is no obvious separation into discrete taxa by cell size in any of the lake populations. The vegetative, heterocyst, and akinete cell shapes also have no obvious discontinuities. The ranges in cell size overlap but are distinct (vegetative cells, end cells, and heterocysts). There are no obvious differences among lake populations in cell size or shape (vegetative cell, heterocyst, or akinete).

There is a discontinutiy in end cell shape. The end cells are either hemispherical or very rarely conical

(or ovoid-shaped).

Filaments with end cells that are conical were found in low numbers in the Carman Bay, Halsted Bay, and Spencer Pond populations but not in the Squaw or Elk Lake populations.

The end cells with a string-like-protoplasm were found only in Carman Bay, Halsted Bay, and Spencer Pond populations in a similarly dimensioned filament. These end cells are present in all the epilimnetic populations but not in the metalimnetic (they were found in another metalimnetic population in Cassidy Lake). Within the same culture or colony some end-cell protoplasm may be string-like, others hyaline, and others partially vacuolated. Therefore, it is a variable character within a strain, and its absence is not a reliable character to distinguish taxa. The capacity to produce this type of end cell may be restricted to certain strains.

The most eutrophic lakes (Spencer Pond and Halsted Bay) have populations with the largest cells. The population in Carman Bay (a less productive lake) has the smallest cells. The metalimnetic populations do not have a distinctive cell size. The range in akinete dimensions is similar for the Halsted Bay, Carman Bay, and Spencer Pond populations. The mean length and width increases from the Carman Bay and Halsted Bay to the Spencer Pond populations.

Very little seasonal variation was found in cell dimensions in the Carman Bay and Halsted Bay populations.

In the Spencer Pond population the vegetative cells, end cells, and heterocysts increased in length and width. However, seasonal differences in mean and range of vegetative-cell, end-cell, and heterocyst length and width for each lake population was less than differences among lake populations.

Because there is less variation within a population seasonally than among different populations, these populations may differ genetically. Alternatively, the alga is very polymorphic, and the environment may vary less within a lake seasonally than among lakes. All the phenotypic variation possible may then not be expressed within a population.

Blue-green algae may be polymorphic (very variable strains) or it may be that the species are composed of a series of strains all different genotypically and phenotypically and with little polymorphism. With field data there is no direct way to determine whether the algae are polymorphic or whether the environment selects certain strains in different lake populations. Culture work with unialgal cultures from different locations would provide more information.

CULTURES

In cultures grown under the same environment, cell morphology would be similar if the alga is polymorphic or very different if the strains from the populations differ genotypically and phenotypically.

As with the lake populations, there is a separation

in the ranges of vegetative and end-cell dimensions in the Halsted Bay cultures. These ranges are distinct but overlapping.

The heterocyst and akinete size ranges are variable within a culture and therefore aren't good taxonomic characters. The heterocyst size range in some cultures and individual colonies is equal to the range found in the lake populations. The akinetes were not found in culture, but the length variation of akinetes in one colony is equal to the length variation found in the lake population.

The cell shapes found in the lake populations were also found in culture. Each culture has a narrow range of cell shape, as does a colony, with only one or two of the cell-shape categories present.

The differences present in the range of the vegetative and end-cell sizes between cultures is therefore genetic. That is, strains were selected that differed genetically in their vegetative and end-cell size and shape. The environment was the same in each culture initially -- same nutrient medium, same temperature, same light, and no stirring. This implies that the differences of cell sizes and shapes among cultures is from a series of strains (each culture a strain) not from a polymorphic population. The standard deviation and standard error in vegetative and end-cell size varies the least within a colony and more within a culture and a lake population (Table 6). However, the range in phenotypic variation of

cell size may be greater if a culture is subjected to a greater variety of environmental conditions.

Narrow filaments and those with conical or ovoid end cells in the Carman Bay lake population were not found in culture nor in colonies. Single filaments may be correlated with narrow cell size and conical or ovoid end cells. However, there is no discontinuity in cell size between these filaments and others.

The total range of cell dimensions for vegetative cells in the Halsted Bay lake population was found in culture. The cultures lacked the range in heterocyst dimensions and end-cell length.

3. TAXONOMY

The genus Aphanizomenon (Class Cyanophyceae, Fam. Nostocaceae) was first described by Linnaeus (1753), who named it Byssus flos-aquae. Morren (1838) subsequently renamed the genus Aphanizomenon with the type epithet A. incurvum.

Morren's species description is incomplete and unclear, so that the combination of Morren's generic epithet (Aphanizomenon) and Ralf's (1850) specific epithet (flos-aquae) is used. The starting point for nomenclature in the Nostocaceae is Bornet and Flahault (1886-1888). The present citation for A. flos-aquae is Ralfs ex Bornet et Flahault.

Morren in 1838 described Aphanizomenon as a colonial blue-green alga with planktonic trichomes that are bent or straight and tapered at the ends. The end

cells are long, vacuolated, and without pigment. The cross-walls may be shorter or longer than the lateral walls. Vegetative cells are barrel-shaped to cylindrical. The single akinetes are distant from the single intercalary heterocysts (weakly ellipsoid to cylindrical) (Komarek 1958).

Aphanizomenon has been differentiated from similar genera (Oscillatoria, Anabaena, Cylindrospermum, Rhaphidiopsis, and Anabaenopsis) by cell shape, end-cell shape, and heterocyst placement. Oscillatoria has no heterocysts and has cells with a lesser length-to-width ratio. Anabaena has barrel-shaped vegetative cells (rarely cylindrical) and end cells that are indistinguishable from the remainder of the vegetative cells (non-tapering trichomes). Both Cylindrospermum and Anabaenopsis have heterocysts that are located terminally. Rhaphidiopsis lacks heterocysts, but the trichome tapers (Komarek 1958).

The primary characters that have been used to differentiate Aphanizomenon species include the shapes and dimensions of 1) vegetative cells, 2) end cells, 3) heterocysts, and 4) akinetes. Other characters include the location and number of akinetes and heterocysts (Komarek 1958).

Taxonomic characters that are useful in distinguishing between these cultures and natural populations were vegetative cell and end-cell width, which overlap but have separate ranges. Heterocyst and

akinete dimensions are more variable.

To offer an explanation of the variations and to classify and name these blue-green populations, background information on the concept of a species is needed.

The controversy over useful taxonomic characters and the concept of a species is also an issue in other algal groups, but knowledge is in its infancy. In recent years several studies have been initiated on not only the blue-green algae but also green algae and diatoms to investigate polymorphism. In the diatom Mastogloia environment stress may cause alteration of frustule markings (Stoermer 1967). Also, the morphology of Anhistrodismus and Tetraedron is maintained by essential magnesium, nitrogen, and micro-elements (Schlicting & Bruton 1970).

Definition of a blue-green algal species requires a knowledge of its genetics and its ability to exchange genetic information in the natural environment. There is evidence of recombination under laboratory conditions (Bazin 1968). But to what extent recombination occurs in nature is unanswered.

Until more is known about the genetics of procaryotes, the morphology, physiology, and ecology of these organisms must be used to determine the affinities of strains and/or populations.

Fjerdingstad (1971) defines a blue-green species as

> "a collection of individuals with common characters, but varying within certain, more or less narrow limits."

This is in contrast to Drouet's (1973) definition, in which a blue-green species includes;

> "all individuals in the world which are clonally related to each other, no matter how desparate their morphology or physiology may be."

> "Descriptions should not only include morphological characteristics that are "typical" or "normal" but also variations produced during growth in every kind of environment."

This definition would be difficult to apply practically because it is impossible to know the past history of a species. Desikachary (1970) has a less extreme definition. He advocates studying the extent of variation of isolates under different culture conditions to

> "arrive at a picture of their taxonomic distances from a central species."

He uses the central species concept of "type" species. Golubic (1969) found that

> "sepeciation is a more or less continuous process resulting in statistically detectable but highly overlapping microspecies, each following normal distribution lines."

The result would be a taxon composed multidimensionally of "swarms" of taxoformae. He feels that clear delineation of taxa would be possible only when natural selection has cut out a "hiatus" between groups of continuously diverging microspecies. These are called group species, macrospecies, or composed species. He also mentions the possibility that some taxa may be

genetically restricted to a given form and others may be genetically capable of growing additional forms.

Taxonomic principles for blue-green algae may develop from the example of bacterial taxonomy because they are both procaryotes. However, certain basic differences may require modified or unique approaches to blue-green taxonomy.

How are procaryotic species defined? To some microbiologists;

> "the microbial species does not exist, it is impossible to define except in terms of a nomenclature type, and it is one of the greatest myths of microbiology" (Cowan 1962).

As more information is gathered we shall see not clear-cut species but a continuum of strains, grading from one extreme to another (Brock 1970; Staley 1973). The best approach might be to characterize each culture on its own merits over a wide range of environmental conditions and record the results. Each culture or strain can be treated as an entity (Skerman 1961).

Other systematists feel that

> "no less among bacteria than among complex forms of life one finds discontinuous clusters of morphologically and physiologically related populations rather than a continuous spectrum of types" (Ravin 1963).

The controversy may be resolved as more characters are involved in separating organisms. Also, there may be no fixed species with a single description. The variation within strains may be great enough to indicate

> "the species is merely a stage in an evolutionary process, a stage in a precarious equilibrium" (Cowan 1962).

I feel a reasonable approach is as follows:

> "to abandon the concept of species would be unfortunate... It seems that the only practicable method of classifying and naming micro-organisms is to establish a series of nodal points along the continuous chain of variants and to record the organisms at these nodes, and for some distance on either side of them as constituting species" (Wilson 1961 in Cowan 1955).

The taxonomic unit in bacteriology is the clone or strain, a population of genetically identical cells derived from a single cell (Brock 1970). Rather than classifying microbes by breaking them down into orders, families, etc., it might be better to build up from the smallest practical unit, the strain (isolate) or, if it has been derived from a single cell, the clone (Cowan 1962).

The opposing view is that a workable taxonomy cannot be based on the clone as a taxonomic unit. It would be necessary to culture samples from populations and separate strains and compare with known strains, although some may not survive.

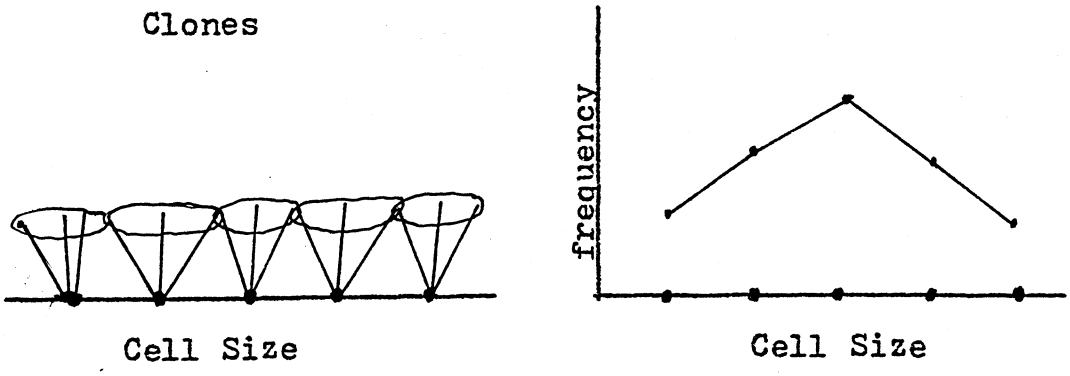
I feel it is important first to know range of variation of populations in lakes and then culture for deviation and range of variation for single strains. Then one must have knowledge at least of morphological variation in a natural population to which culture data could then be compared.

If the critical taxonomic characters were not

included, the series of strains may appear to be continuous rather than clustered (Stanier et al. 1971).

A lake population may be a collection of clones. The alga overwinters as akinetes or filaments. Each akinete or filament then divides to produce many filaments. Differences may exist in the cell size, cell shape, or cell contents among the original filaments or akinetes. These differences are then passed on to the clonal offspring. Supportive evidence for this is the continuum of variation within all of the populations, with no consistent and distinctive breaks. Also, the cultures grown under similar conditions have different but overlapping ranges in cell size. How much greater a range may be produced by a colony grown under a variety of conditions is unknown. The size range of the vegetative and end cells differs among populations.

Example



Overwintering Akinetes or Filaments

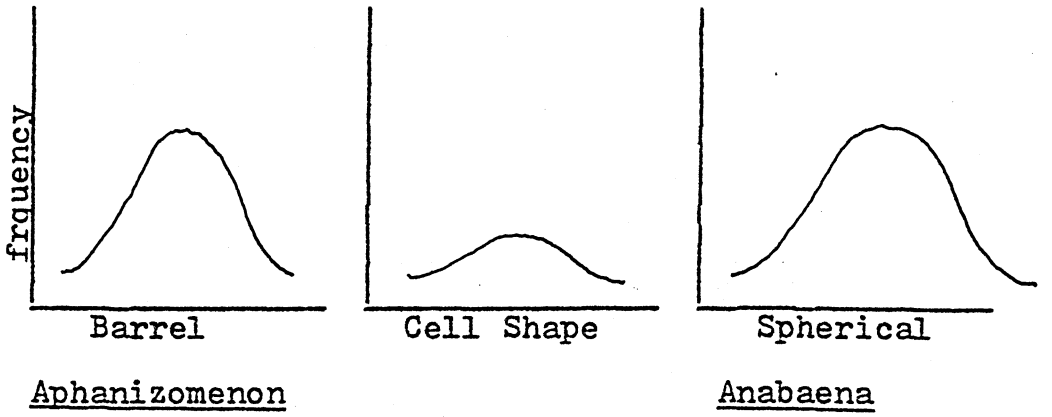
The environment may select out a greater proportion of several strains over the other strains present. Depending on the strains selected, the mean

cell size of the population may vary. The means of the vegetative cell dimensions for four populations clustered except for the Spencer Pond population. The same size was selected out of the ranges present. The means of the end-cell, heterocyst, and akinete size did not cluster. The Spencer Pond population had the highest mean cell size and the Carman Bay population the lowest. Perhaps, if a population were placed in a different environment, a different size strain would be selected. One culture was selected from the Halsted Bay population which had the range of vegetative cell size found in the Spencer Pond population.

There was a hiatus between forms with a conical or ovoid end cell and those with a cylindrical end cell. Characters correlated with filaments of this type included a greater length-to-width ratio and a slightly tapering filament. These filaments were rare.

Aphanizomenon (cylindrical cells) and Anabaena (spherical, barrel-shaped cells) are usually distinct taxa. But there is a gradation of filaments with cylindrical cells to filaments with spherical and barrel-shaped cells (Fig. 50). Also, filaments with both cylindrical and spherical cells are rare. There are also filaments with spherical akinetes, heterocysts, or end cells. It is questionable whether these are rare mutants that look morphologically like links between the two genera or are actually filaments from

strains with characters between two "groups of strains" (Anabaena and Aphanizomenon).



Blue-green algae reproduce asexually. But recombination and also mutation are reported in culture at the rate of 4.5-491 x 10^{-9} cells and 1 x 10^{-8} cells respectively (Baxin 1968; Hungate 1962). Mutations or recombination are immediately expressed in a procaryote.

For example, if the recombinant or mutant occurs during the spring in Halsted Bay, its density at the end of a summer can be computed if it is assumed that:

a. the volume of water is 8.63 x 10^{12} ml
b. 32 x 10^{16} cells are present (a very high estimate - 2000 filaments per ml)
c. the doubling rate is four days for all four months for the recombinant or mutant with all the descendants surviving
d. approximately two mutations or recombinations occur with the above density of cells

There would be less than one cell per liter of this mutant or recombinant at the end of a four-month season, assuring no new mutations after the initial two.

Therefore, the filaments with characteristics of both Aphanizomenon and Anabaena probably develop from akinetes or filaments that overwinter but are not

selected. One conclusion is that nature has selected Aphanizomenon and Anabaena strains for strains that have one or the other groups of characteristics but rarely a combination of them.

The study populations studies would ordinarily be classified as A. flos-aquae, A. flos-aquae var. klebahnii, A. gracile, or A. elenkinii (Table 7).

In these populations classification is based on the cell type and the statistic. If the means or ranges in cell dimensions for the study populations are compared to the range of dimensions in described taxa, the study populations include all four commonly used taxa plus a range outside of these.

For example, in the Carman Bay population the vegetative cell mean length and width are within the range described for A. flos-aquae var. klebahnii (Geitler 1932), the akinete mean length and width is within the range described for A. gracile, and the heterocyst mean length and width are not included in any of the ranges (Table 12).

If the range of dimensions for all the study populations is compared to the range of described taxa, all the four taxa are present and a range outside of all of these. Each population has a vegetative cell, heterocyst, and/or an akinete within the range of described taxa and outside all of them (Table 13). Exceptions are the Squaw and Elk Lake populations where

cells were not large enough for Aphanizomenon flos-aquae. This may result from the small sample size.

Komarek's revision of Aphanizomenon includes most of the variation present in the study populations (Table 14). He divided the species Aphanizomenon flos-aquae into two forms separated by cell width, colony formation, and end-cell contents. He found a bimodal curve (2-4.5, 4.5-7 μm) for cell width that separated the two forms. This separation was not found in my study populations, for there was a continuous range in cell width. However, end cell contents and colony formation may be correlated characters.

Drouet (1973) divided Aphanizomenon taxa into two new taxa based on end-cell shape (Calothrix and Rhaphidiopsis). The present study supports his view that the ovoid and conical end-cell shape are distinct from a cylindrical and hemispherical end-cell shape. Gradations between these two groups of end-cell shapes were not found. Therefore, A. elenkinii is distinct from the other four taxa on the basis of its end cell (also length-to-width ratio of cells, and tapering filament).

I feel strongly that Drouet's revision of the Nosocaceae with cylindrical trichomes should not be utilized! I feel Drouet lumps species prematurely without published evidence to substantiate his revision. In this study filaments with a spherical end cell on one end and cylindrical end cell on the other end were found. Drouet's classification would place such

a filament into two genera.

Whether to lump or split taxa is controversial. Splitting taxa is useful when it results in a highly descriptive precision and when causes of variability and relations between forms are not clear (Golubic 1969). Descriptions add information about character variation in relation to the environment.

Lumping gives a clearer indication of relationships among forms and also reduces the number of names (Golubic 1969). The reasons for lumping must be clearly documented.

At present there is no adequate definition of what constitutes a "lump," or a species of a blue-green alga. Unless supportive data (especially genetic) on character variation is provided for field populations, it is premature to combine taxa.

Because of the lack of any reliable separating character, it seems reasonable to group all of the study lake populations into one taxon (except the 14 filaments measured that were clearly A. elenkinii).

For the future identification of populations two options are possible. If the description of a population falls definitely into the range of a previously described taxon such as A. flos-aquae var. klebahnii, I feel the variety epithet should be added. The additional epithet adds information on the range of variation in the population. An alternative, which I

feel is preferable, is to use the species citation with a range of variation for the cell types in a population.

I advocate use of the taxon Aphanizomenon flos-aquae Ralfs ex Bornet et Flahault, plus additional information on range of cell size, shape, and contents. The range of variation is similar to that of Komarek's populations except for akinete length and multiple heterocysts and akinetes (Table 14).

Many of the previously described taxa could be included in this specific name. Table 15 lists these taxa. Group I contains all the taxa included by Komarek plus taxa that fit the description I have used. Group II include taxa with end cell shapes that are conical or ovoid and are lumped by Drouet and probably belong to a distinct taxon. Group III taxa are questionable until more information is available. To undertake a more complete revision of the genus requires more field and lab information and a more detailed study of previous descriptions.

For future research, the possible morphological variations within a population in different environmental conditions should be examined. Reciprocal lake transplants of a sample of a population cultured in the field or in the lab would provide information. Field cultures are possible with chambers enclosed will millipore filters. More phenotypic variability may be produced by the same genotype, and/or the variation of the strains selected could differ. This

approach does not indicate the cause or origin of the variation.

To obtain more precise information on the nature of morphological variation, a clonal culture grown under lab or field conditions is needed. The range of variation produced in a clonal culture would presumably be phenotypic. In cultures grown in the field the variation presumably occurs in a lake population. In lab cultures, where the environmental conditions can be controlled, relationships between environment and morphological variation can be studied, for example morphological variation during different phases of growth.

Also information on percent frequency and time of formation of heterocysts and akinetes would be provided by lab cultures. Some strains may have a higher possible maximal percent heterocysts or akinetes than others.

The formation of end cells would also most effectively be studied in lab culture. How are they formed? Are the numbers and percent concentration related to the phase of growth or to the amount of combined nitrogen in the medium?

Culture of filaments with one-half spherical cells and the other half cylindrical would be very interesting.

SUMMARY

1. The Aphanizomenon populations in this study occurred as a summer bloom of relatively long duration - six months (Halsted Bay); a perennial population (Carman Bay); a summer bloom of short duration - two months (Spencer Pond); and two metalimnetic populations (Squaw and Elk Lakes).

2. Aphanizomenon populations increased in the epilimnion (Halsted Bay, Carman Bay, Spencer Pond), and metalimnion (Squaw and Elk Lake), also throughout the lake when water was not thermally stratified in Halsted Bay and Carman Bay. The population maxima occurred at various times between May and October.

3. In the Halsted Bay and Spencer Pond populations the initial exponential increase in concentration occurred through the epilimnion, and surface blooms resulted from lack of wind mixing.

4. The maximum specific rate of change during the exponential phases of all the populations was .12-.18 or a doubling rate of 3 to 4 days.

5. In the Halsted Bay population growth phases similar to phases reported in bacterial cultures were observed - no lag phase but an exponential increase phase, a stationary phase, and an exponential decrease phase. These growth phases have not been reported for natural populations of algae previously.

6. The range of temperature tolerance for the Aphanizomenon populations includes times of maximal

specific rates of change and maximal biomass. The maximal specific rates may relate to times of optimal temperature 16-20° C Halsted Bay; 12-18° C Spencer Pond; 10-16° C Carman Bay (spring 1971) and 16-24° C Carman Bay (fall 1971 and 1972). The temperature range at times of maximal biomass was more broad, 8-26° C.

7. The position of the algae in the lake vertically in the epilimnion is probably controlled by thermal mixing patterns.

8. Heterocysts occurred in all of the populations but with varying frequency. The maximal percent of heterocysts in the populations decreased from Spencer Pond, Halsted Bay, Carman Bay, and Elk Lake to Squaw Lake. They were present only during spring through fall. Akinetes were present only in the Halsted Bay, Carman Bay, and Spencer Pond populations. The maximal concentrations of akinetes occurred usually after the heterocyst maximum.

In the Halsted Bay population the percent heterocyst concentration was highest during the exponential phase of increase, the numbers of heterocysts per m^2 highest during the stationary phase, and the numbers of akinetes per m^2 highest during the late stationary phase. These differences in heterocyst and akinete concentrations may be environmentally induced and therefore were not used to distinguish populations or taxa.

9. Nitrogen fixation per unit (acetylene reduction) was maximal in the Halsted Bay algal community in early

summer and decreased through the summer. All three populations (Halsted Bay, Carman Bay, Spencer Pond) reduced acetylene but to varying degrees. The Aphanizomenon colonies isolated from Halsted Bay reduced acetylene, but the results were variable. Therefore, with the present technique acetylene reduction as a taxonomic character would be more valuable (less variable) in culture (either field or laboratory) than it is in natural populations.

10. The ranges in cell size (vegetative cells, end cells, and heterocysts) for all five populations overlapped yet were distinct. The distributions for each quantitative character had one mode within each populatuion. There was no difference in range for the akinete cell size among populations.

11. There is no indication by cell size that these populations in nature consist of different taxa among or within populations. There was a greater variation in means and ranges of vegetative cell size and end-cell size among populations than within a population seasonally.

12. There were no obvious discontinuities in distributions of vegetative, heterocyst, or akinete shapes.

13. The distribution of end-cell shapes was discontinuous. Cells were either cylindrical with a hemispherical end, or conical or ovoid. Very few (14 of 3000 filaments measured) conical or ovoid end cells were seen.

14. The ranges of vegetative and end-cell size differed among cultures but overlapped. The range in heterocyst size differed among cultures, but one culture and some colonies had a range found in the Halsted Bay population. The size of the akinete was also variable within a colony. Therefore, vegetative-cell and end-cell size and shape are more reliable taxonomic characters.

15. The cell shape (vegetative and end-cell) and cell size overlapped but were distinct among cultures. There was no indication of different taxa. If the algae are polymorphic the strain in each culture grown under similar conditions should be similar in cell size and shape.

As an alternative a population may be composed of a continuous series of strains that differ in minor ways in cell size and cell shape. In each lake population a range of strains is present, but certain strains are selected and form the dominant biomass. This would explain overlapping ranges but different means in cell size.

16. It is questionable how discrete are the Aphanizomenon and Anabaena strains. Rare filaments were seen with characters of both.

17. I recommend use of the taxon Aphanizomenon flos-aquae Ralfs ex Bornet et Flahault, with a range of variation, that includes all of the populations studied (except for the few filaments with ovoid or conical end

cells). Komarek's (1958) description of this taxon includes most of the size variation I found. However, filaments with spherical cells and multiple (up to 3) heterocysts or akinetes would also be included. This lumping is recommended on the basis of the lack of any reliable separating character. However, if a population's cell dimensions are similar to a taxon published then the previously published epithet should be used because it conveys information on the range of variation present.

18. I do not advocate Drouet's classification because his data are not published and thus do not allow a comparison with the results of this study. Also, there is no evidence from my populations that the alga is polymorphic.

19. If other natural populations are described in other habitats, then the above epithet could be used along with a range of variation present.

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TABLE 1. Morphometry of the Five Study Lakes

Lake	Area (ha.)	Volume ($10^6 M^3$)	Max. Depth (m)	Mean Depth (m)	Station Depth (m)
Halsted Bay	220	8.63	10.1	3.9	8.5
Upper Lake (Carman Bay Megard 1970)	808	46.97	15.5	6.0	9.0
Spencer Pond					
1969	1.25	.017	2.5	1.4	2.5
1971	.87	.012	1.5	.8	1.5
1972	.77	.011	1.25	.6	1.25
Elk Lake (Megard 1967)	101	11.2	30	11	26
Squaw Lake (Bland 1971)	65		23		23

TABLE 2. Water Chemistry of the Five Study Lakes

Lake	$CaCO_3$ Alkalinity meg/L	Conductivity Micromhos	Ca^{++} meg/L	Mg^{++} meg/L	PO_4^{++} P ppb	NO_3^- N ppb	NH_4^+ N ppb
Minnetonka (Megard 1974)	2.1-2.9	317	1.35	1.32			
Halsted Bay (1972)					1.5-948	3.0-182	0-3100
Carman Bay (1972)					0-13	5.0-136	2- 220
Spencer Pond (1968)	.4- .5	79-105	.07- .57	.02- .39	July 23, 1969 35-67		
Squaw Lake (1968)	1.0-1.17	128-161	.90-1.10	.11- .49	July 23, 1969 9.5-22.6		
Elk Lake (1968)	2.9-3.5	288-363	1.30-2.39	.62-1.32	July 11, 1966 10		(Megard 1967)
					Oct. 29, 1966 17-75		
Farm Pond (1968)					July 23, 1969 1680		

TABLE 3. Variation in Algal Counts on Data From Halsted Bay and Carman Bay Populations

	Halsted Bay July 28, 1974	Carman Bay October 13, 1971
1. Within a Chamber		
N	5	5
$\chi^2_{.05}$	9.49	9.49
χ^2 sample	1.34	4.4
coefficient of variation	2.1%	4.3%
2. Within a Bottle		
N	5	7
$\chi^2_{.05}$	9.49	12.59
χ^2 sample	38.6	22.6
coefficient of variation	11%	7%
3. Same Sampling Station		
N	5	4
coefficient of variation	17%	12%
4. Diff. Sampling Stations		
N	9	
coefficient of variation	19%	

TABLE 4. Variation in Percent Cells Estimates

	Coefficient of Variation C.V.	Chi-square
VII 28 1974 each N=5 (50 filaments)		
$\chi^2_{.05}$ = 9.49 d.f.=4		
Within a Chamber		
vegetative cells	4.7	6.0
end cells	8.8	3.4
heterocysts	15.2	1.8
Within a Bottle		
vegetative cells	4.2	7.8
end cells	6.7	1.2
heterocysts	11.7	1.1
Same Station Different Bottles		
vegetative cells	8.6	6.1
end cells	14.1	7.5
heterocysts	21.9	18.1
Different Stations N=8		
vegetative cells	6.8	
end cells	15.0	
heterocysts	17.5	

TABLE 5. Comparison of Lugol's Solution and H_2SO_4 for Effectiveness in Stopping the Acetylene reduction Reaction

	Incubation Period Minutes	moles - Ethylene/Bottle
Lugol's	20	7.9
	40	13.9
	60	20.5
H_2SO_4	20	10.4
	40	21.7
	60	30.2

TABLE 6. Variation in Cell Dimensions (Microns) for a Colony, Culture, Lake Sample (One Date), and Lake Population (All Dates) in the Halsted Bay Population

	Colony					
	Vegetative cell		End Cell		Heterocyst	
	L	W	L	W	L	W
Observations	16	16	15	15	5	5
Mean	4.5	3.6	7.3	3.2	.5	5.6
Standard error (mean)	.1	.04	.5	.09	.2	.2
Confidence limits for pop. mean (95%)	+-.2 4.3-4.6	.1 3.5-3.7	1.0 6.3-8.3	.2 3.0-3.4	.2 8.0-8.9	.2 5.1-6.0
Standard deviation	.3	.2	1.8	.4	.4	.4
Coefficient of Variation %	7.4	4.8	25	11	4	7

TABLE 6. con't. Variation in Cell Dimensions (Microns) for a Colony, Culture, Lake Sample (One Date), and Lake Population (All Dates) in the Halsted Bay Population

	Culture					
	Vegetative Cell		End Cell		Heterocyst	
	L	W	L	W	L	W
Observations	64	64	51	16	25	25
Mean	5.2	4.4	10.0	4.1	7.7	5.0
(mean) Standard error	.15	.05	.50	.19	.15	.10
	.3	.1	1.0	.4	.3	.2
Confidence limits for pop. mean (95%)	1.9-5.5	4.3-4.5	9.0-11.0	3.7-4.5	7.4-8.0	4.8-5.2
Standard deviation	1.21	.37	3.6	.76	.76	.48
Coefficient of Variation %	23	8	36	19	10	10

TABLE 6. Variation in Cell Dimensions (Microns) for a Colony, Culture, Lake con't. Sample (One Date), and Lake Population (All Dates) in Halsted Bay Population

	Lake Sample					
	Vegetative Cell		End Cell		Heterocysts	
	L	W	L	W	L	W
Observations	26	26	21		7	7
Mean	5.0	3.8	9.9		8.6	4.9
Standard error (mean)	.2	.1	.9		.4	.2
Confidence limits for pop. mean (95%)	.3 4.7-5.3	.1 3.7-4.0	1.8 9.1-11.7		.9 7.8-9.5	.5 4.4-5.4
Standard deviation	.8					
Coefficient of Variation %	15					

TABLE 6. Variation in Cell Dimensions (Microns) for a Colony, Culture, Lake con't. Sample (One Date), and Lake Population (All Dates) in the Halsted Bay Population

	Lake Population					
	Vegetative cell		End Cell		Heterocyst	
	L	W	L	W	L	W
Observations	2022	2022	1585	953	494	494
Mean	5.2	3.8	9.5	3.5	9.2	5.0
(mean) Standard error	.02	.01	.08	.05	.07	.03
Confidence limits for pop. mean (95%)	.04 6.2	.02 3.8	.15 9.4-9.7	.09 3.4-3.6	.15 9.1-9.4	.05 5.0-5.1
Standard deviation	1.0		3.1	1.4	1.7	.6
Coefficient of Variation %	19	11	33	40	19	12

TABLE 7. Six of the Commonly Used Taxa Within the Genus Aphanizomenon

Aphanizomenon flos-aquae Ralfs ex Born. et Flah. 1888

Aphanizomenon flos-aquae Var. Klebahnii Elenkin 1909

Aphanizomenon gracile Lemm. 1910

Aphanizomenon elenkinii Kisel 1951

Komarek 1958

Aphanizomenon flos-aquae f. flos-aquae

Aphanizomenon flos-aquae f. gracile (Lemm.) Elenk., 1938

TABLE 8. The Distribution of Cell Shapes for Each Lake Population (See Fig. 29 for Cell-Shape Types)

Cell-Types	Halsted Bay	Carman Bay	Spencer Pond	Squaw Lake	Elk Lake
Vegetative Cell					
		32			
1.	101	25			
2.	1455	268	2	6	22
3.	1285	148	201	85	75
4.	23	3	33	9	3
Heterocyst					
1.	73	7	7		
2.	331	33	113		
3.	11	4	2		
4.					
Akinete					
1.	20		5		
2.	113	42	25		
3.	6				
4.					

TABLE 9. Comparison of Range of Cell Dimensions (Microns) for Filaments with String End Cells and for All Filaments in a Lake Population

Filaments	Halsted Bay	Carman Bay	Spencer Pond	Carman Cultures	Cassidy Lake
String End Cells					
WV	3.5-6.0	3.0-5.5	4.5-6.0	2.7-4.7	3.1-4.3
WE	3.0-5.0	3.0-4.5	3.5-6.0	1.8-4.9	5.2-8.2
All Filaments					
WV	2.5-6.0	1.0-5.5	3.0-6.0		
WE	1.5-5.5	1.0-5.5	3.0-6.0		

TABLE 10. Range in Temperature (°C) for the Maximum S.R.C., Optimum Biomass, and Presence of *Aphanizomenon* Populations

Lake	S.R.C.	Optimum Biomass	Presence
Halsted Bay	12-18	8-26	4-28
Carman Bay			
	10-16(1971 Spring)	8-20	4-28
	10-24(1971 & 1972 Fall)		
Spencer Pond	12-18	22-26	10-28
Squaw Lake			6-10
Elk Lake			7-11

TABLE 11. Presence of Cell Types Seasonally (Sterile Filaments-SF, Filaments with Heterocysts-H, Filaments with Akinetes-A, Filaments with a Heterocyst and Akinete-AH

		J	F	M	A	M	J	J	A	S	O	N	D	f=few
Lemmermann (1900)	SF	+	+	+	+	+	+	+	+					
	H	+	+	+	+	+	+	+	+	+	+	+	+	
	A	+								+	+	+	+	
	AH	+								+	+	+	+	
Halsted Bay	SF	+			+	+	+	+	+	+	+	+	+	
	H				+	+	+	+	+	+	f	f		
	A						f	f	f	f	+	+		
	AH								rare					
Carman Bay	SF	+	+	+	+	+	+	+	+	+	+	+	+	
	H				+	+	+	+	+	+	+	f	f	
	A										+	+	f	
	AH													
Spencer Pond	SF				+	+	+	+	+	+	f			
	H				+	+	+	+	+	+	+			
	A				+	+	+	+	+	+	+			
Squaw Lake	SF					+	+	+	+					
	H					+	+	+	+					
	A													
Elk Lake						+	+	+	+					
								+	+					

TABLE 12. Classification of Lake Populations on the Basis of Mean Cell Size for Vegetative Cells, Heterocysts, and Akinetes

	Aphanizomenon flos-aquae	Aphanizomenon flos-aquae var. Klebahnii	Aphanizomenon gracile	Aphanizomenon elenkinii	None
Halsted Bay	H	VC, A			
Carman Bay		VC	A		H
Spencer Pond	VC, H				A
Squaw Lake		VC			
Elk Lake		VC			H

TABLE 13. Classification of Lake Populations on the Basis of Range of Cell Size for Vegetative Cells, Heterocysts, and Akinetes

	Aphanizomenon flos-aquae Ralfs ex Born et Flah 1888	Aphanizomenon flos-aquae Var. klebahnii elenkin 1909	Aphanizomenon gracile Lemm. 1910	Aphanizomenon elenkinii Kisel. 1951	None
Halsted Bay	VC, H	VC, H, A	VC, A	VC, H, A	VC, H, A
Carman Bay	VC, H	VC, H, A	VC, A	VC, H, A	VC, H, A
Spencer Pond	VC, H, A	VC, H, A	A	VC, H, A	VC, H, A
Squaw Lake		VC	VC	VC	VC
Elk Lake		VC, H	VC	VC, H	VC, H

TABLE 14. Comparison of Range of Variation of Cell Size in the Study Populations and Komarek's Populations (Microns)

	Vegetative Cell		End Cell		Heterocyst		Akinete	
	L	W	L	W	L	W	L	W
Minnesota Populations	2-10	1.8-5.8	1-25	1.8-5.8	5.5-15.5	2.3-6.8	7-82	3.0-11.0
Komarek (1958)	2.5-16.5	2-8	35	1.2-5.5	3.5-18	2.6-9.5	20-220	3.5-9.6
f. flos-aquae	4.5-8	4.5-7			7-28	5.5-9.5	30-220	6.7-10
f. gracile	2-5.2	2-5.0			3.5-22	2.6-6.5	20-85	3.5-7

TABLE 15. Published taxa of Aphanizomenon (Group I probably taxa, Group II taxa distinguished by end-cell shape, Group II questionable taxa)

Group I		
Aphan. flos-aquae f. flos-aquae		1958
Byssus flos-aquae	L.	1753
Aphan. flos-aquae	(L.)Ralfs	1850
Aphan. flos-aquae	Ralfs ex Bornet et Flah.	1888
Aphan. flos-aquae f. typicum	Elenk.	1883
Aphan. incurvum	Morr.	1838
Aphan. incurvum	Morr. ex Born. et Flah.	1888
Aphan. holsaticum	P. Richt.	1896
Aphan. flos-aquae f. holsaticum	Elenk.	1938
Aphan. platensis	Seckt	1922
Aphan. flos-aquae f. gracile	(Lemm.) Elenk.	1938
Aphan. flos-aquae V. gracile	Lemm.	1898
Aphan. gracile	Lemm.	1907
Aphan. flos-aquae f. gracile	Elenk.	1938
Aphan. flos-aquae V. Klebahnii	Elenk.	1909
Aphan. flos-aquae f. Klebahnii	Elenk.	1938
Aphan.	Morren	1838

TABLE 15. con't. Published taxa of Aphanizomenon (Group I probably taxa, Group II taxa distinguished by end-cell shape, GroupIII questionable taxa)

Group I		
Aphan.	Morr. ex Born. et Flah	1888
Aphan. platensis	Seckt	1921
Aphan. flos-aquae	Breb.	
Aphan. morreni	Kufferath	1942
Aphan. flos-aquae (Lyngb.) Breb. V. gracilis Nov. var.	Lemm.	1898
Limnochlide (flos-aquae)	Kutzing	1843
Anabaena flos-aquae V. gracile	Lemm.	1898
Rhaphidiopsis	Fritsch et Rich	1929
Calothrix	Agardh	1824
Aphan. flos-aquae var. hercynicum	Kutzing (as "hercynica") ex Forti	1907
Aphan. cyaneum	Ralfs	1850
Aphan. flos-aquae fa. incurvatum	Tschernov	1950
Aphan. flos-aquae var. Haerdtlii	Fjerdingstad (as "Hardtlii")	1966
Aphan. Ussaczevii	Proskkina-Lavrenko	1968
Aphan. ovalisporum var. capsicum	Usaczev (as "caspica") ex Proshkina-Lavrenko et Markova	1968
Aphan. flos-aquae fa. macrosporum	Fedorov	1970
Aphan. flos-aquae var. minus	Nair (as "minor")	1967

TABLE 15. con't. Published taxa of Aphanizomenon (Group I probably taxa, Group II taxa distinguished by end-cell shape, Group III questionable taxa)

Group I		
Aphan. Klebahnii	Kufferath	
Oscillatoria flos-aquae	Agardh	1817
Group II		
Aphan. elenkinii	Kisel	1951
Aphan. kaufmanii	Schmidle in Kaufmann	1897
Aphan. elenkinii v. gracile	Kast.	1955
Aphan. elenkinii f. maroticum	Picyk	1956
Aphan. americanum	Reinhard	1941
Aphan. elenkinii f. gracile	(Kast) Komarek	1958
Aphan. minnesotaense	Hill	1968
Group III		
Aphan. ovalisporum	Forti	1911
Aphan. sphaericum	Kisel	1954
Aphan. manguinii	Bourrelly	1952
Aphan. chinese	Negoro	1943
Aphan. Issatschenkoi	Proschkina-Lavrenko	1962
Aphan. ovalispoium fa. bievicellum	Ulomsky	1956
fa. oblongum	Ulomsky	1956

FIGURE 1. Diagram of Aphanizomenon flos-aquae filament

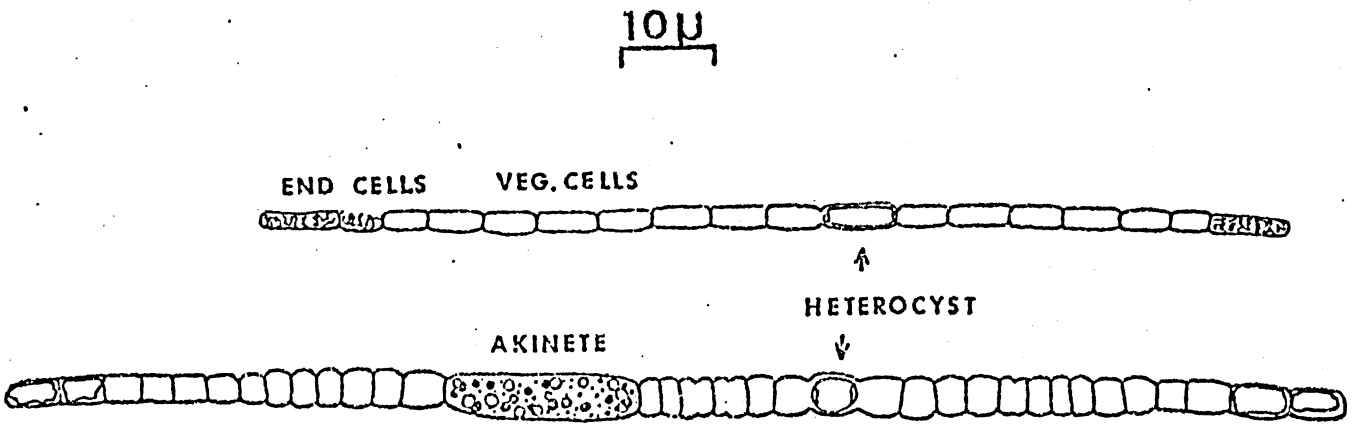

10μ
END CELLS
VEG. CELLS
HETEROCYST
AKINETE

FIGURE 2. Map of Lake Minnetonka (Halsted and Carman Bay)

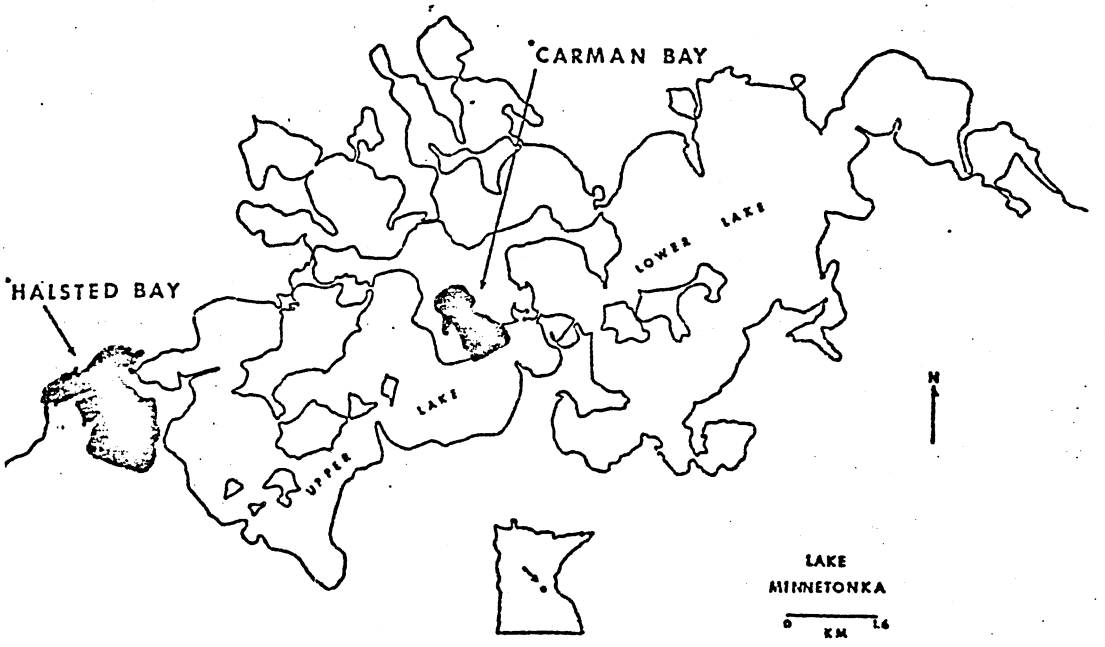
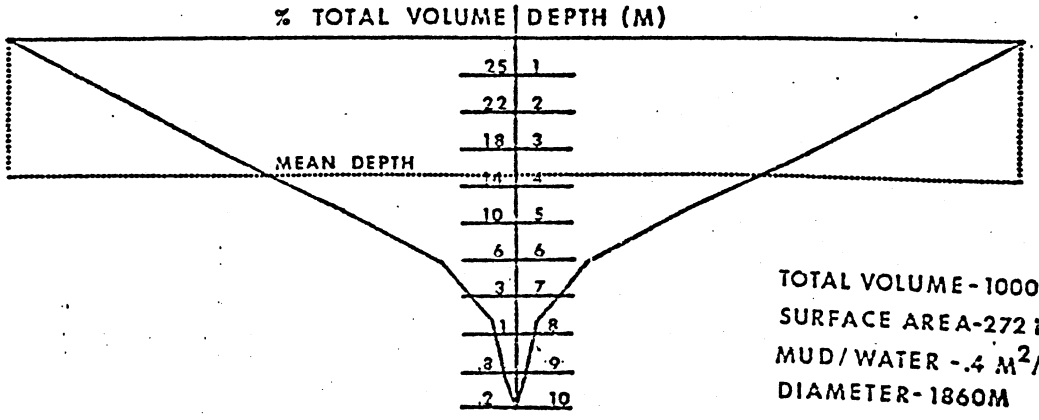

CARMAN BAY
HALSTED BAY
LOWER LAKE
LAKE
UPPER
N
LAKE
MINNETONKA
0 KM 1.6

FIGURE 3. Hypsograph (depth-area curve) of Halsted Bay



TOTAL VOLUME - 1000 HA-M
SURFACE AREA-272 HA
MUD/WATER -.4 M^2/M^3
DIAMETER-1860M

HALSTED BAY

FIGURE 4. Orthophosphate, nitrate, and ammonia concentrations in Halsted Bay during 1972

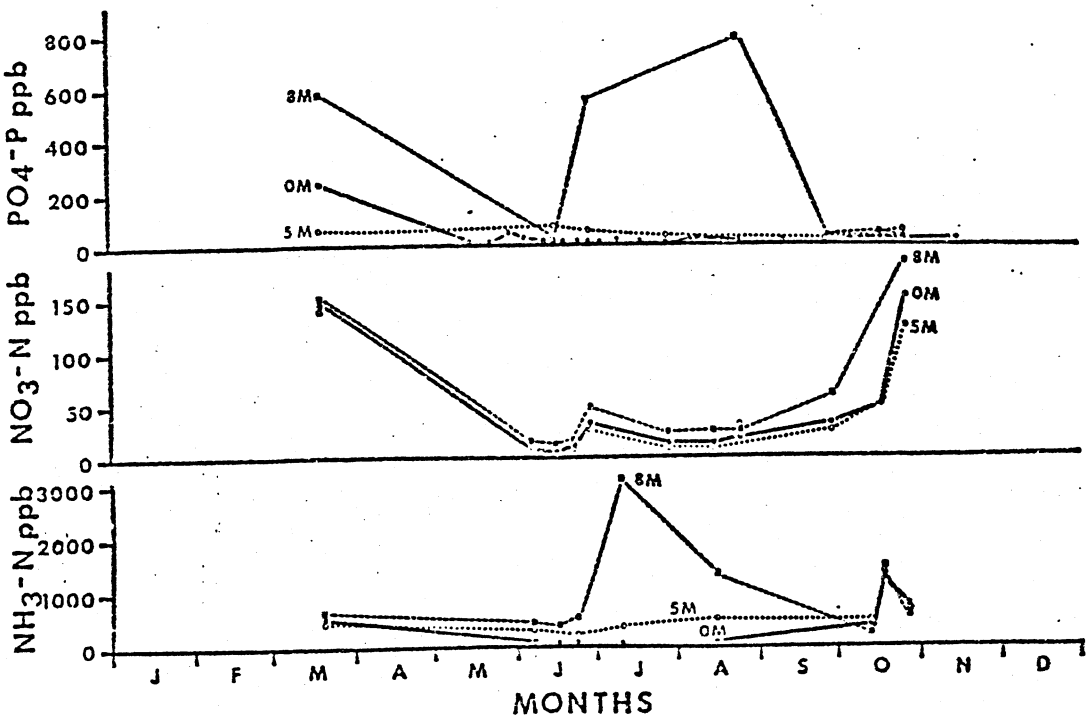

PO4-P ppb
800
600
400
200
0
8M
0M
5M
NO3-N ppb
150
100
50
0
8M
0M
5M
NH3-N ppb
3000
2000
1000
0
8M
5M
0M
J
F
M
A
M
J
J
A
S
O
N
D
MONTHS

FIGURE 5. Orthophosphate, nitrate, and ammonia concentrations in Carman Bay during 1972

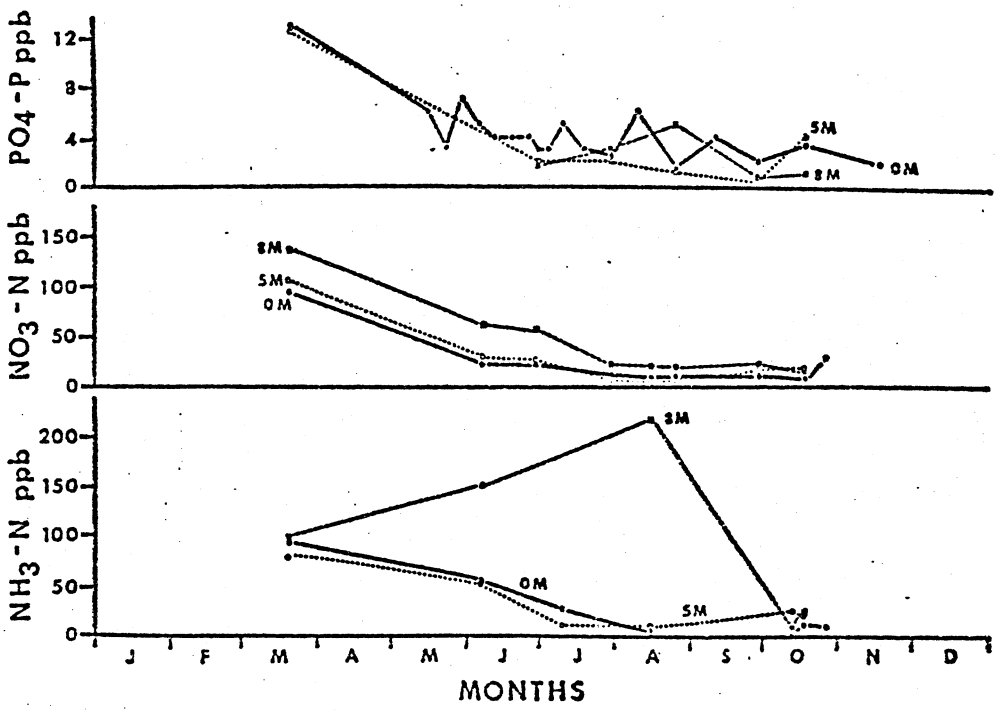

PO4-P ppb
12
8
4
0
8M
5M
0M
NO3-N ppb
150
100
50
0
8M
5M
0M
NH3-N ppb
200
150
100
50
0
8M
0M
5M
J
F
M
A
M
J
J
A
S
O
N
D
MONTHS

FIGURE 6. Map of Itasca State Park (Spencer Pond, Squaw Lake, Elk Lake

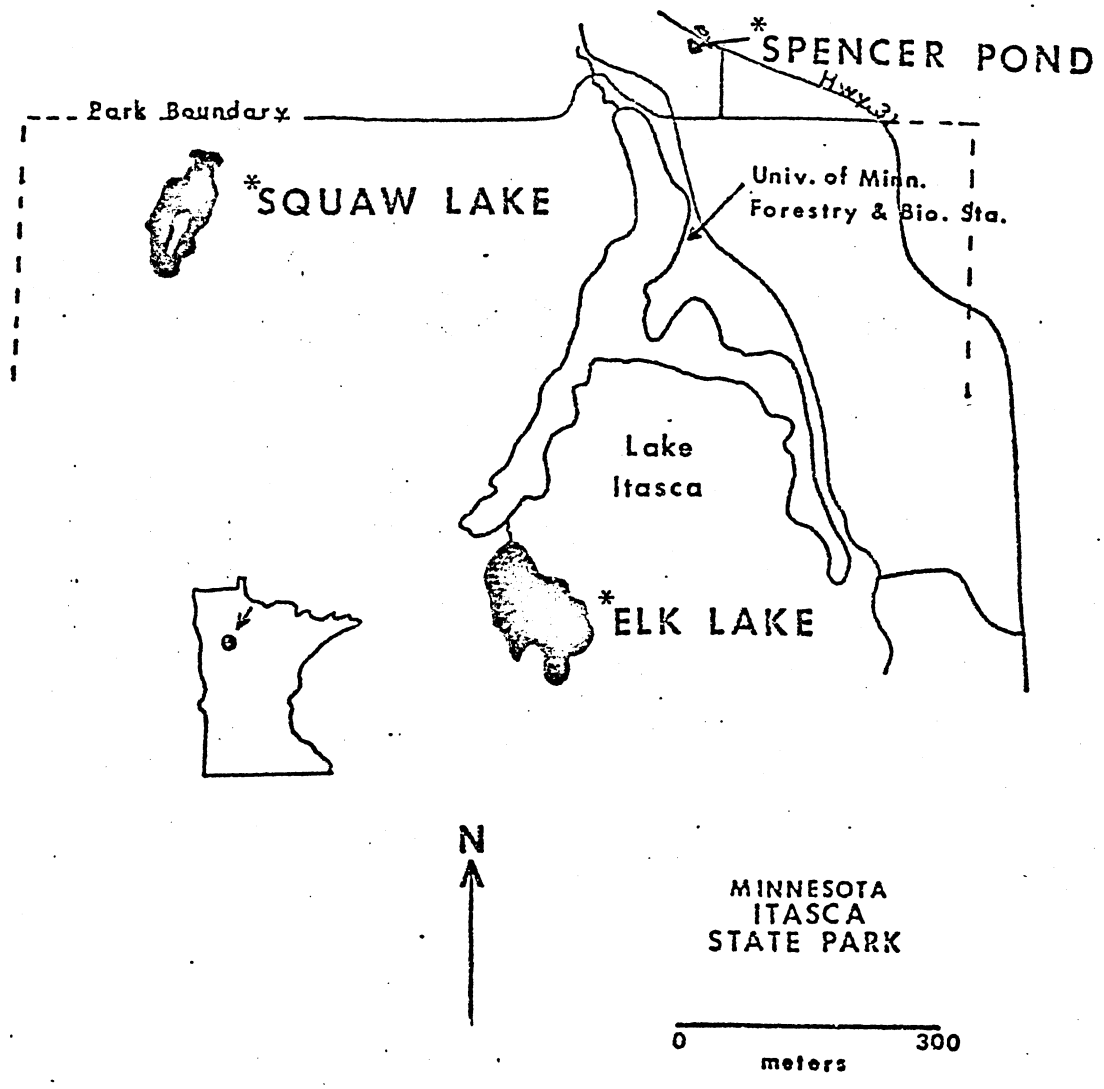
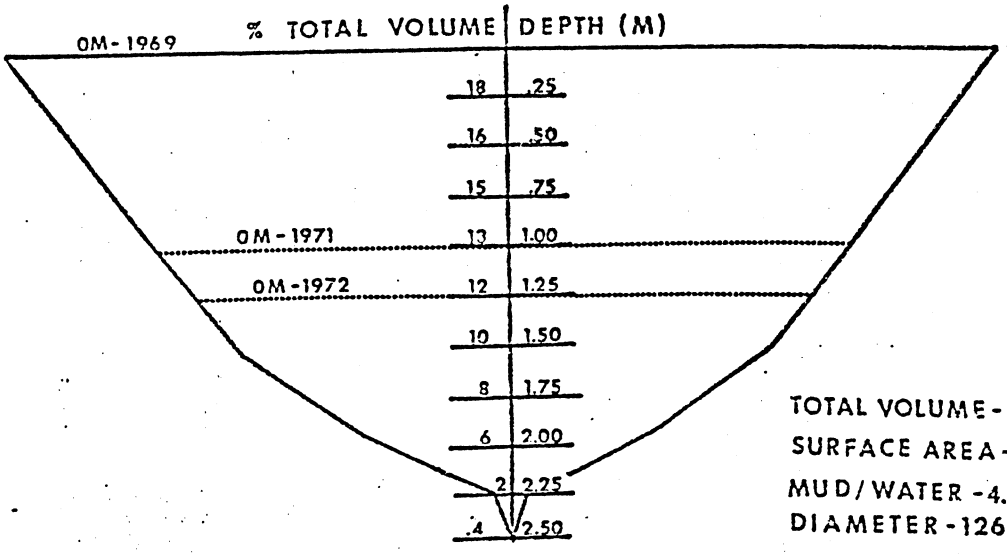

*SPENCER POND
Hwy 71
Park Boundary
*SQUAW LAKE
Univ. of Minn.
Forestry & Bio. Sta.
Lake
Itasca
*ELK LAKE
N
MINNESOTA
ITASCA
STATE PARK
0
300
meters

FIGURE 7. Hypsograph (depth-area curve) of Spencer Pond



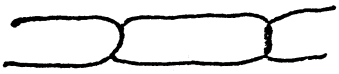
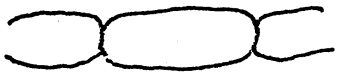
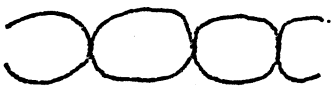
TOTAL VOLUME - 1.7 HA-M
SURFACE AREA - 1.25 HA
MUD/WATER - 4.1 M^2/M^3
DIAMETER - 126 M

SPENCER POND 1969

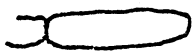
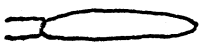
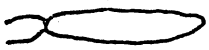
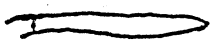
FIGURE 8. Categories for cell shapes and end cell contents

FIGURE 8. CATEGORIES FOR CELL SHAPES AND END CELL CONTENTS

VEGETATIVE CELL, HETEROCYST, AND AKINETE CELL SHAPE

1.  CYLINDRICAL
2. 
3.  BARREL-SHAPED
4.  SPHERICAL

END CELL SHAPE

1.  HEMISPHERICAL END
2.  CONICAL END
 OVOID CELL
3. SHARP CONICAL END

4.  SPHERICAL

END CELL CONTENTS

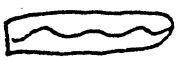
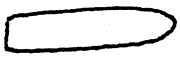
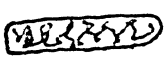
1.  STRING
2.  HYALINE
3.  "PALE" PROTOPLASM
4.  VEGETATIVE LIKE CONTENTS
5.  VACUOLATED

FIGURE 9. Seasonal change in Aphanizomenon cell concentration per M^2 in Halsted Bay for 1971, 1972, and 1974

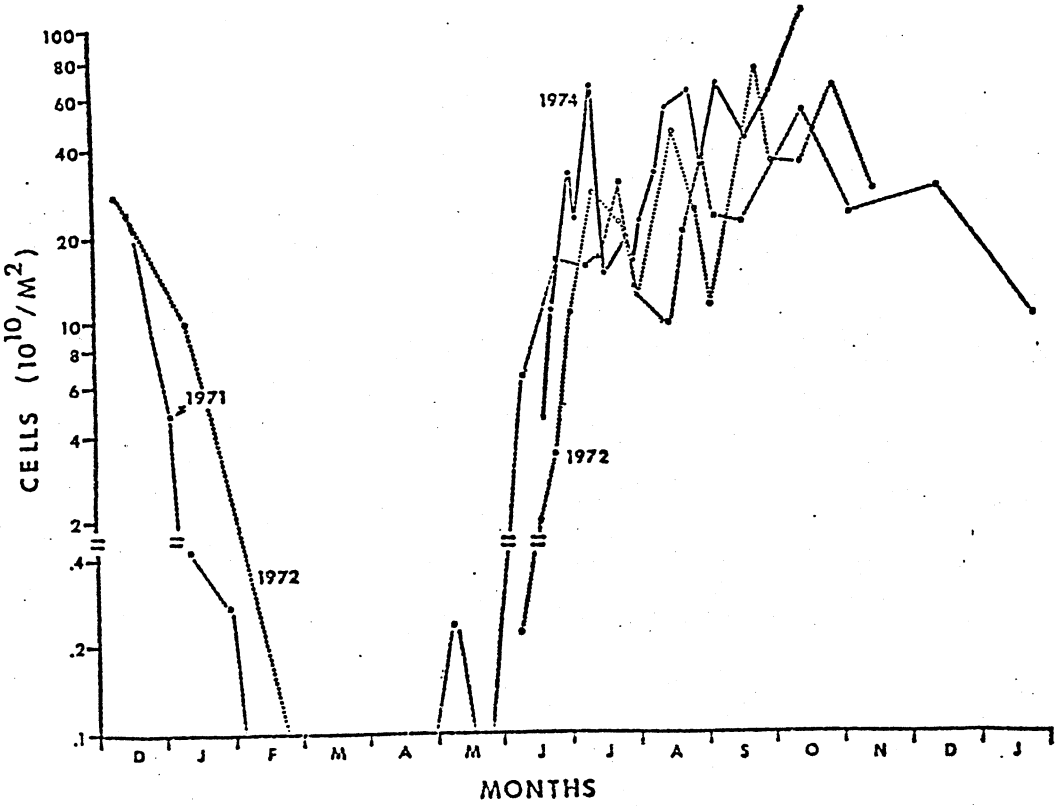

CELLS ($10^{10}/M^2$)
100
80
60
40
20
10
8
6
4
2
.4
.2
.1
1971
1972
1974
1972
D
J
F
M
A
M
J
J
A
S
O
N
D
J
MONTHS

FIGURE 10. Seasonal change in specific rate of change per day for Aphanizomenon cell concentrations per M^2 in Halsted Bay for 1971, 1972, and 1974

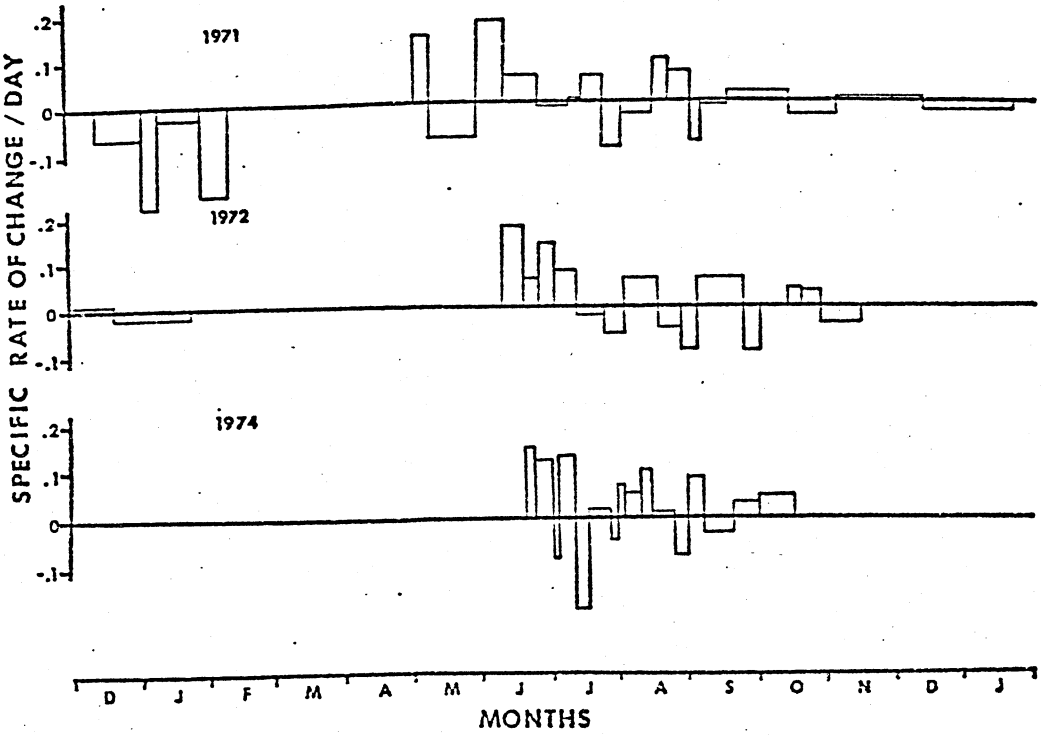

SPECIFIC RATE OF CHANGE / DAY
1971
1972
1974
.2
.1
0
-.1
D
J
F
M
A
M
J
J
A
S
O
N
D
J
MONTHS

FIGURE 11. Isopleths of filament concentration, isopleths of temperature (°C), and Secchi disc depths for 1971 in Halsted Bay

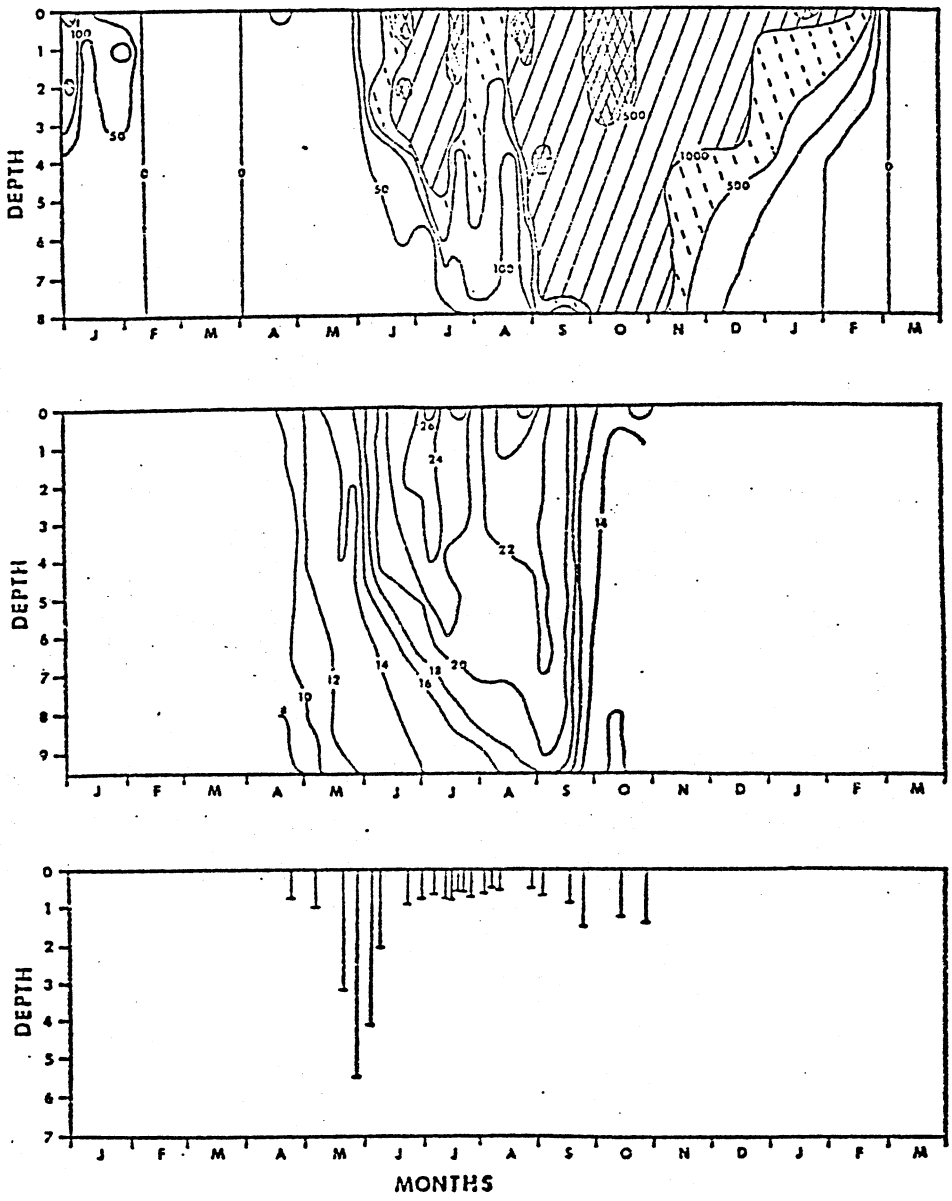

DEPTH
0
1
2
3
4
5
6
7
8
9
100
50
0
500
1000
J F M A M J J A S O N D J F M
MONTHS

FIGURE 12. Isopleths of filament concentration, isopleths of temperature (^{o}C), and Secchi disc depths for 1972 in Halsted Bay

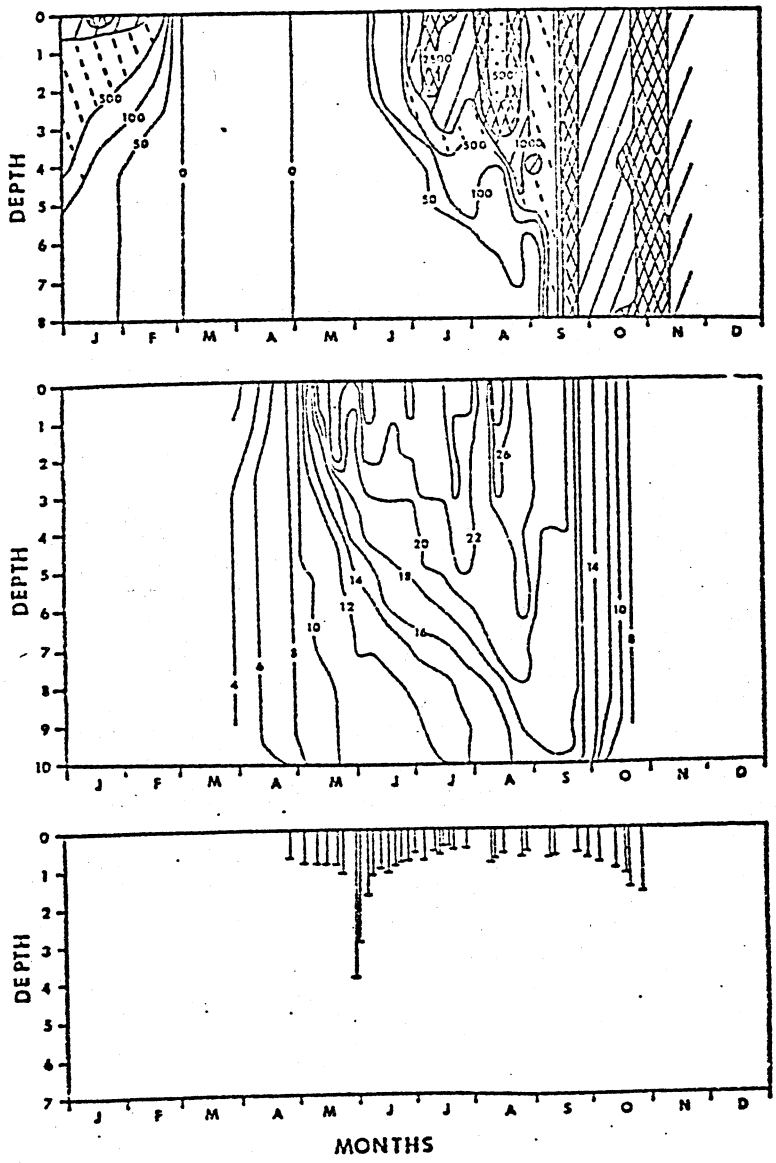
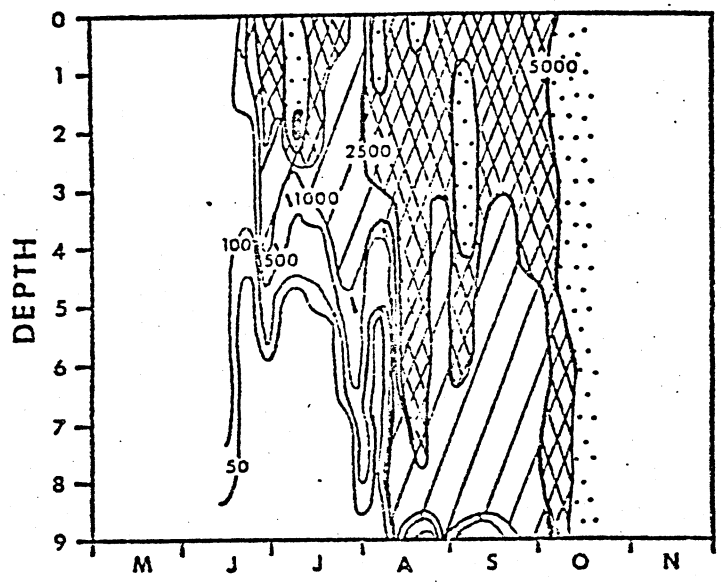

DEPTH
0
1
2
3
4
5
6
7
8
500
100
50
0
0
2500
500
300
1000
50
100
J F M A M J J A S O N D
DEPTH
0
1
2
3
4
5
6
7
8
9
10
4
6
8
10
12
14
16
18
20
22
24
14
10
8
J F M A M J J A S O N D
DEPTH
0
1
2
3
4
5
6
7
J F M A M J J A S O N D
MONTHS

FIGURE 13. Isopleths of filament concentration and temperature (°C) for 1974 in Halsted Bay


DEPTH
0
1
2
3
4
5
6
7
8
9
M
J
J
A
S
O
N
5000
2500
1000
100
500
50

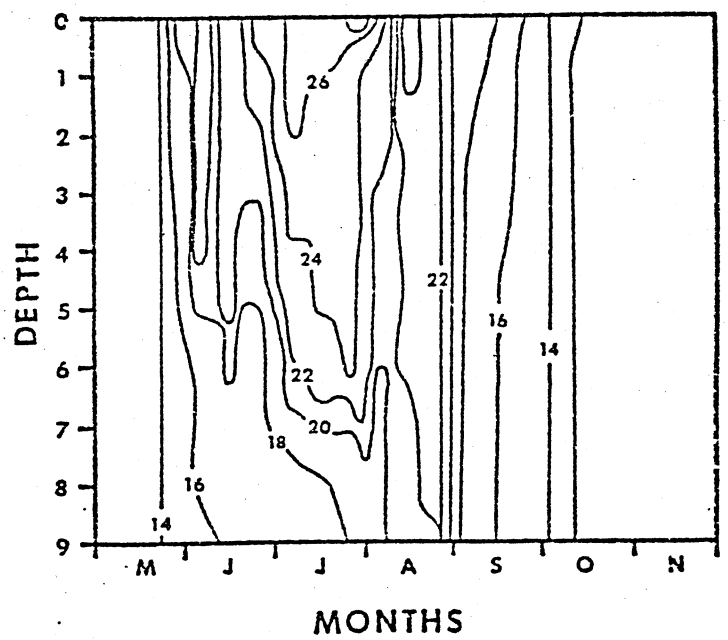

DEPTH
0
1
2
3
4
5
6
7
8
9
M
J
J
A
S
O
N
MONTHS
26
24
22
22
20
18
16
16
14
14

FIGURE 14. Seasonal change of phytoplankton concentration other than Aphanizomenon (blue-green algae, green algae, diatoms) for 1974 in Halsted Bay

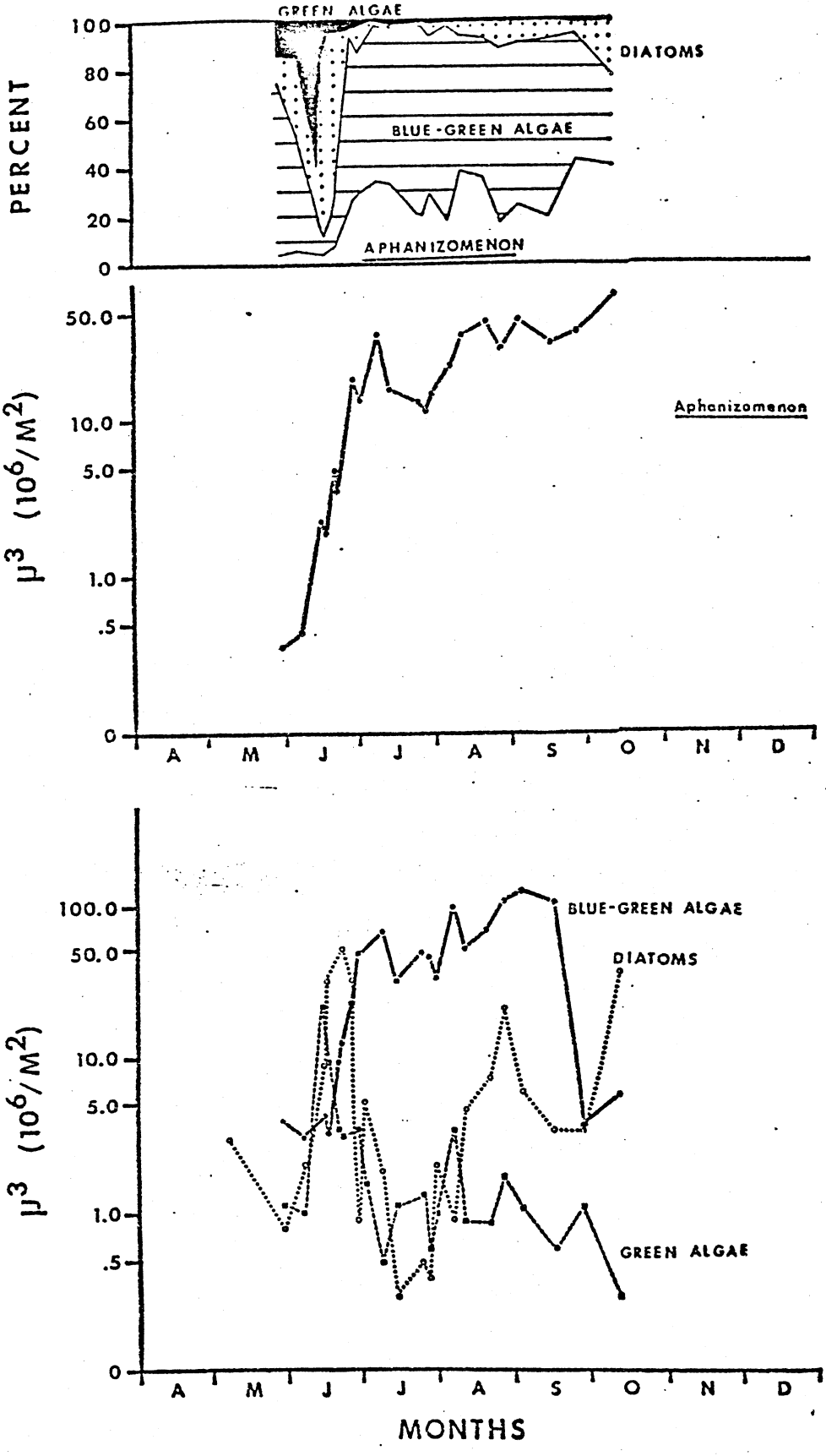

GREEN ALGAE
DIATOMS
BLUE-GREEN ALGAE
APHANIZOMENON
PERCENT
100
80
60
40
20
0
μ3 (10⁶/M²)
50.0
10.0
5.0
1.0
.5
0
Aphanizomenon
A
M
J
J
A
S
O
N
D
BLUE-GREEN ALGAE
DIATOMS
GREEN ALGAE
MONTHS

FIGURE 15. Seasonal change in Aphanizomenon filament concentration per M^2 in Carman Bay for 1971 and 1972

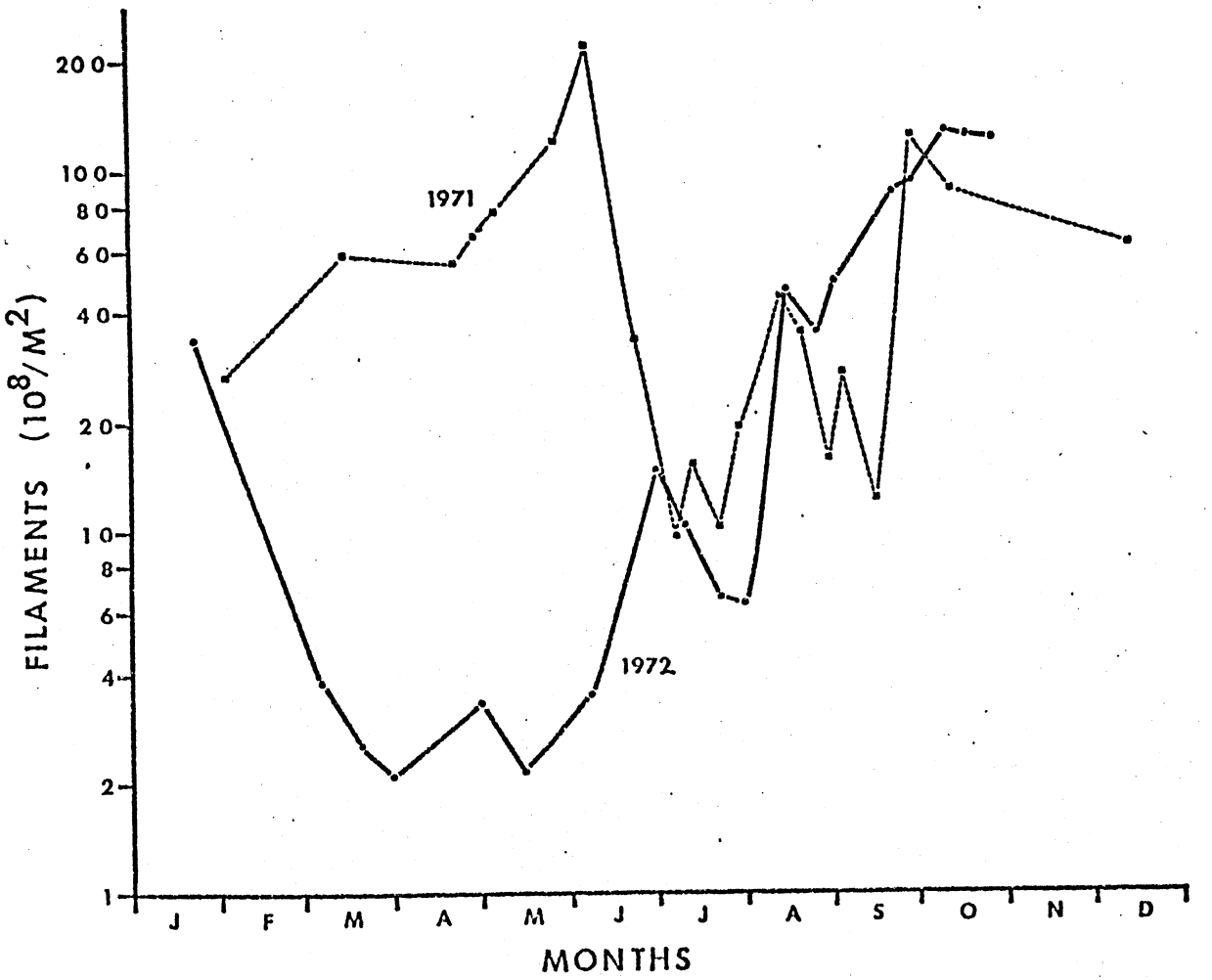

200
100
80
60
40
20
10
8
6
4
2
1
FILAMENTS ($10^8/M^2$)
1971
1972
J
F
M
A
M
J
J
A
S
O
N
D
MONTHS

FIGURE 16. Seasonal change in specific rate of change per day for Aphanizomenon filament concentration per M^2 in Carman Bay for 1971 and 1972

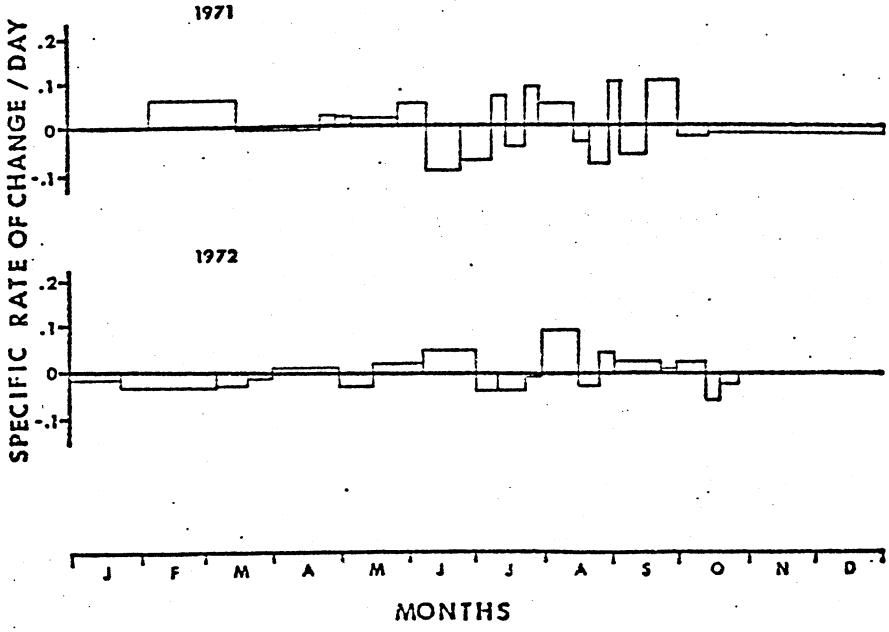

1971
1972
SPECIFIC RATE OF CHANGE / DAY
.2
.1
0
-.1
J
F
M
A
M
J
J
A
S
O
N
D
MONTHS

FIGURE 17. Isopleths of filament concentration, isopleths of temperature (^{o}C), and Secchi disc depth in Carman Bay for 1971

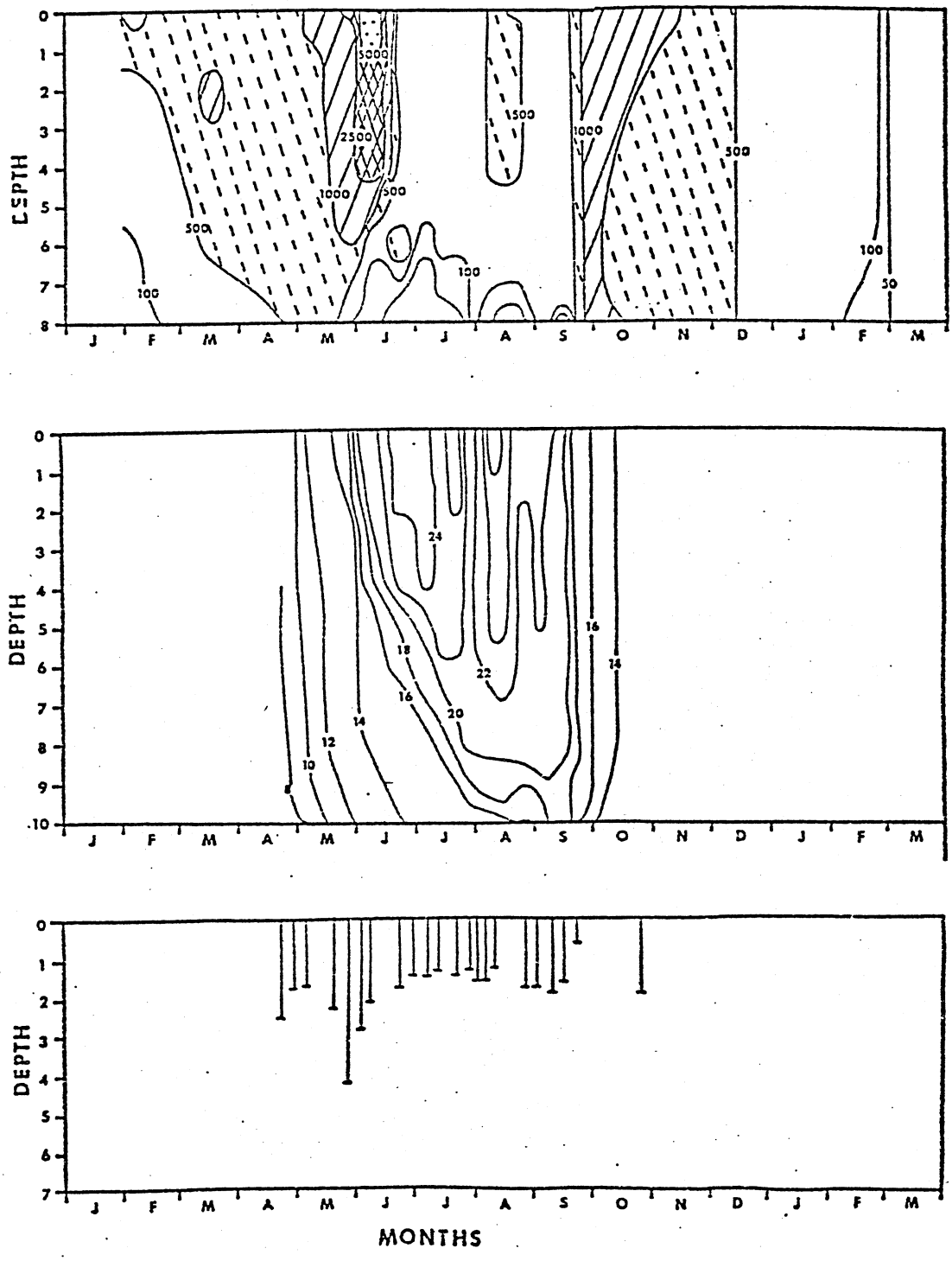

DEPTH
0
1
2
3
4
5
6
7
8
9
10
5000
2500
1500
1000
500
100
30
J F M A M J J A S O N D J F M
DEPTH
24
22
20
18
16
14
12
10
8
DEPTH
MONTHS

FIGURE 18. Isopleths of filament concentration, isopleths of temperature (°C), and Secchi disc depth in Carman Bay for 1972

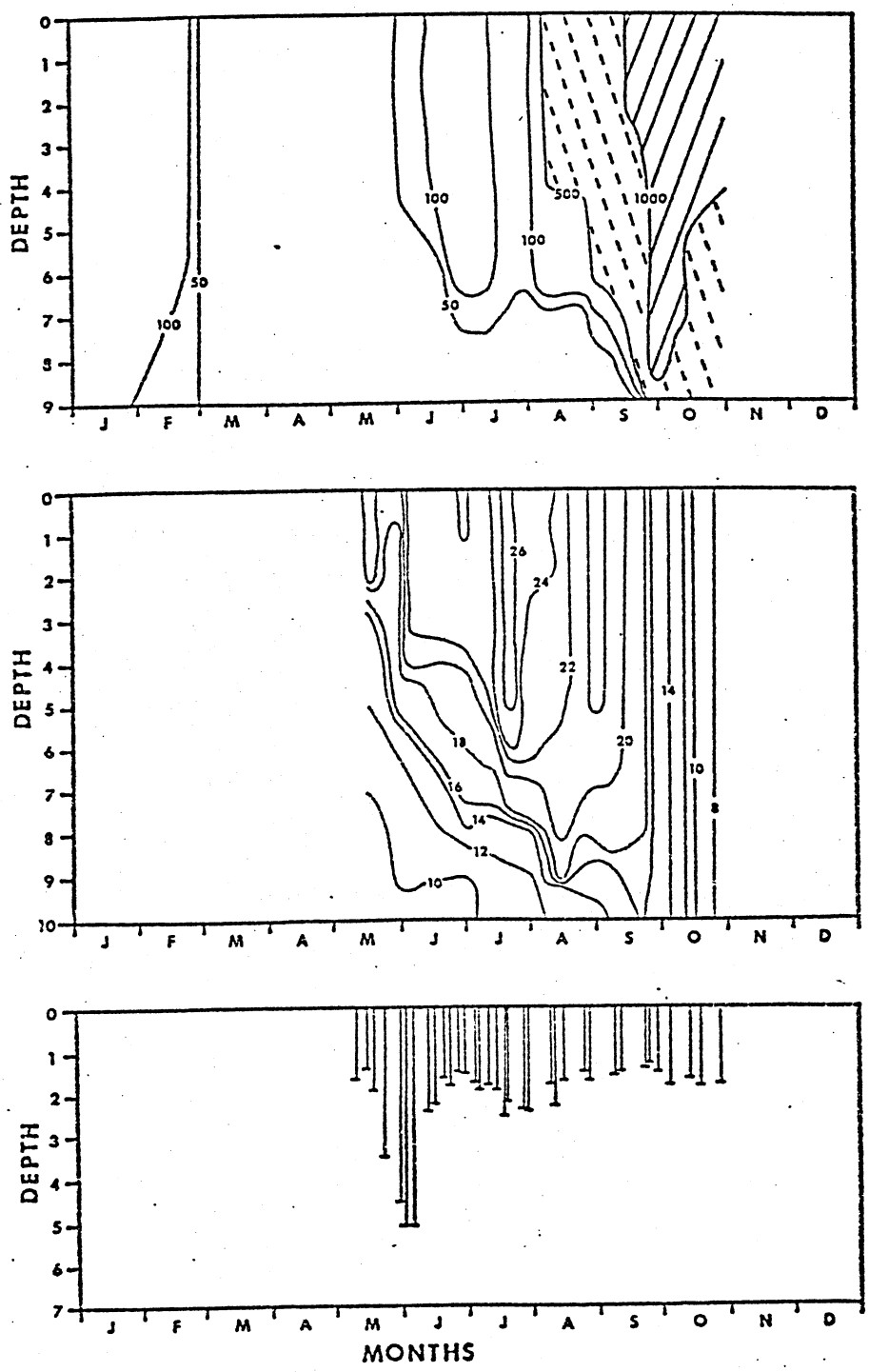

DEPTH
0
1
2
3
4
5
6
7
8
9
J F M A M J J A S O N D
100
50
100
100
50
500
1000
1
DEPTH
0
1
2
3
4
5
6
7
8
9
10
J F M A M J J A S O N D
26
24
22
20
18
16
14
12
10
14
10
8
DEPTH
0
1
2
3
4
5
6
7
J F M A M J J A S O N D
MONTHS

FIGURE 19. Seasonal change in Aphanizomenon filament concentration per M^2 in Spencer Pond for 1969, 1971, and 1972

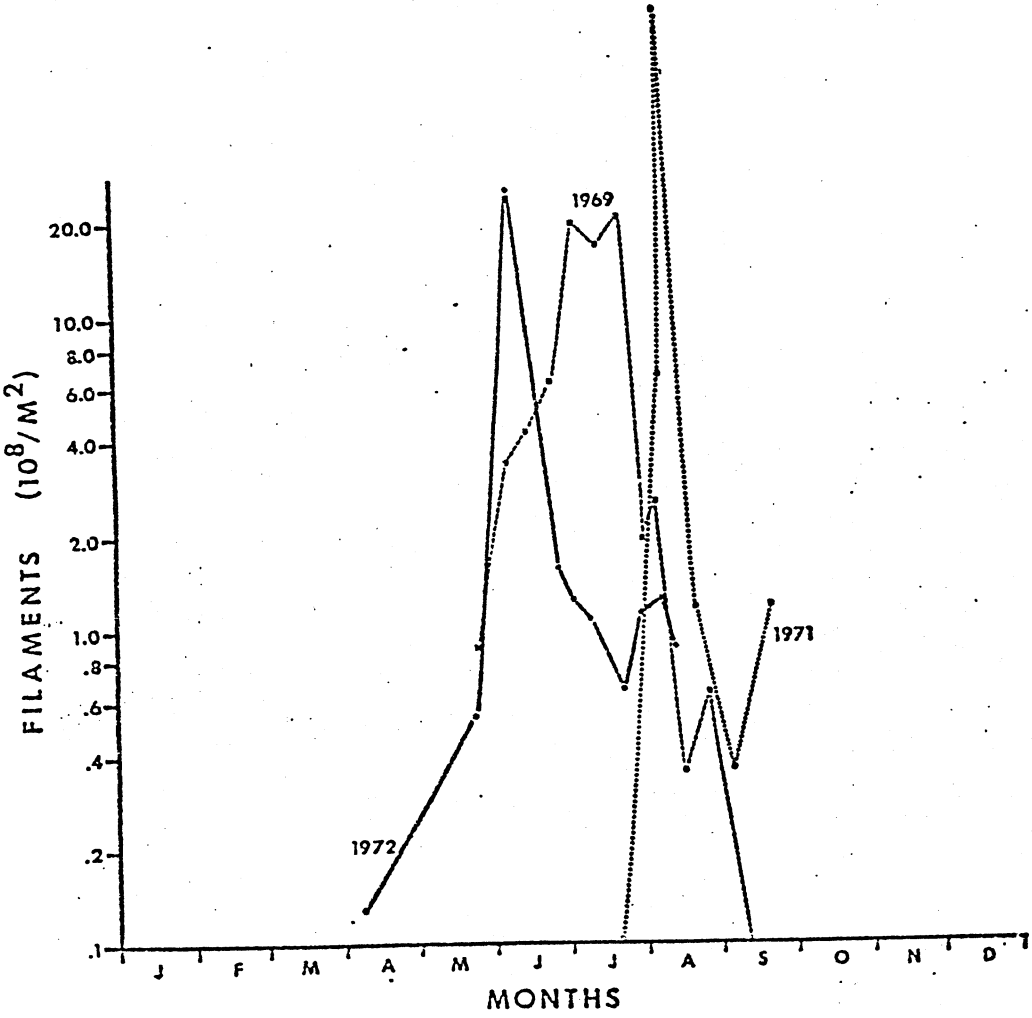

FILAMENTS (10⁸/M²)
20.0
10.0
8.0
6.0
4.0
2.0
1.0
.8
.6
.4
.2
.1
1969
1971
1972
J
F
M
A
M
J
J
A
S
O
N
D
MONTHS

FIGURE 20. Seasonal change in specific rate of change per day for Aphanizomenon filament concentration per M^2 in Spencer Pond for 1969, 1971, and 1972

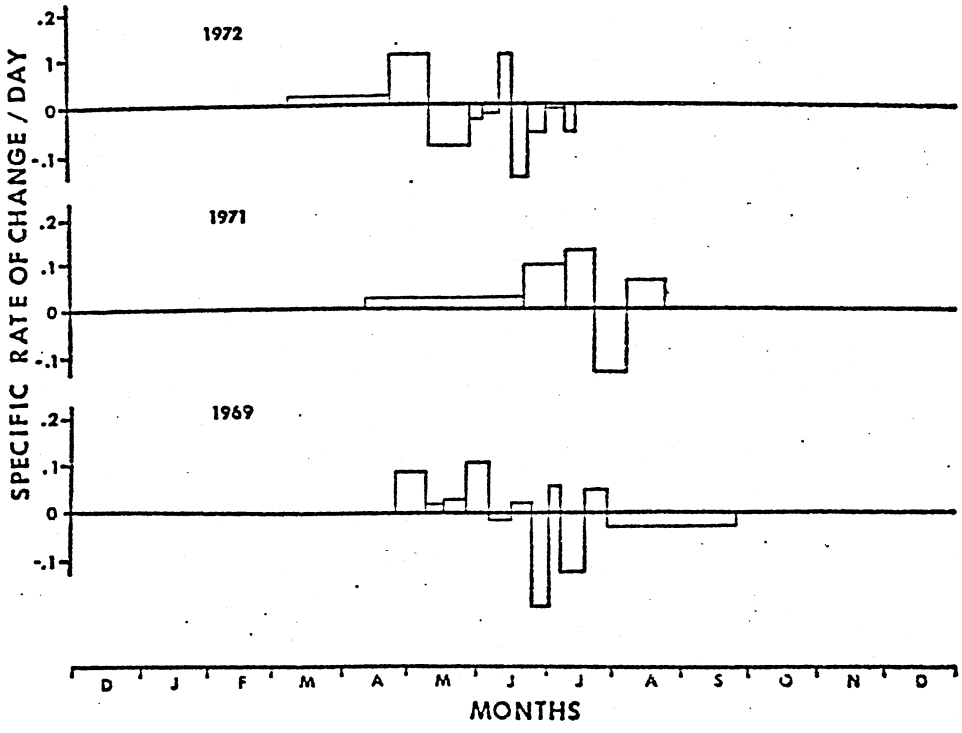

1972
1971
1969
.2
.1
0
-.1
SPECIFIC RATE OF CHANGE / DAY
D
J
F
M
A
M
J
J
A
S
O
N
D
MONTHS

FIGURE 21. Isopleths of filament concentration, temperature (°C), and oxygen concentration (ppm) in Spencer Pond for 1969

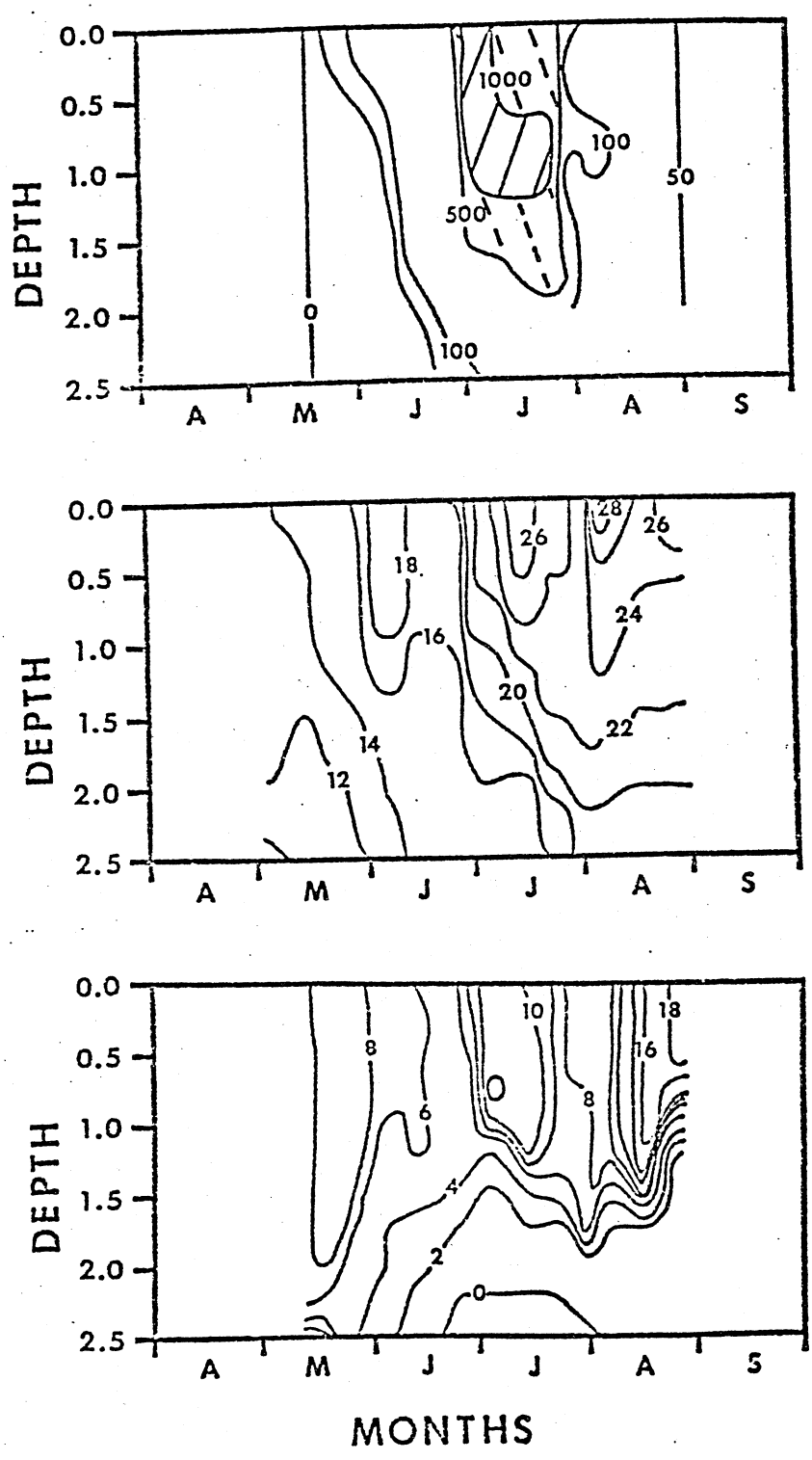

DEPTH
0.0
0.5
1.0
1.5
2.0
2.5
A
M
J
J
A
S
1000
100
50
500
0
100
28
26
26
18
24
16
20
22
14
12
10
18
8
16
8
6
4
2
0
MONTHS

FIGURE 22. Depth profiles of percent maximum Aphanizomenon filament concentration, temperature (^{o}C), and oxygen concentration (ppm) in Squaw Lake during 1969

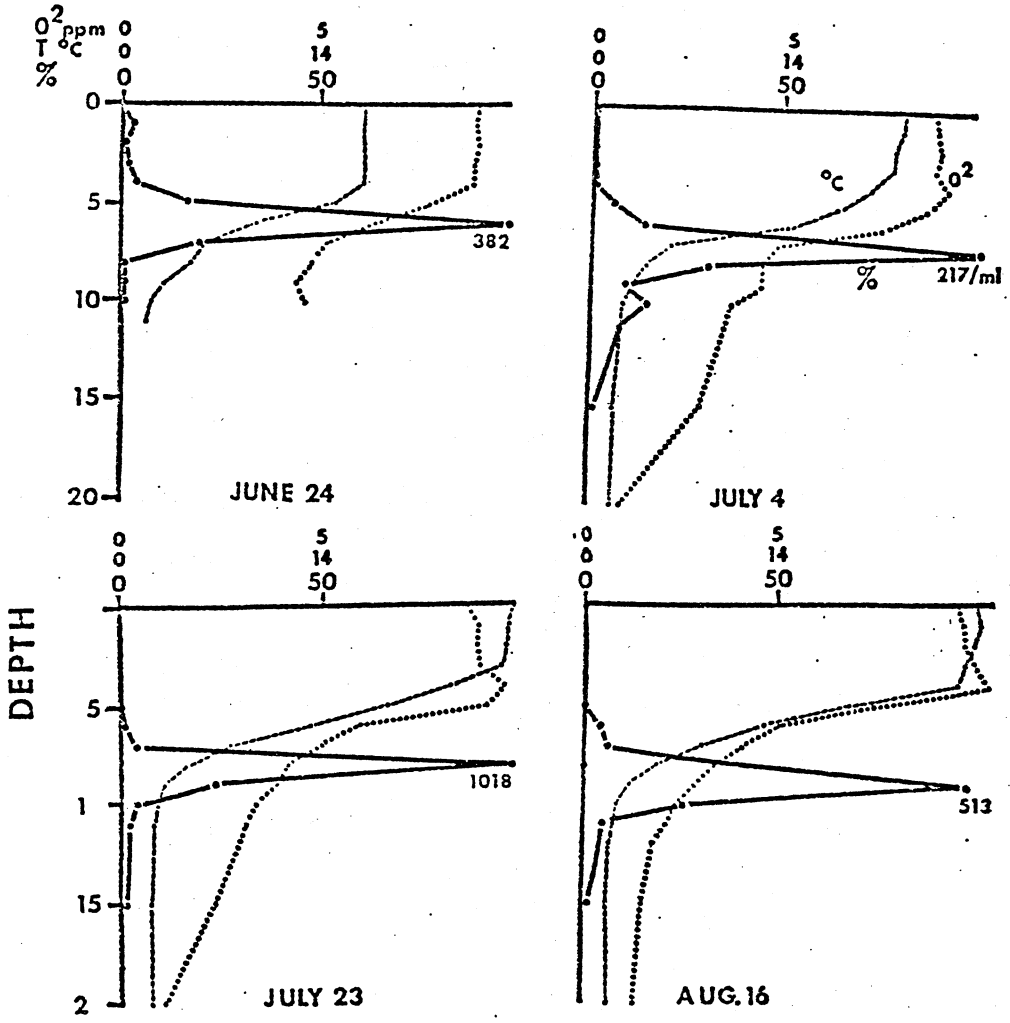

O^2 ppm
T °C
%
0
0
0
5
14
50
0
5
10
15
20
382
JUNE 24
°C
O^2
%
217/ml
JULY 4
DEPTH
5
1
15
2
1018
JULY 23
513
AUG. 16

FIGURE 23. Depth profiles of percent maximum Aphanizomenon filament concentration, temperature (°C), and oxygen concentration (ppm) in Elk Lake during 1969

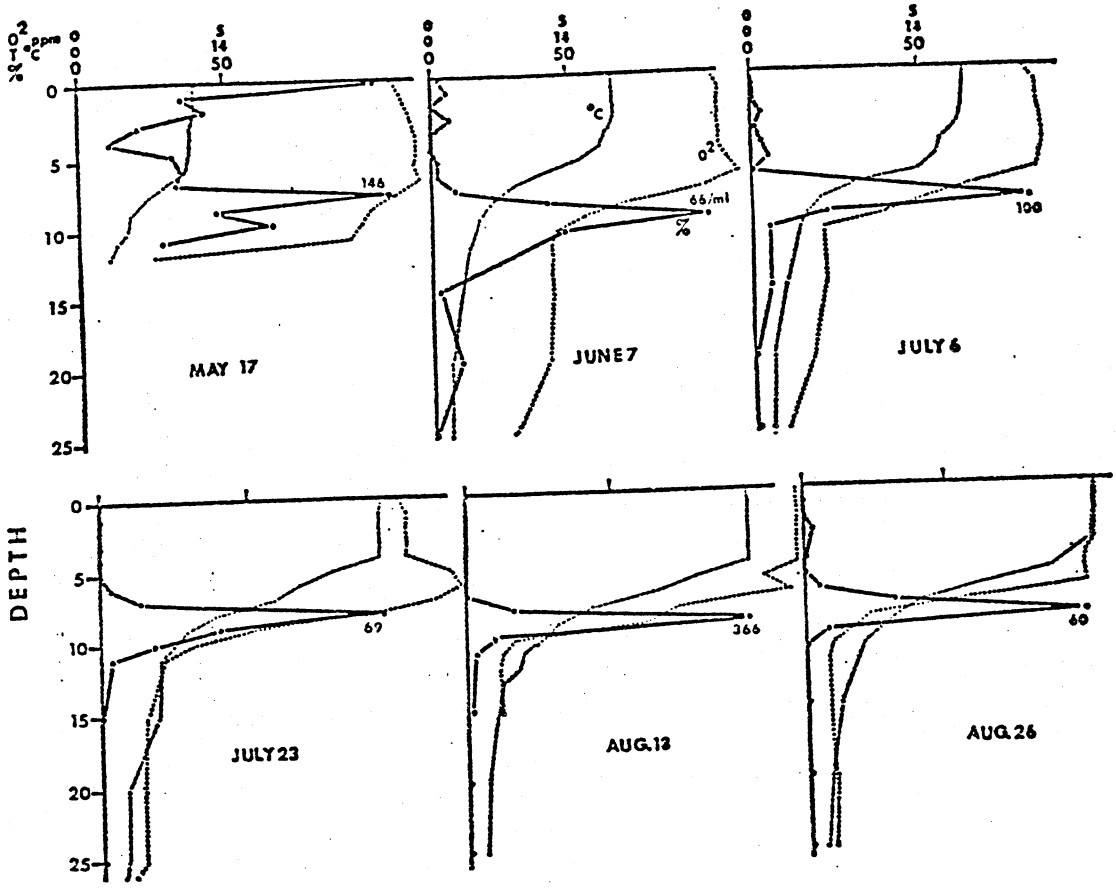

DEPTH
0
5
10
15
20
25
MAY 17
JUNE 7
JULY 6
JULY 23
AUG. 13
AUG. 26
146
66/ml
100
69
366
60

FIGURE 24. Seasonal change of heterocyst, akinete, and end cell concentration per M^2 in Halsted Bay for 1971, 1972, and 1974

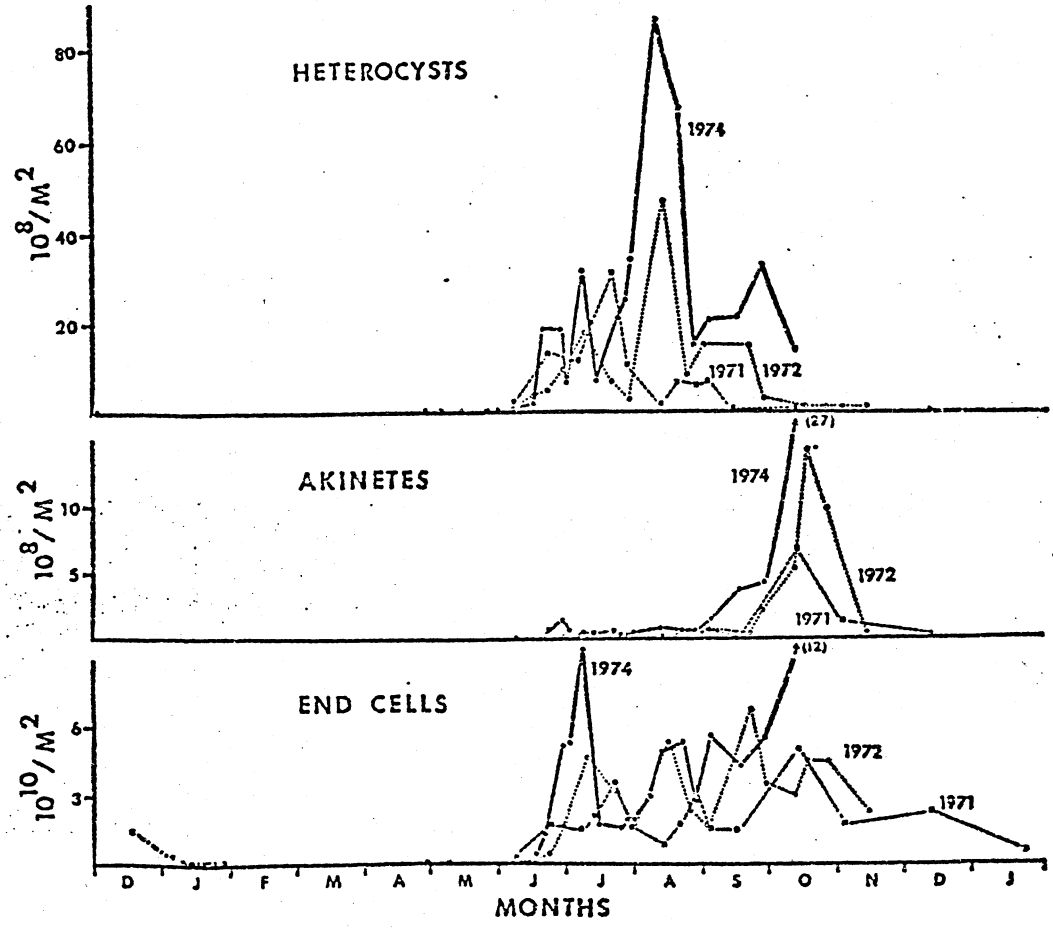

HETEROCYSTS
$10^8/M^2$
80
60
40
20
1974
1971
1972
AKINETES
$10^8/M^2$
10
5
(27)
1974
1972
1971
END CELLS
$10^{10}/M^2$
6
3
†(12)
1974
1972
1971
D J F M A M J J A S O N D J
MONTHS

FIGURE 25. Seasonal variation in percent vegetative cells, end cells, heterocysts, and akinetes in Halsted Bay for 1971, 1972, and 1974

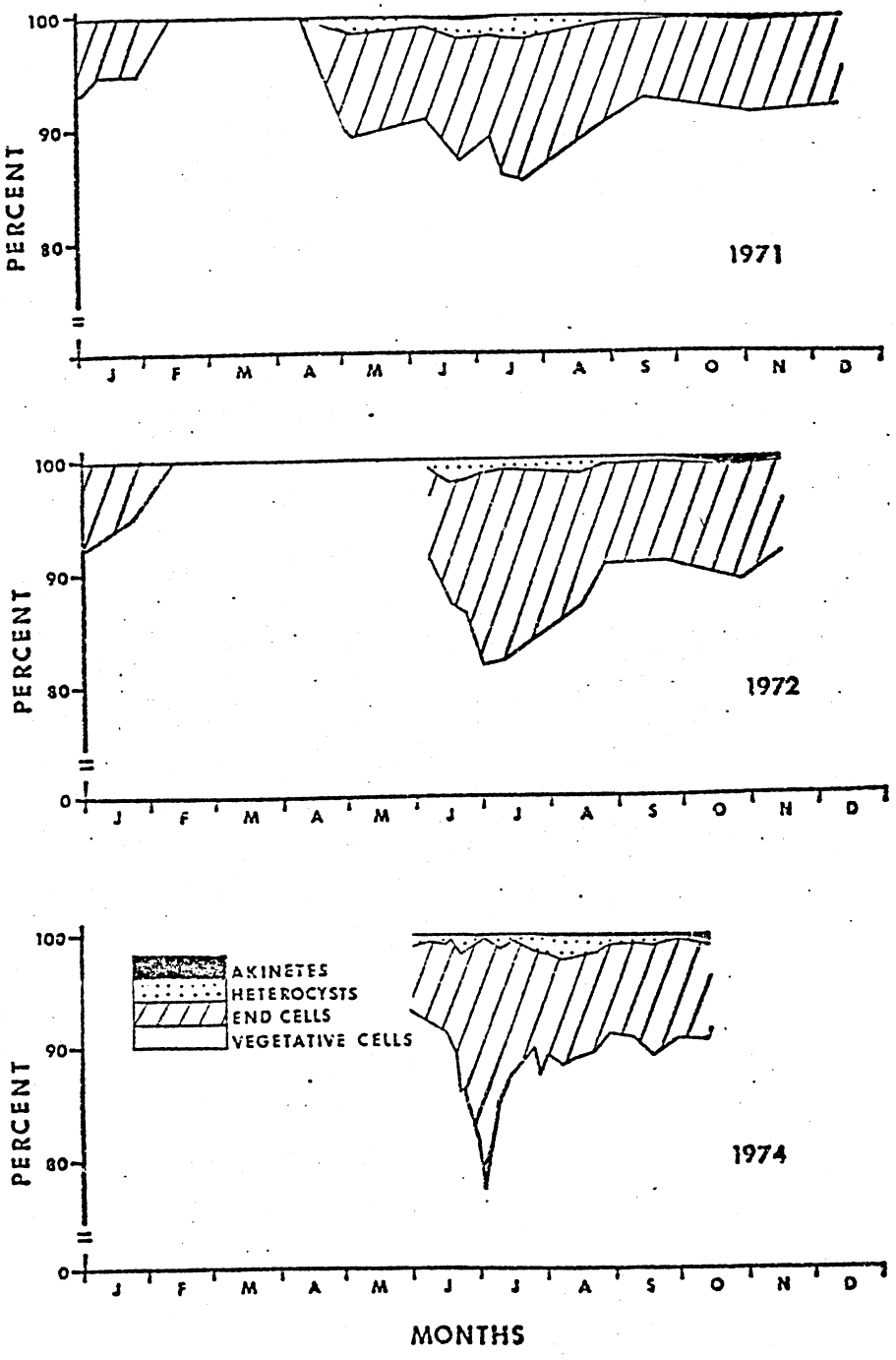

100
90
80
PERCENT
1971
J F M A M J J A S O N D
100
90
80
0
PERCENT
1972
J F M A M J J A S O N D
100
90
80
0
PERCENT
AKINETES
HETEROCYSTS
END CELLS
VEGETATIVE CELLS
1974
J F M A M J J A S O N D
MONTHS

FIGURE 26. Seasonal change of heterocyst and akinete concentration per M^2 in Carman Bay for 1971 and 1972

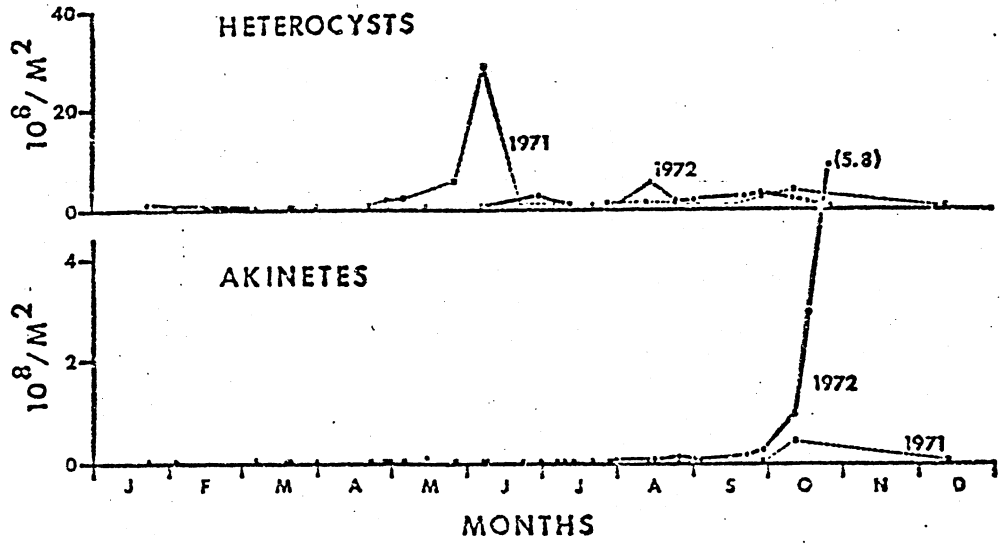

HETEROCYSTS
$10^6/M^2$
40
20
0
1971
1972
(5.8)
AKINETES
$10^8/M^2$
4
2
0
1972
1971
J F M A M J J A S O N D
MONTHS

FIGURE 27. Seasonal change of heterocyst and akinete concentration per M^2 in Spencer Pond for 1969, 1971, and 1972

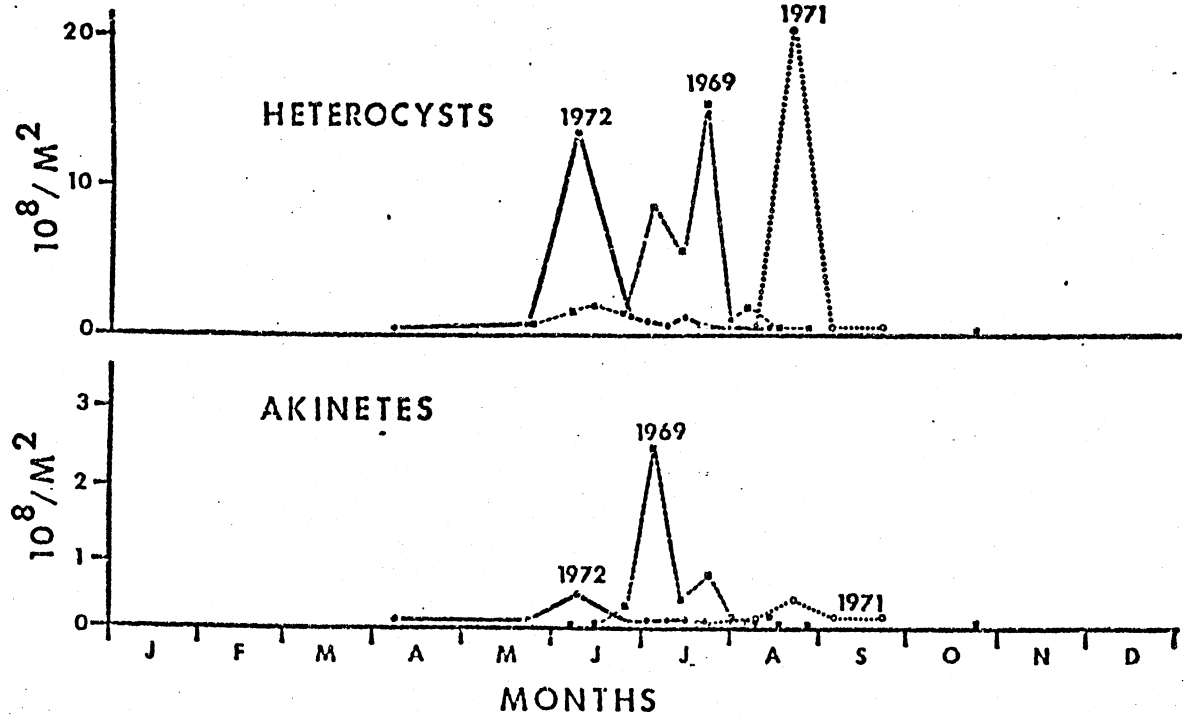

HETEROCYSTS
1971
1969
1972
20
10
0
$10^8/M^2$
AKINETES
1969
1972
1971
3
2
1
0
$10^8/M^2$
J
F
M
A
M
J
J
A
S
O
N
D
MONTHS

FIGURE 28. Nitrogen fixation (acetylene reduction) by net concentrated plankton in Halsted Bay for 1972

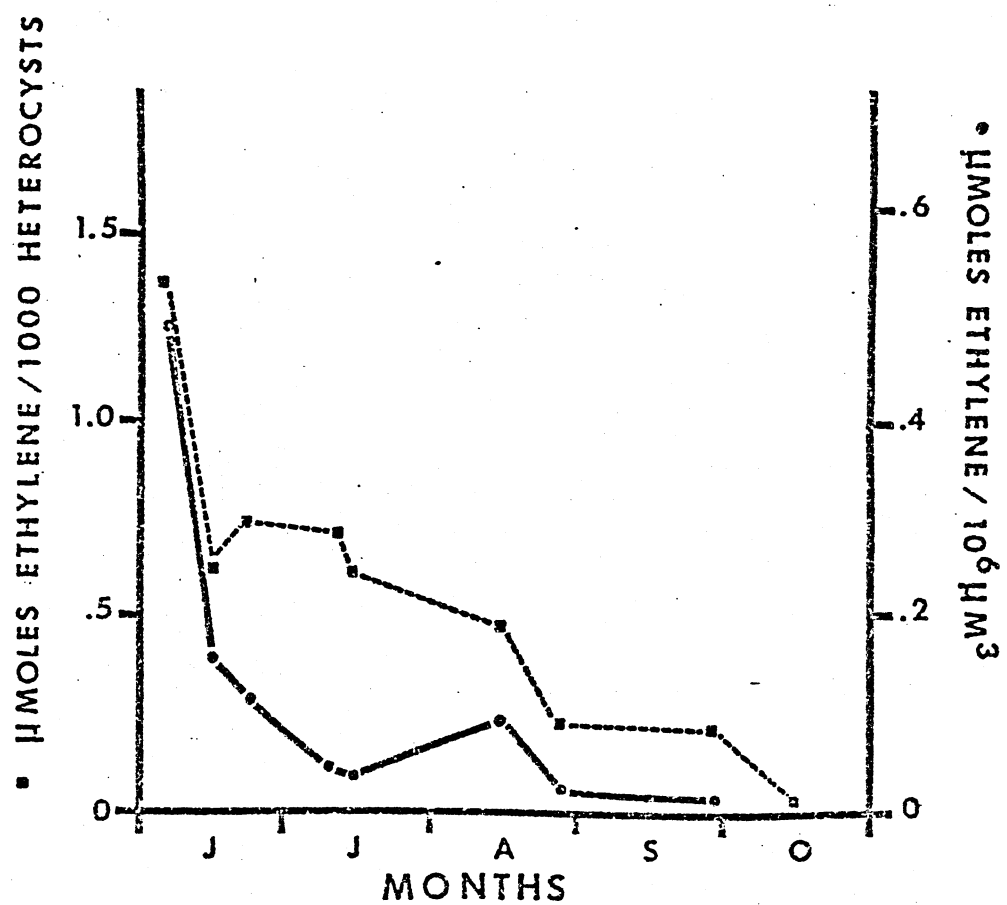

■ μMOLES ETHYLENE/1000 HETEROCYSTS
1.5
1.0
.5
0
J
J
A
S
O
MONTHS
.6
.4
.2
0
• μMOLES ETHYLENE/10^6 μM^3

FIGURE 29. Frequency polygons, mean, and standard deviation of cell width (vegetative cells, end cells, heterocysts, and akinetes) for all the study populations

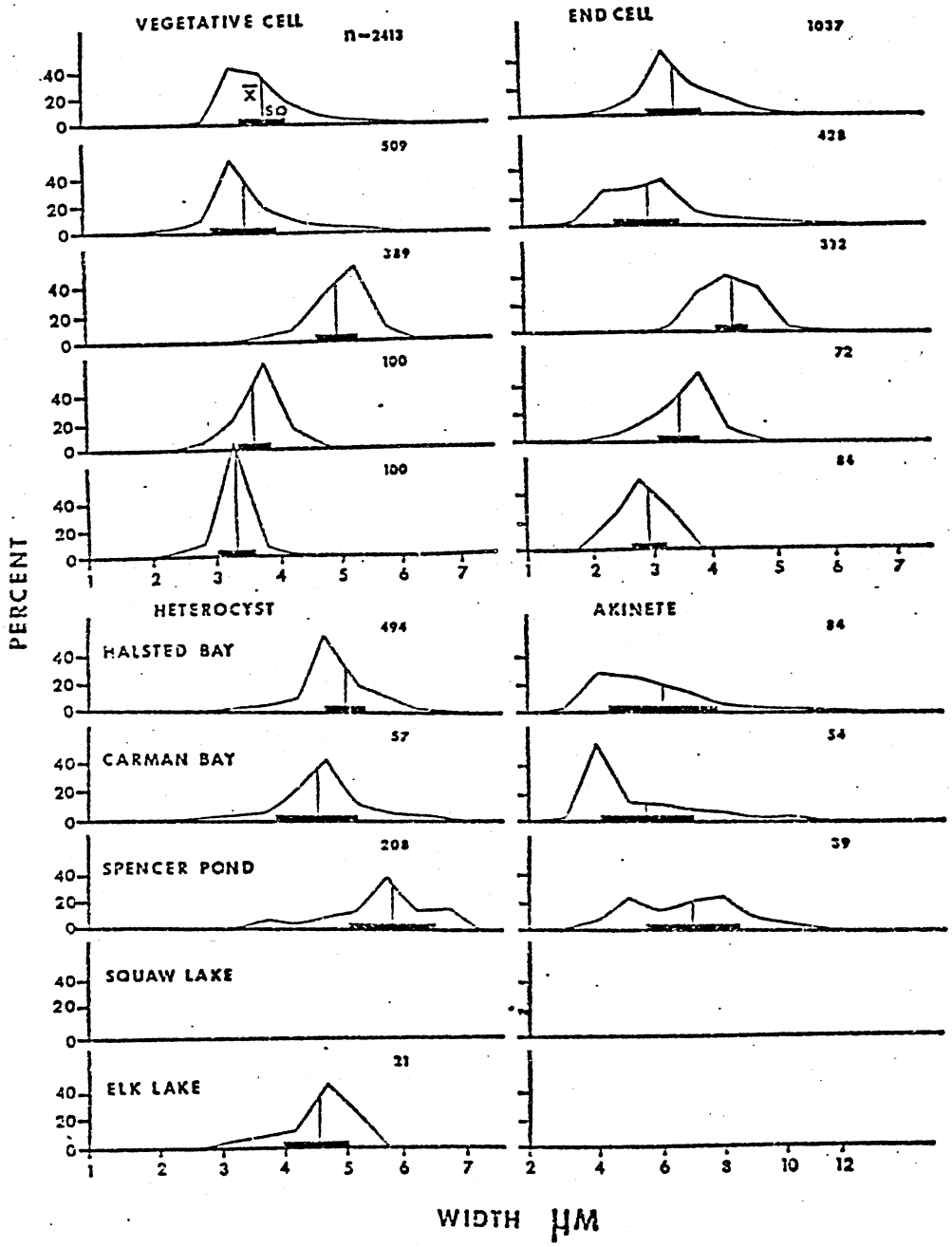

VEGETATIVE CELL
n=2413
END CELL
1037
509
428
389
332
100
72
100
84
HETEROCYST
AKINETE
494
84
HALSTED BAY
57
54
CARMAN BAY
208
39
SPENCER POND
SQUAW LAKE
21
ELK LAKE
PERCENT
WIDTH µM

FIGURE 30. Frequency polygons, mean, and standard deviation of cell length (vegetative cells, end cells, heterocysts, and akinetes) for all the study populations

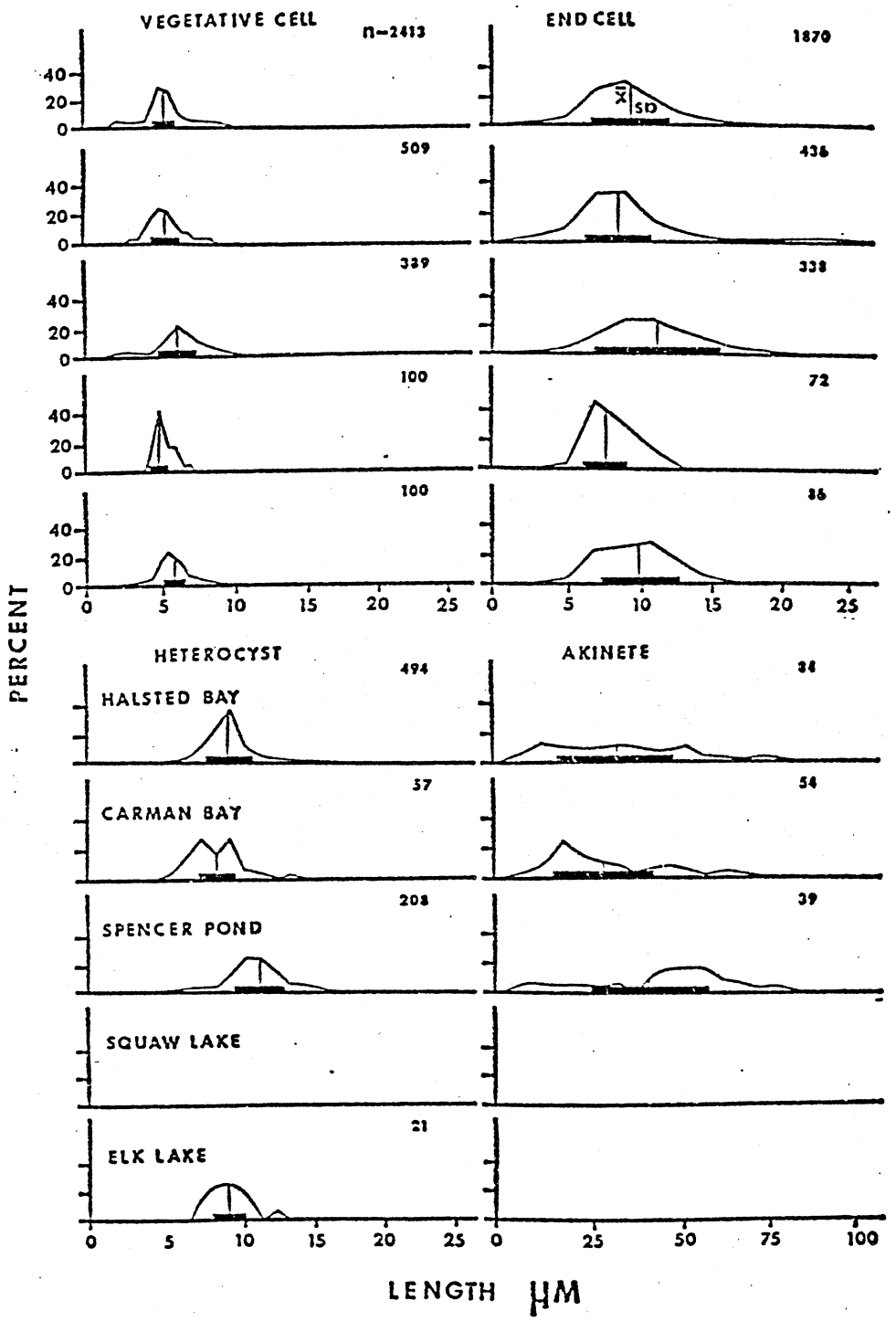

VEGETATIVE CELL
n=2413
END CELL
1870
509
436
339
338
100
72
100
86
HETEROCYST
494
AKINETE
36
HALSTED BAY
37
54
CARMAN BAY
208
39
SPENCER POND
SQUAW LAKE
21
ELK LAKE
X̄
SD
PERCENT
LENGTH μM

FIGURE 31. Frequency polygons, mean, and standard deviation of cell length to width ratios (vegetative cells, end cells, heterocysts, and akinetes) for all the study populations

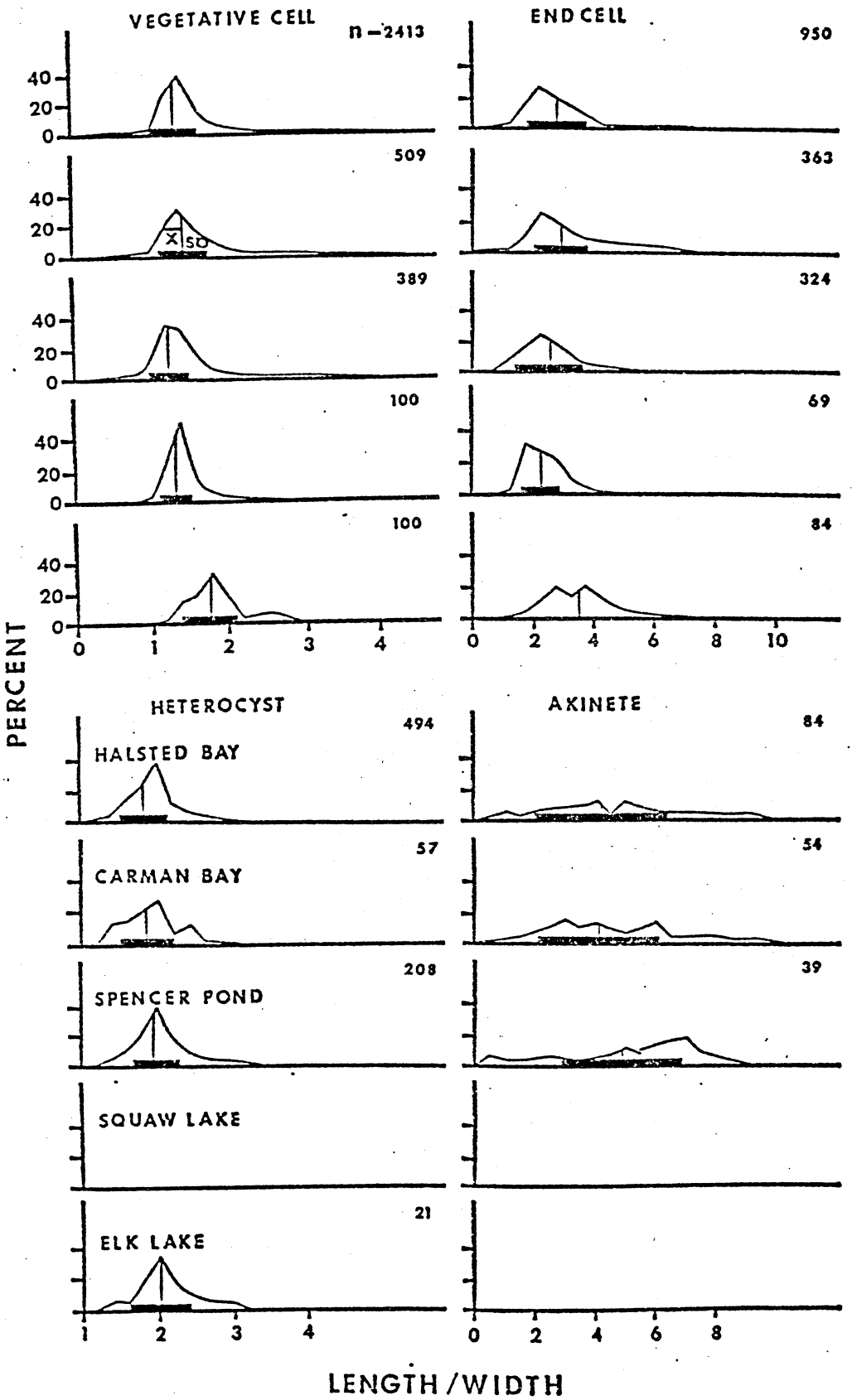

VEGETATIVE CELL
n = 2413
END CELL
950
509
363
389
324
100
69
100
84
HETEROCYST
494
AKINETE
84
HALSTED BAY
57
54
CARMAN BAY
208
39
SPENCER POND
SQUAW LAKE
21
ELK LAKE
PERCENT
LENGTH / WIDTH

FIGURE 32. Range, mean, and standard deviation of cell length and width (vegetative cells, end cells, heterocysts, and akinetes) for the Halsted Bay population

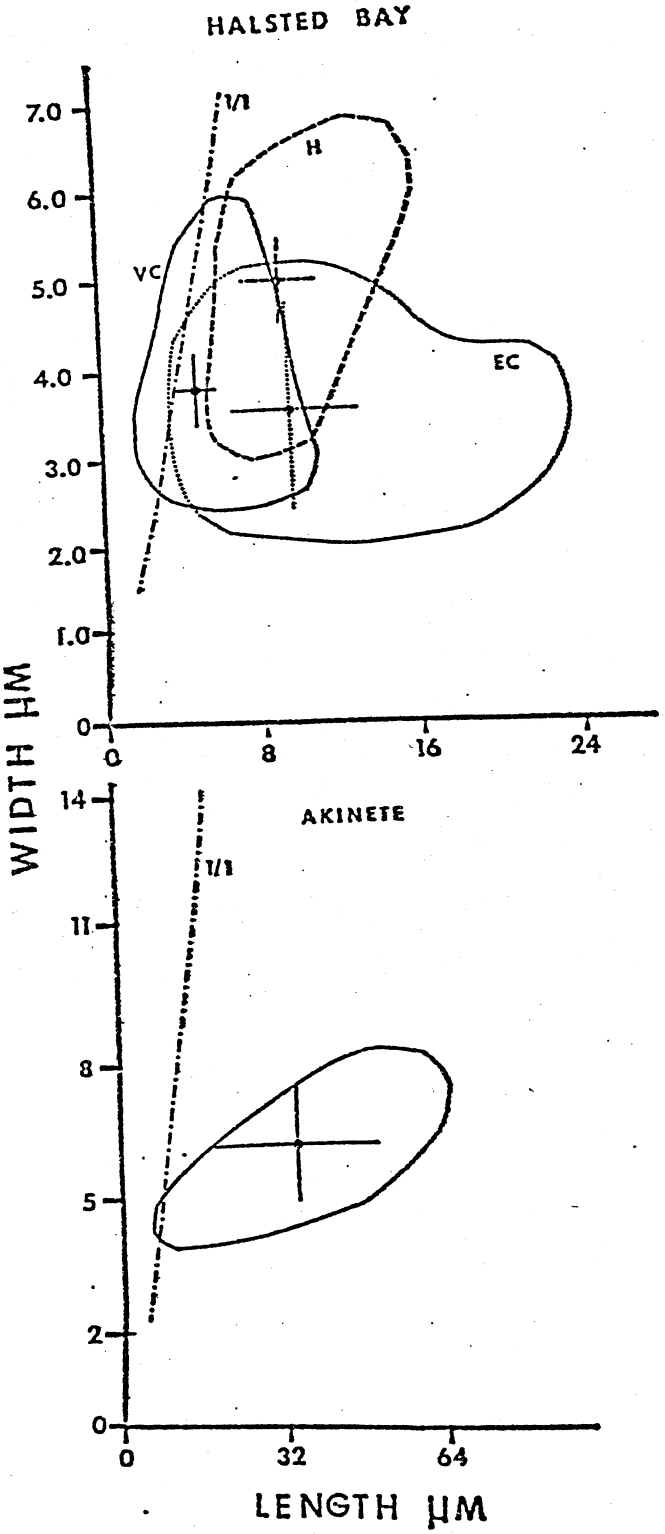

HALSTED BAY
T/1
H
VC
EC
7.0
6.0
5.0
4.0
3.0
2.0
1.0
0
0
8
16
24
WIDTH µM
AKINETE
T/1
14
11
8
5
2
0
0
32
64
LENGTH µM

FIGURE 33. Range, mean, and standard deviation of cell length and width (vegetative cells, end cells, heterocysts, and akinetes) for the Carman Bay population

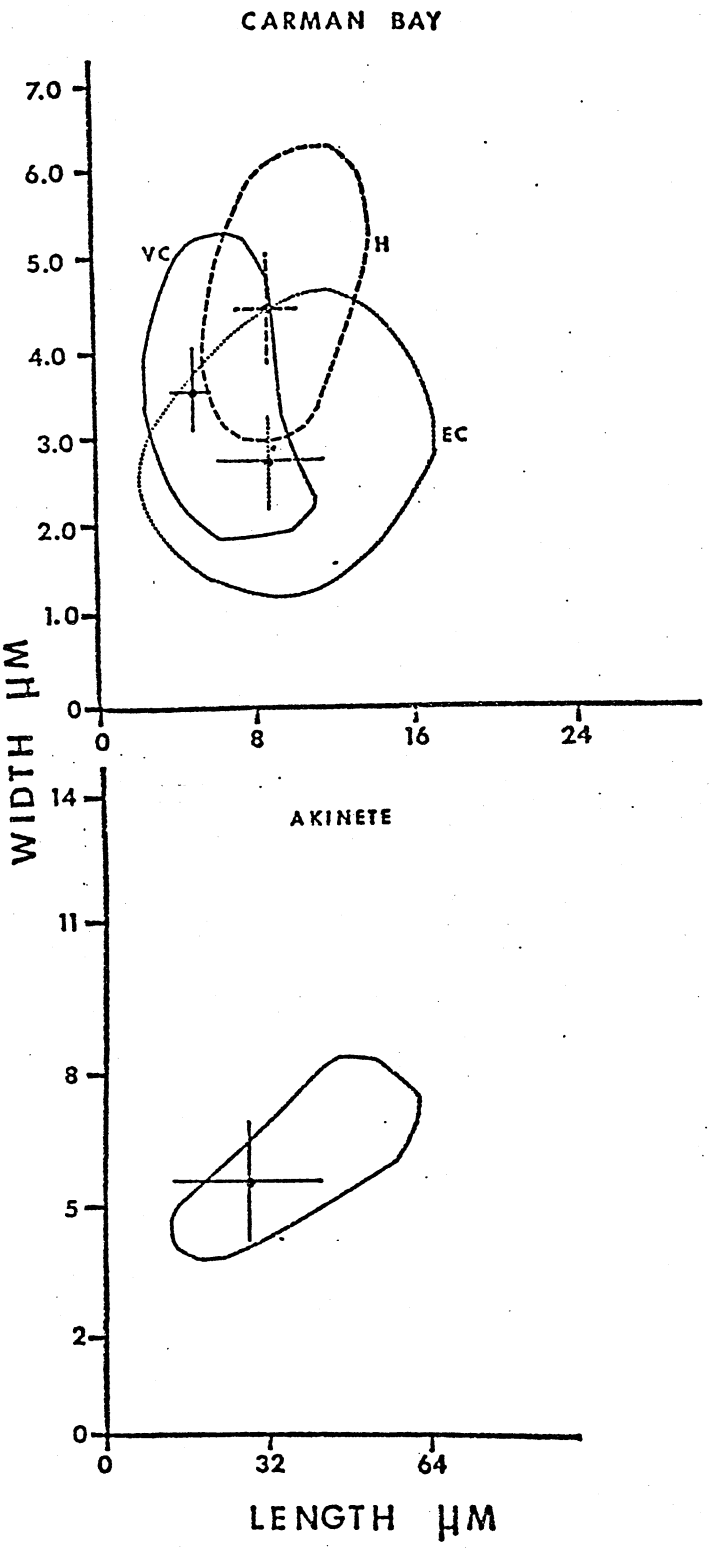

CARMAN BAY
7.0
6.0
5.0
4.0
3.0
2.0
1.0
0
VC
H
EC
0
8
16
24
WIDTH µM
AKINETE
14
11
8
5
2
0
0
32
64
LENGTH µM

FIGURE 34. Range, mean, and standard deviation of cell length and width (vegetative cells, end cells, heterocysts, and akinetes) for the Spencer Pond population

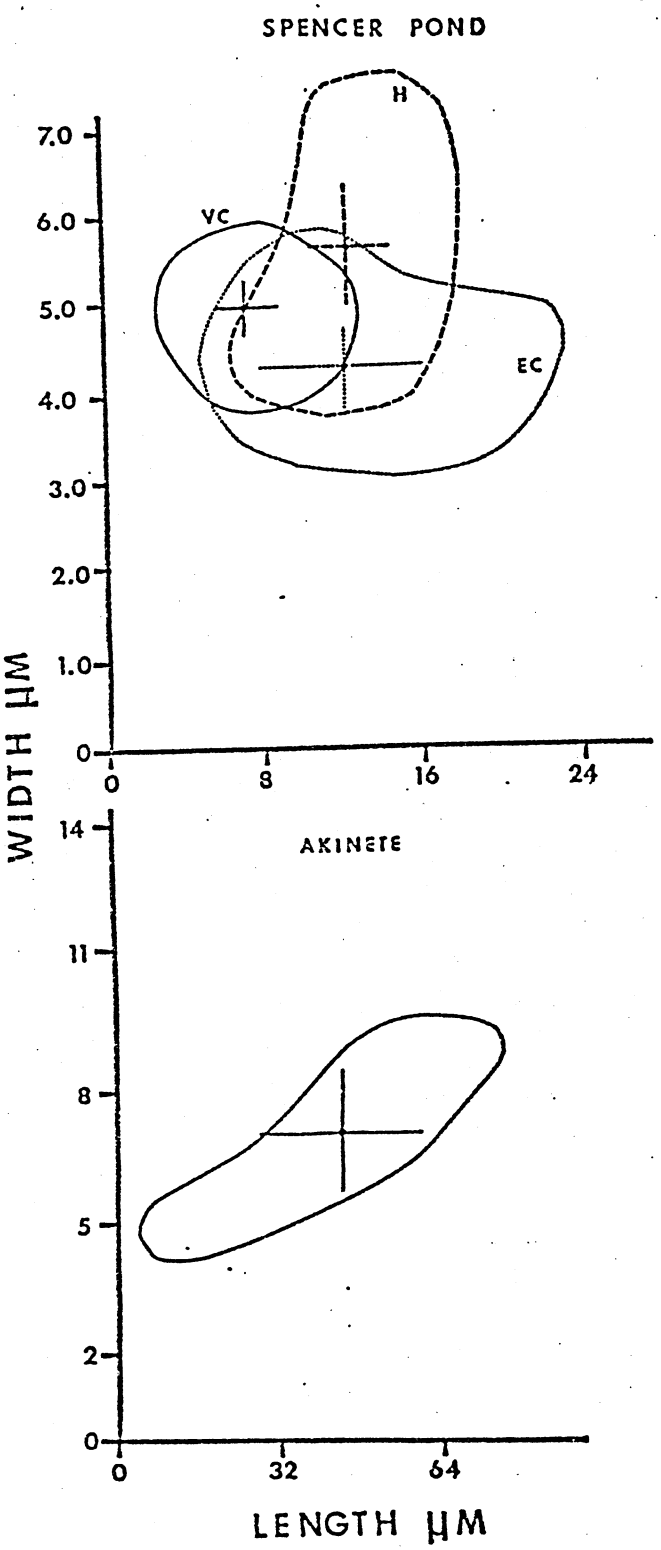

SPENCER POND
H
VC
EC
7.0
6.0
5.0
4.0
3.0
2.0
1.0
0
0
8
16
24
WIDTH µM
AKINETE
14
11
8
5
2
0
0
32
64
LENGTH µM

FIGURE 35. Range, mean, and standard deviation of cell length and width (vegetative cells, end cells, and heterocysts) for the Squaw and Elk Lake populations

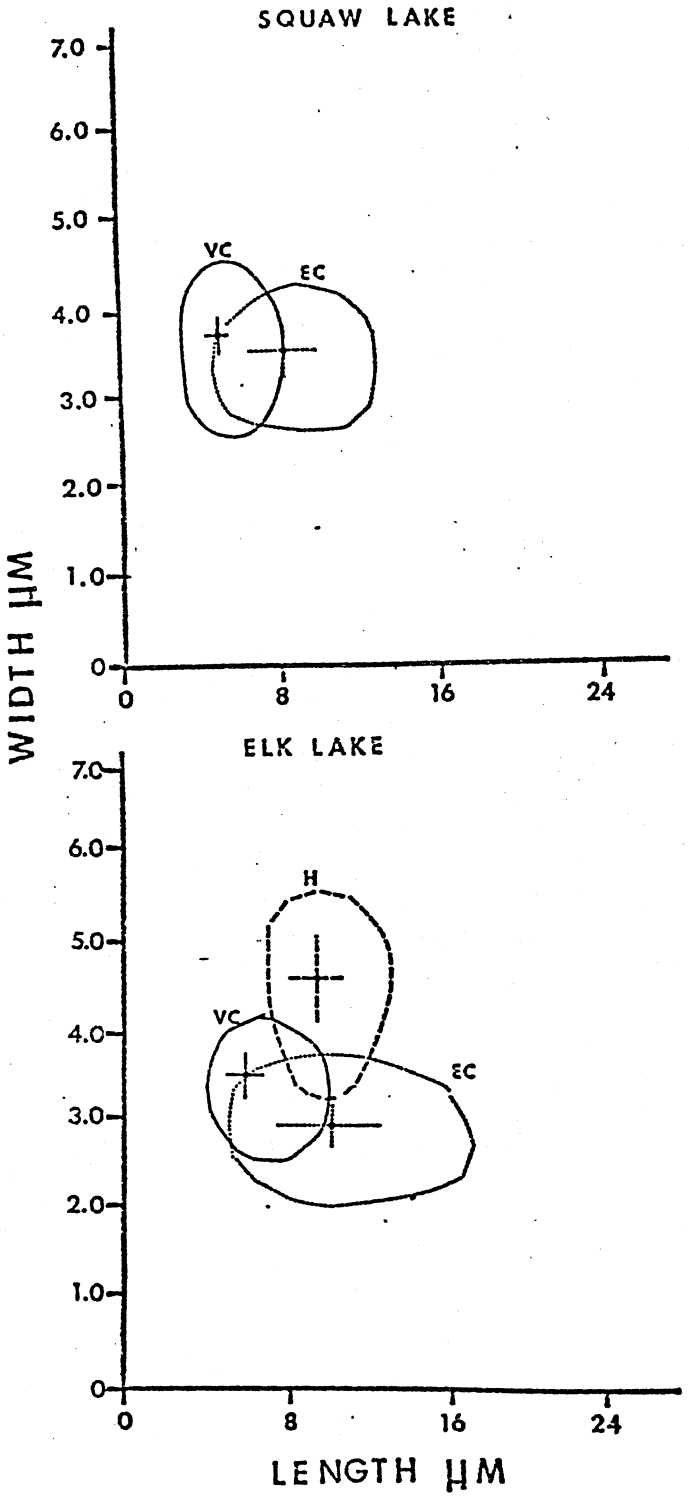

SQUAW LAKE
7.0
6.0
5.0
4.0
3.0
2.0
1.0
0
VC
EC
0
8
16
24
WIDTH µM
ELK LAKE
7.0
6.0
5.0
4.0
3.0
2.0
1.0
0
H
VC
EC
0
8
16
24
LENGTH µM

FIGURE 36. Range, mean, and standard deviation of vegetative cell length and width for all the study lakes, and range of vegetative cell length and width for described taxa

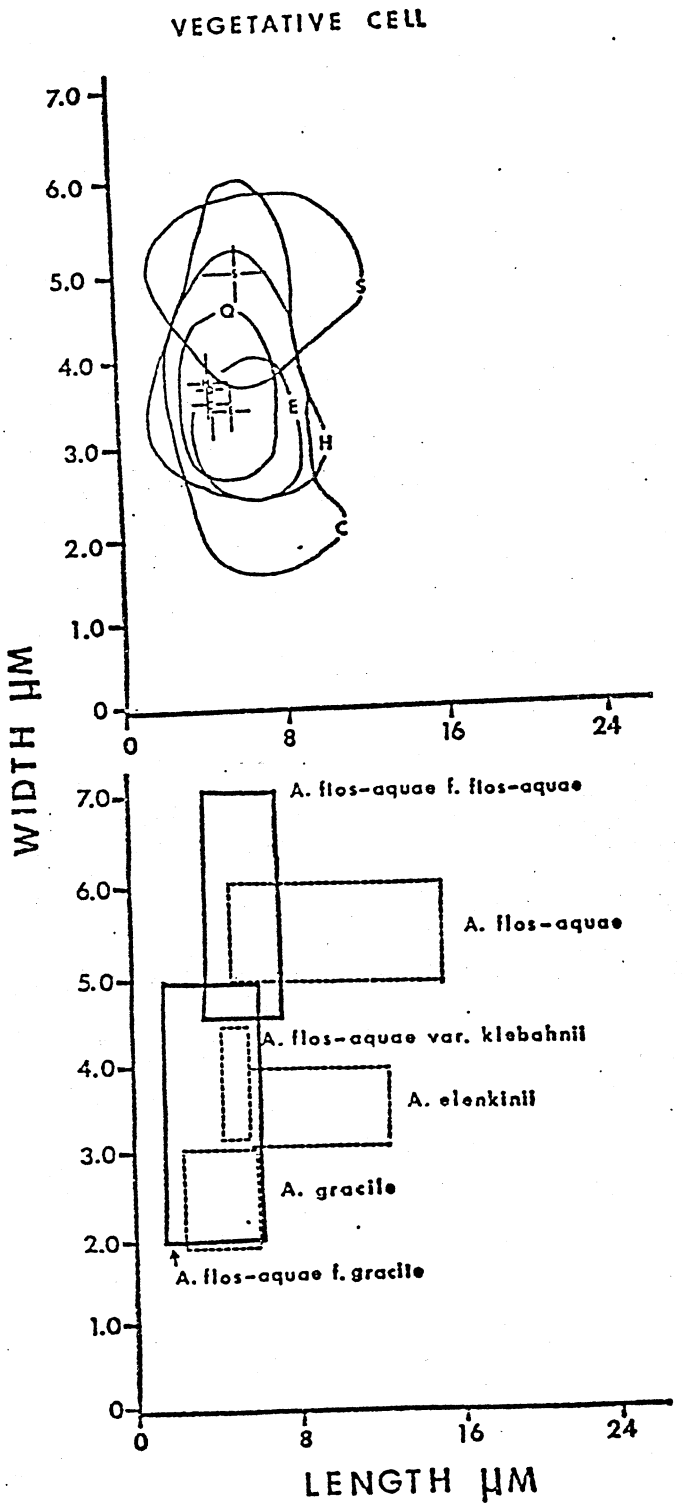

VEGETATIVE CELL
7.0
6.0
5.0
4.0
3.0
2.0
1.0
0
0
8
16
24
S
O
E
H
C
WIDTH µM
A. flos-aquae f. flos-aquae
A. flos-aquae
A. flos-aquae var. klebahnii
A. elenkinii
A. gracile
A. flos-aquae f. gracile
LENGTH µM

FIGURE 37. Range, mean, and standard deviation of end cell length and width for all the study lake populations

END CELL

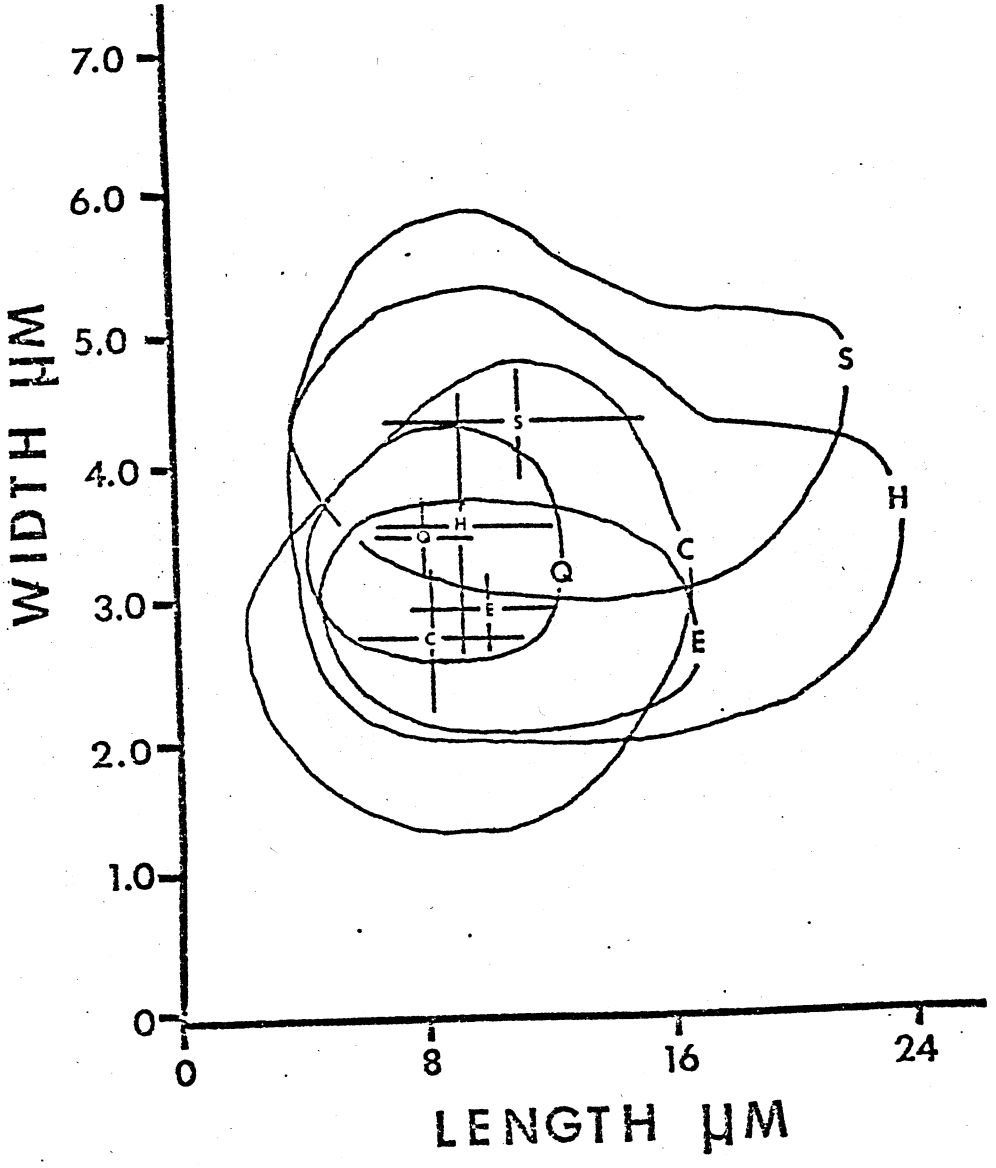


FIGURE 38. Range, mean, and standard deviation of heterocyst length and width for Halsted Bay, Carman Bay, Spencer Pond, and Elk Lake populations, and range of heterocyst length and width for described taxa

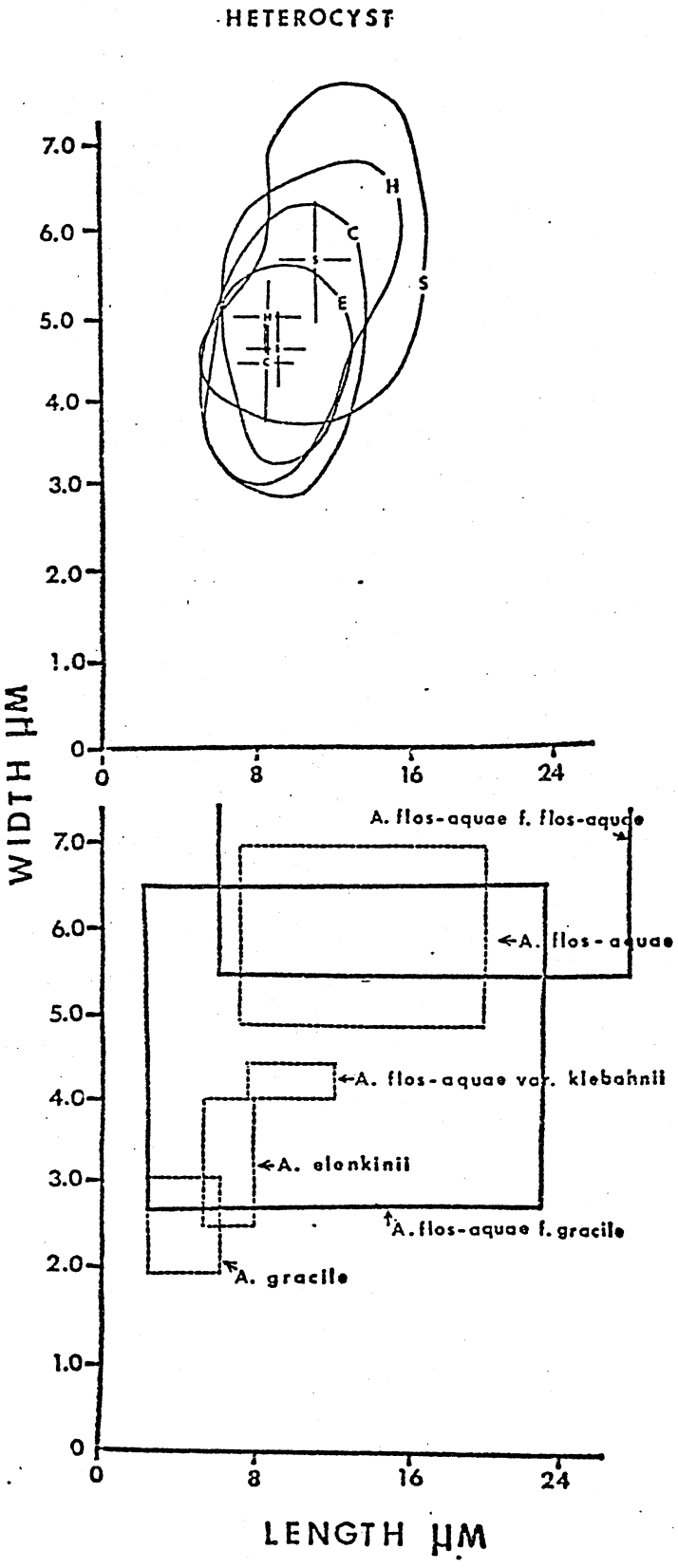

HETEROCYST
H
C
S
E
7.0
6.0
5.0
4.0
3.0
2.0
1.0
0
0
8
16
24
WIDTH µM
A. flos-aquae f. flos-aquae
A. flos-aquae
A. flos-aquae var. klebahnii
A. elenkinii
A. flos-aquae f. gracile
A. gracile
LENGTH µM

FIGURE 39. Range, mean, and standard deviation of akinete length and width for Halsted Bay, Carman Bay, and Spencer Pond populations, and range of akinete length and width for described taxa

AKINETE

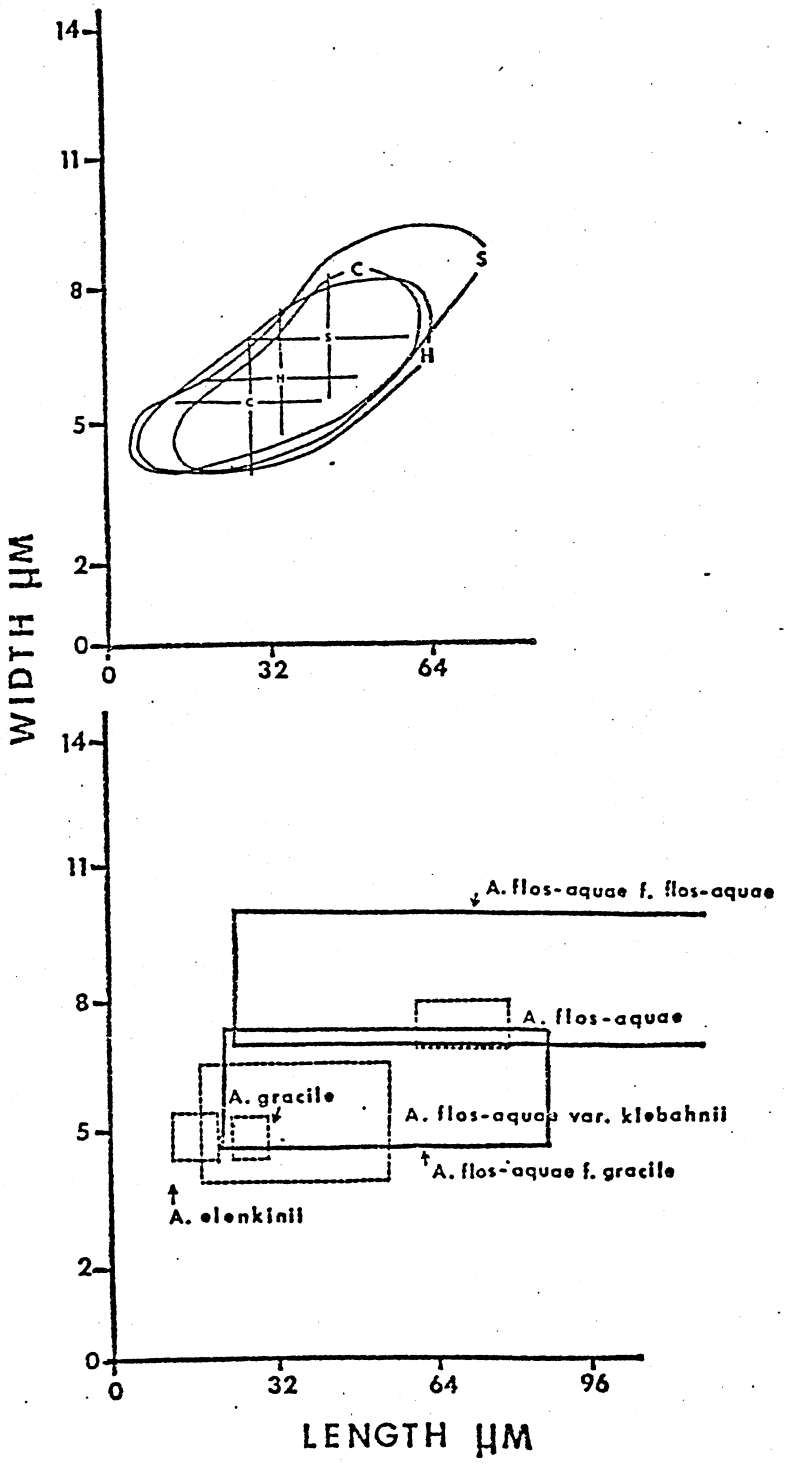

14
11
8
5
2
0
0
32
64
C
S
H
WIDTH µM
A. flos-aquae f. flos-aquae
A. flos-aquae
A. gracile
A. flos-aquae var. klebahnii
A. flos-aquae f. gracile
A. elenkinii
96
LENGTH µM

FIGURE 40. Seasonal variation of range, mean, and standard deviation of length and width of vegetative cells for the Halsted Bay, Carman Bay, and Spencer Pond populations

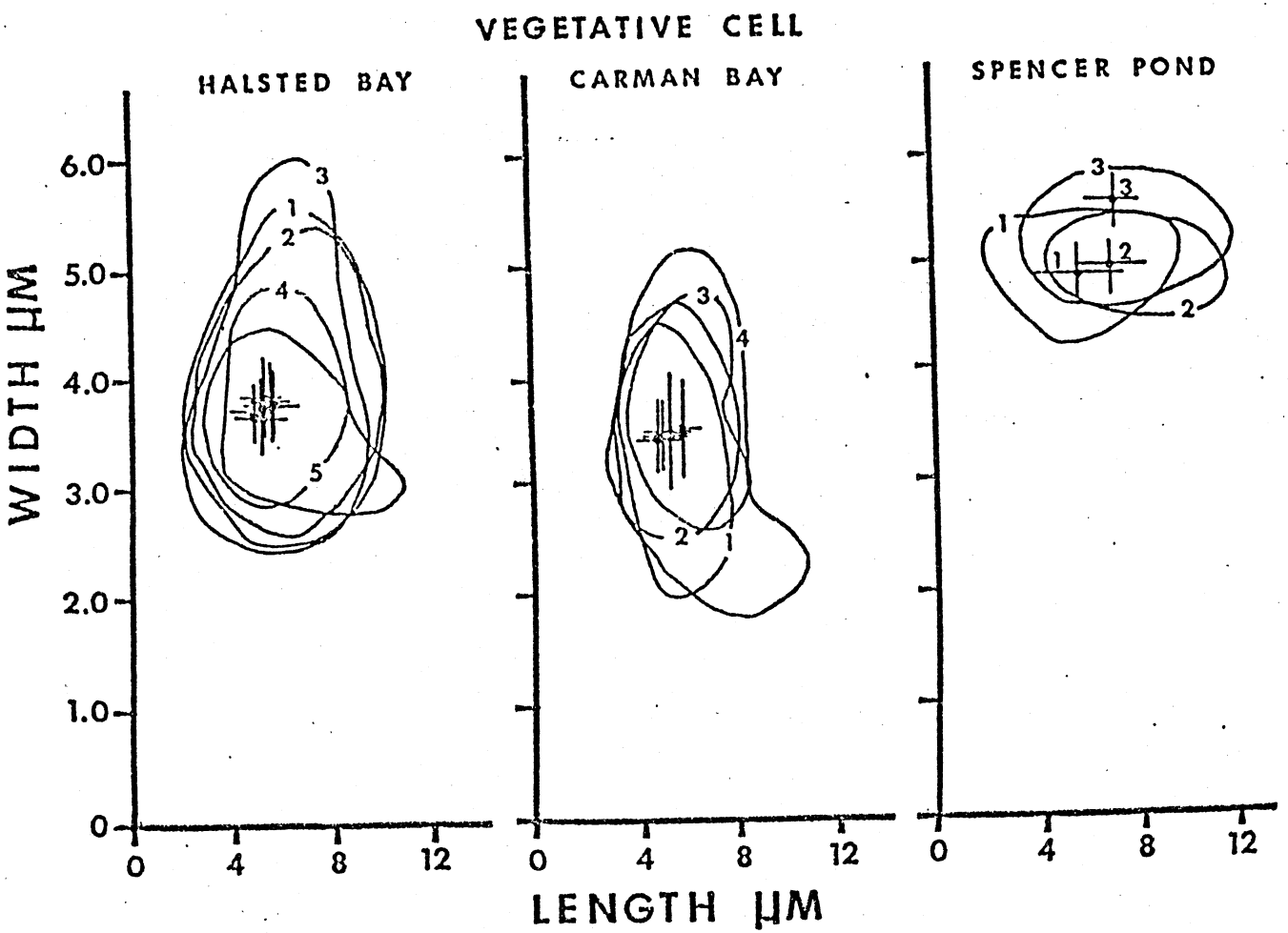

VEGETATIVE CELL
HALSTED BAY
CARMAN BAY
SPENCER POND
WIDTH µM
LENGTH µM
6.0
5.0
4.0
3.0
2.0
1.0
0
0
4
8
12

FIGURE 41. Seasonal variation of range, mean, and standard deviation of length and width of end cells for the Halsted Bay, Carman Bay, and Spencer Pond populations

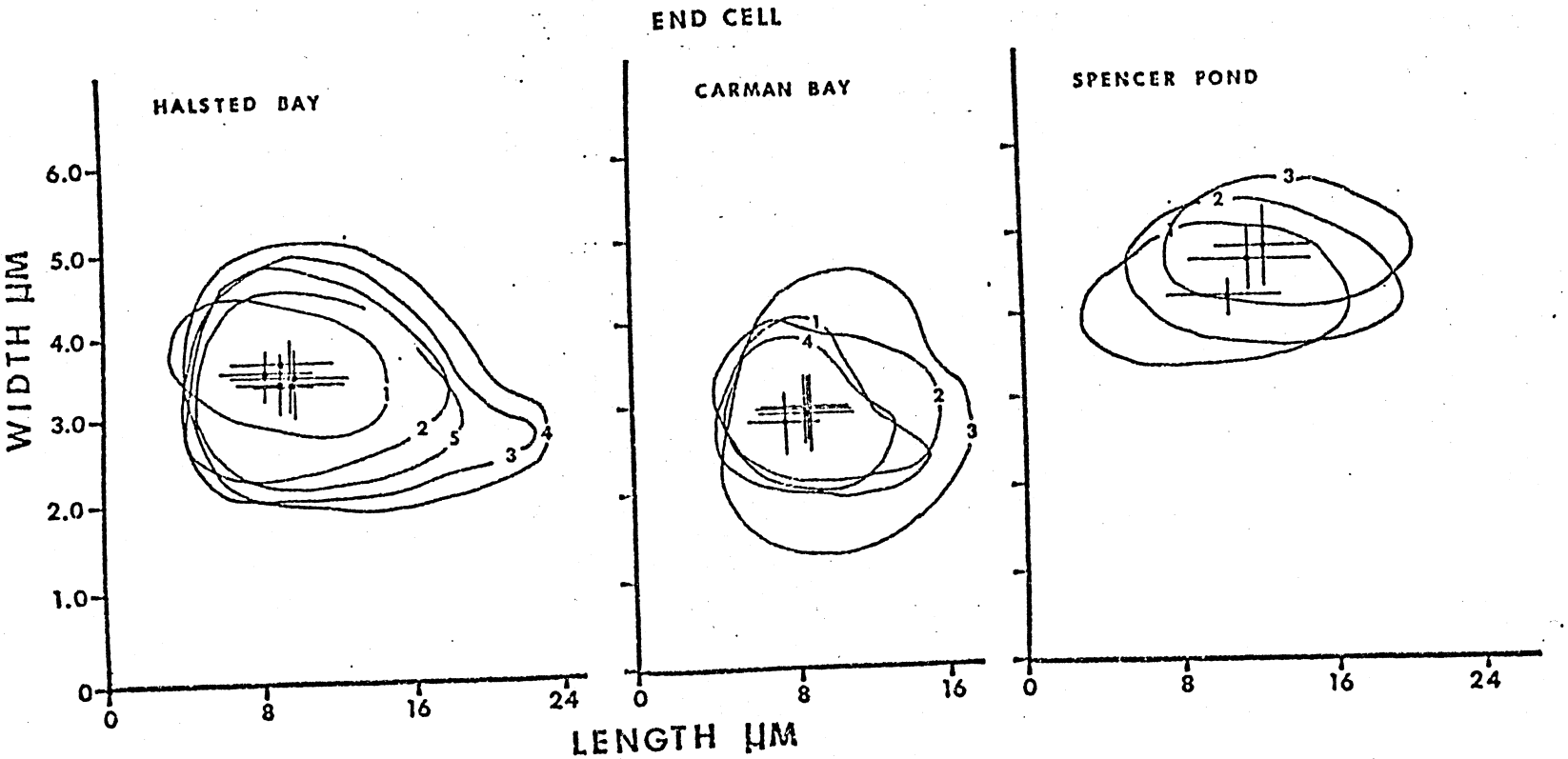

END CELL
HALSTED BAY
CARMAN BAY
SPENCER POND
WIDTH µM
6.0
5.0
4.0
3.0
2.0
1.0
0
0
8
16
24
LENGTH µM
1
2
3
4
5

FIGURE 42. Seasonal variation of range, mean, and standard deviation of length and width of heterocysts for the Halsted Bay, Carman Bay, and Spencer Pond populations

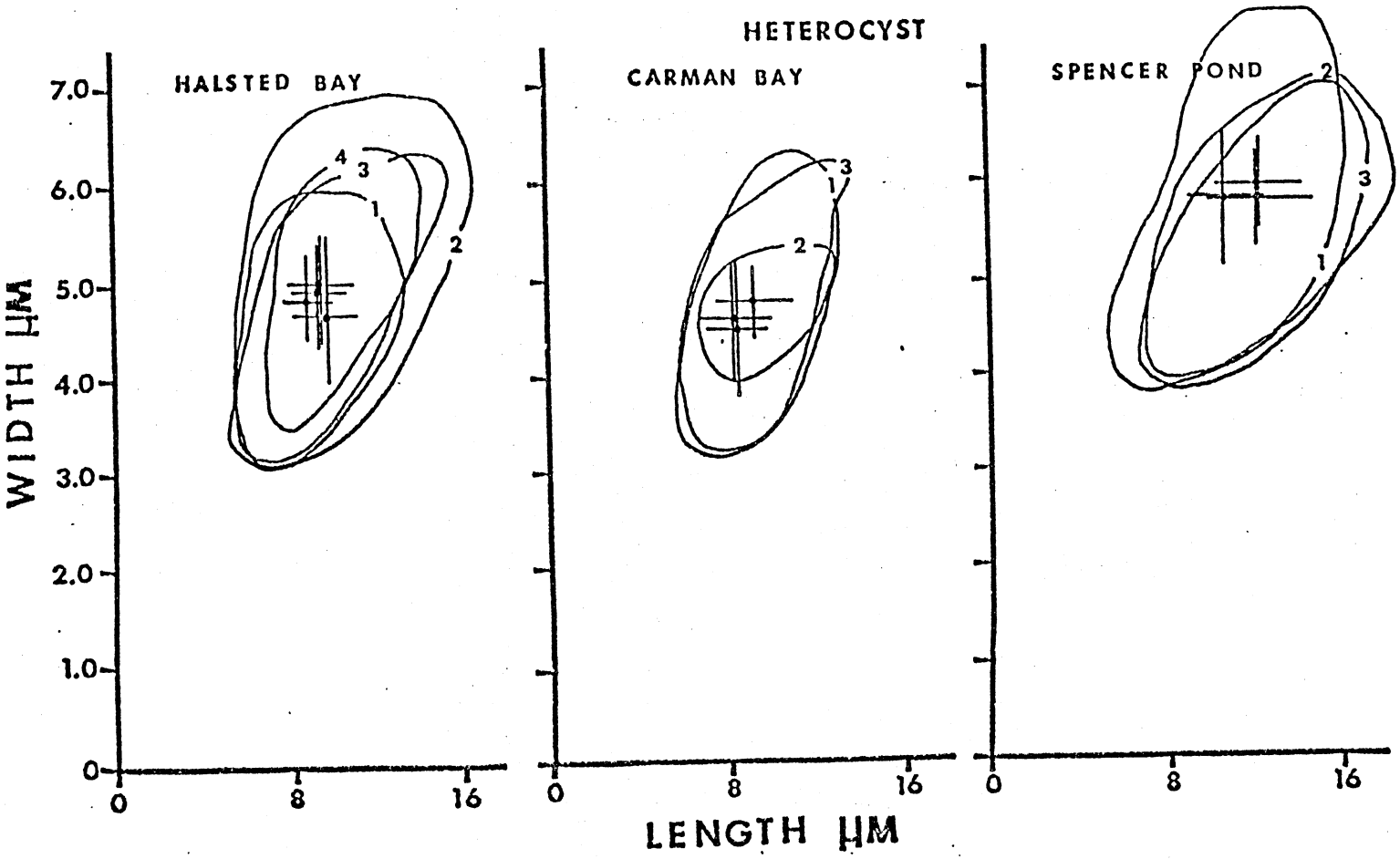

HETEROCYST
HALSTED BAY
CARMAN BAY
SPENCER POND
WIDTH µM
LENGTH µM
7.0
6.0
5.0
4.0
3.0
2.0
1.0
0
8
16
1
2
3
4

FIGURE 43. Range in vegetative cell length and width for colonies and cultures from the Halsted Bay population

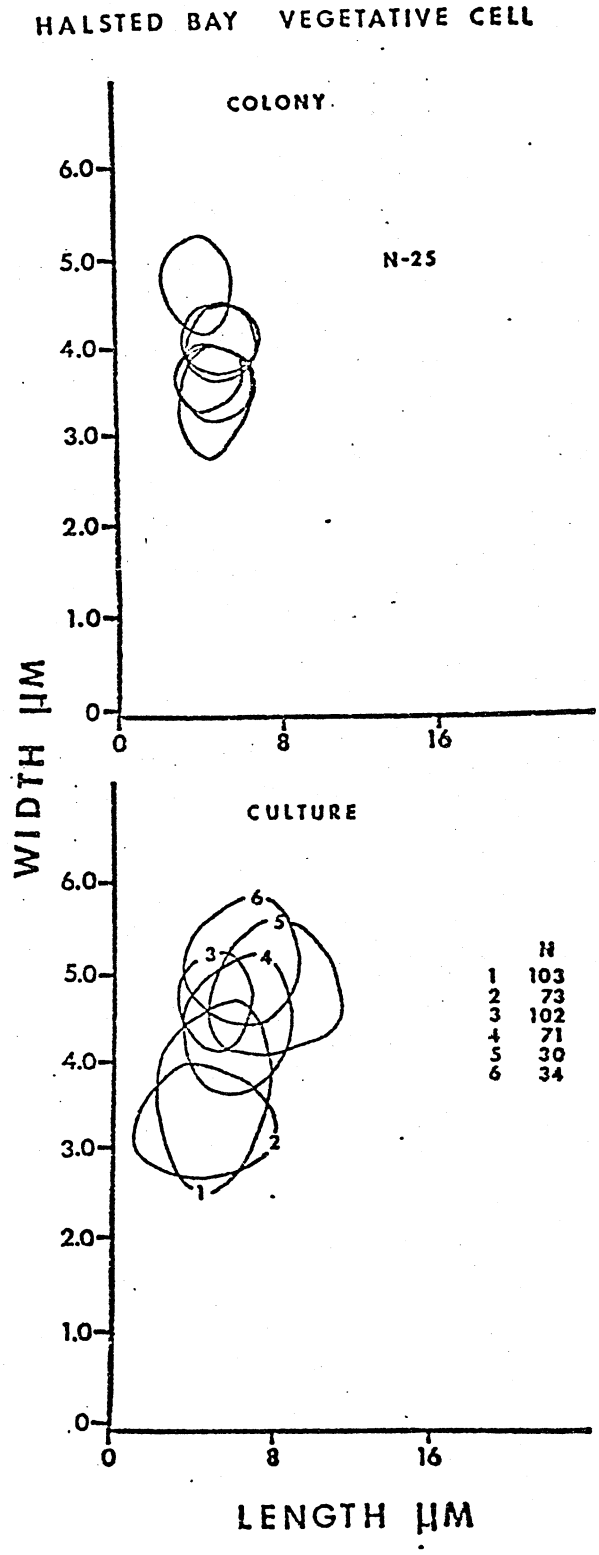

HALSTED BAY VEGETATIVE CELL
COLONY
N-25
CULTURE
WIDTH µM
LENGTH µM
6.0
5.0
4.0
3.0
2.0
1.0
0
8
16
1
2
3
4
5
6
N
1 103
2 73
3 102
4 71
5 30
6 34

FIGURE 44. Range in end cell length and width for colonies and cultures from the Halsted Bay population

HALSTED BAY· END CELL

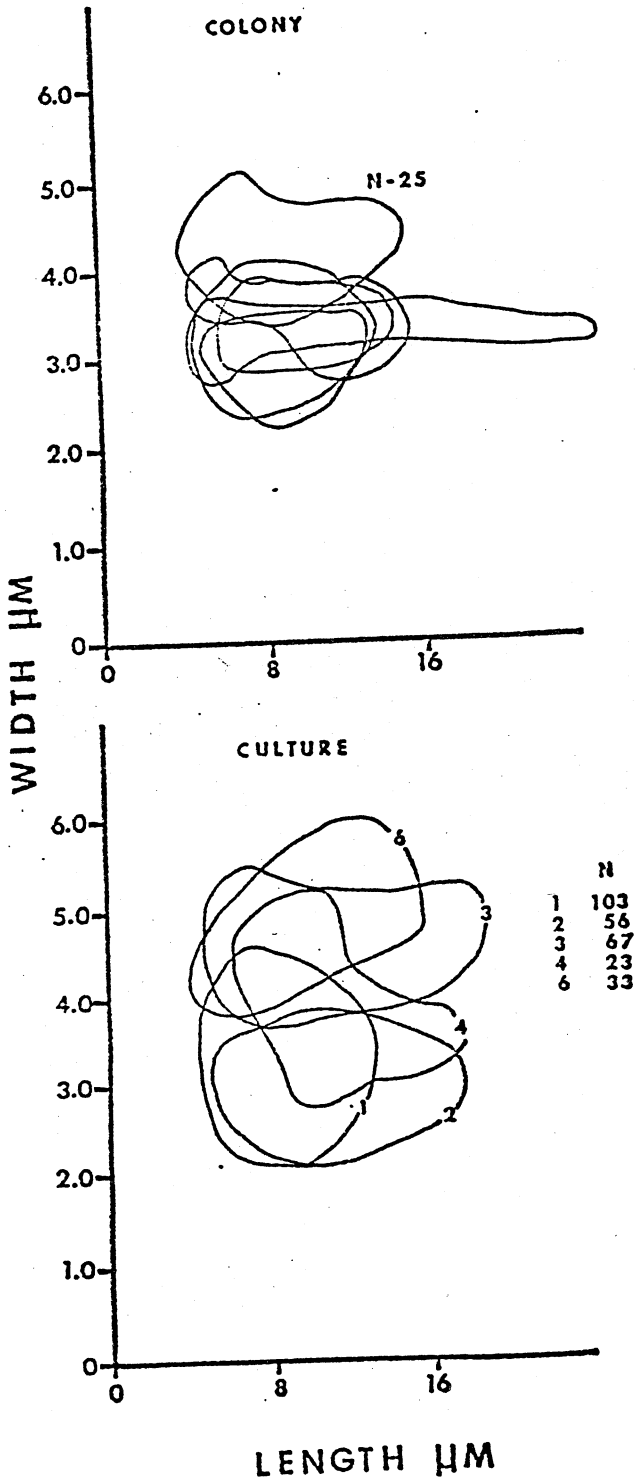


FIGURE 45. Range in heterocyst length and width for colonies and cultures from the Halsted Bay population

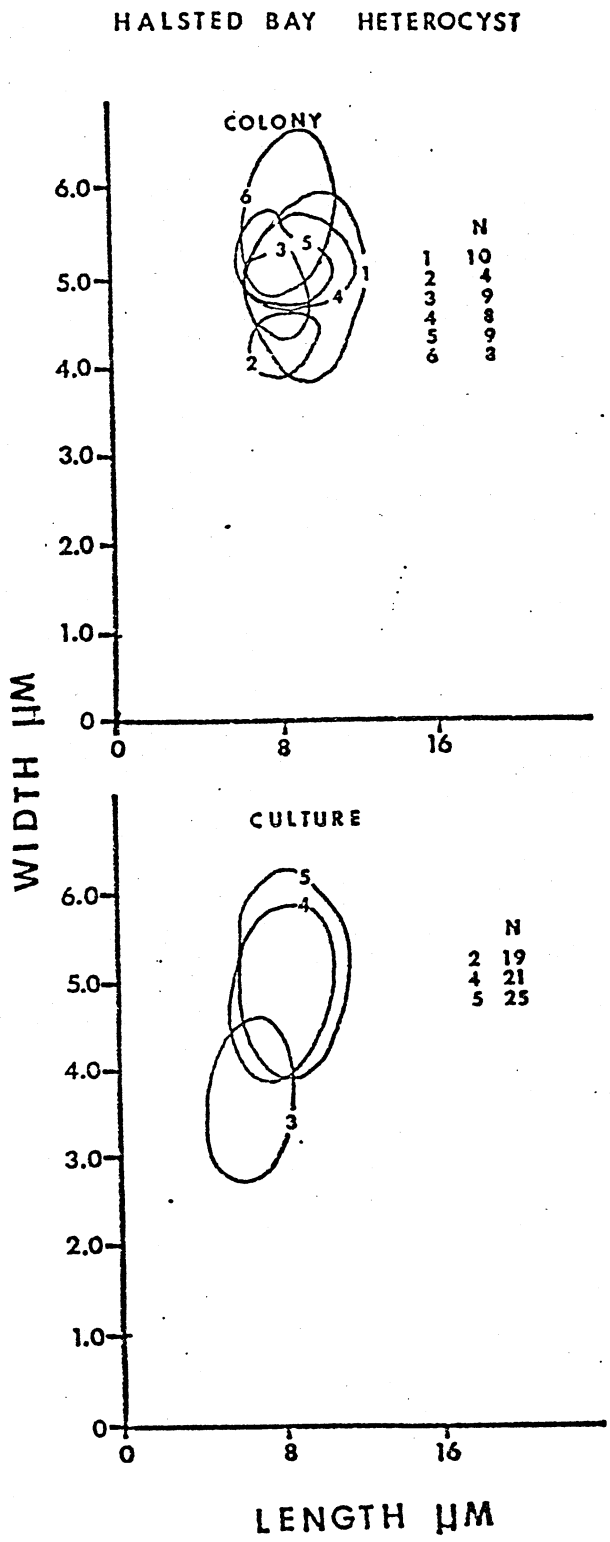

HALSTED BAY HETEROCYST
COLONY
N
1 10
2 4
3 9
4 8
5 9
6 3
CULTURE
N
2 19
4 21
5 25
WIDTH µM
LENGTH µM
6.0
5.0
4.0
3.0
2.0
1.0
0
8
16

FIGURE 46. Range in akinete length and width for colonies from the Halsted Bay population

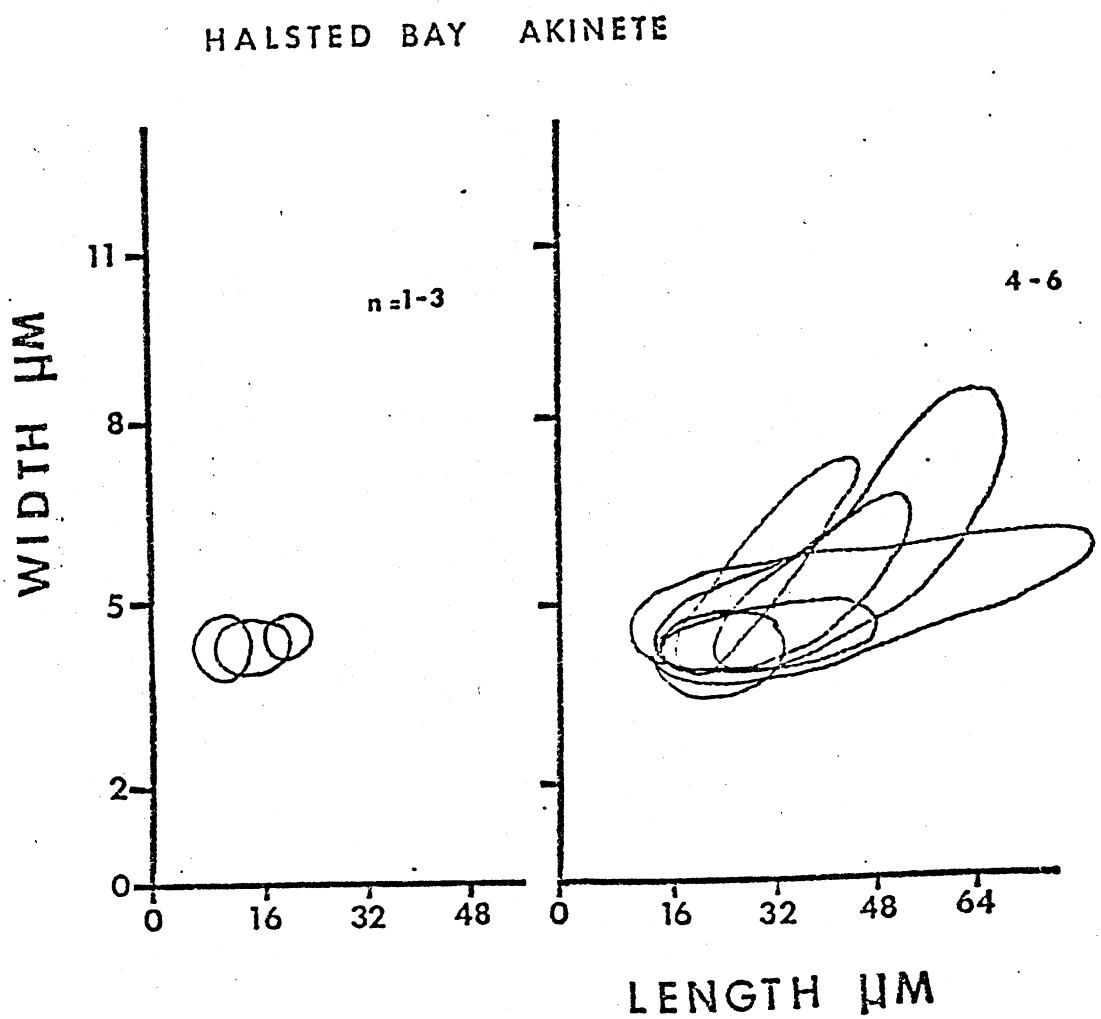

HALSTED BAY AKINETE
WIDTH µM
11
8
5
2
0
n=1-3
4-6
0
16
32
48
0
16
32
48
64
LENGTH µM

FIGURE 47. Range in vegetative and end cell length and width for colonies, cultures, and the lake population in the Carman Bay population

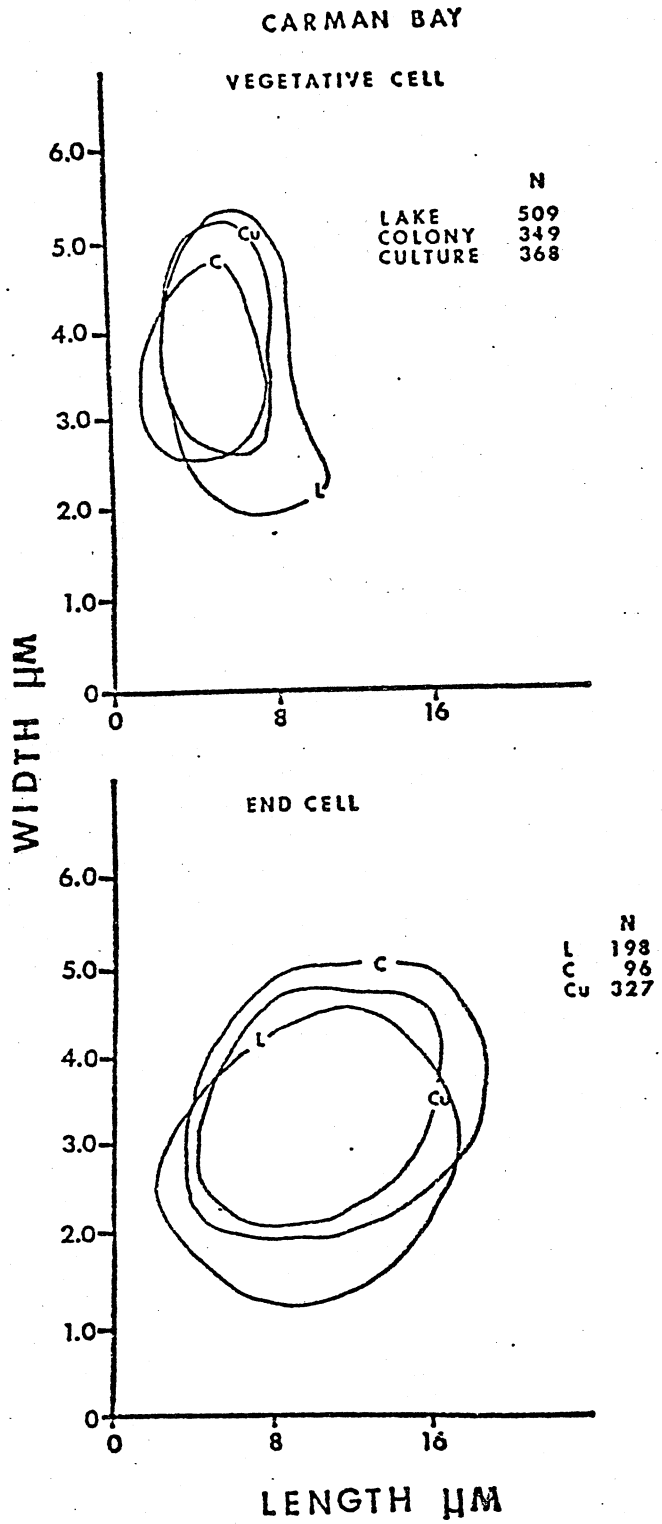
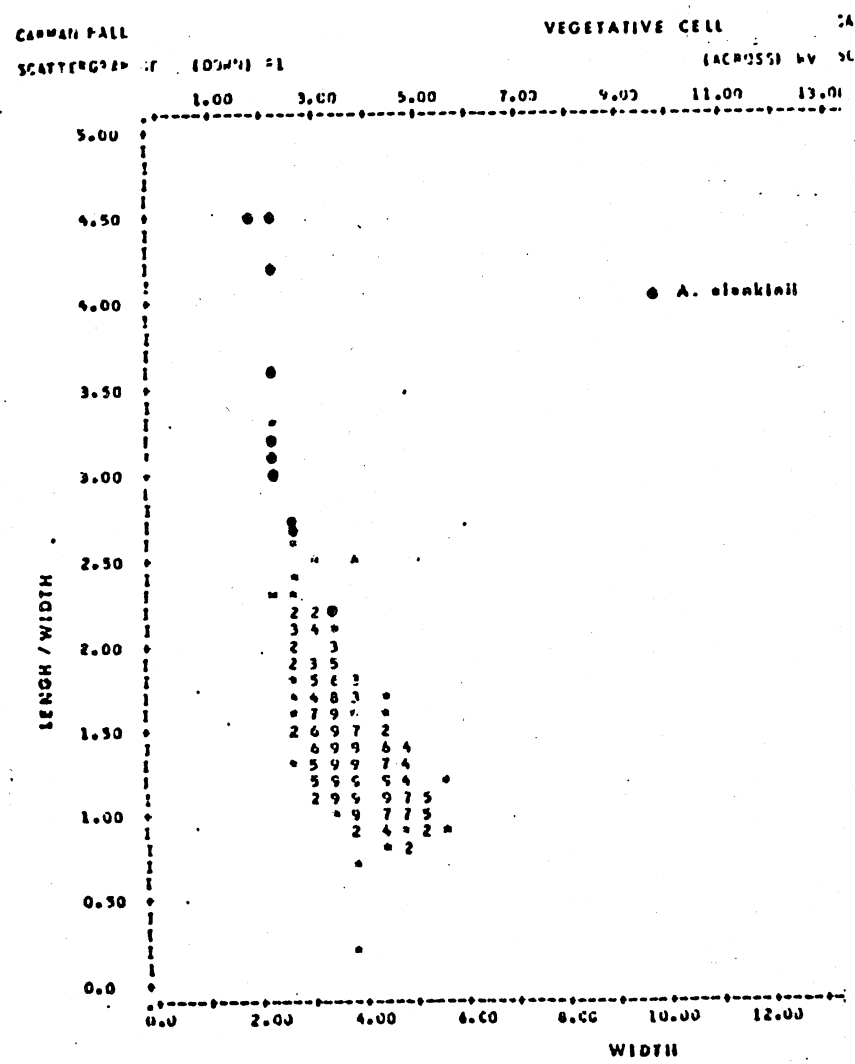

CARMAN BAY
VEGETATIVE CELL
N
LAKE 509
COLONY 349
CULTURE 368
Cu
C
L
6.0
5.0
4.0
3.0
2.0
1.0
0
0
8
16
WIDTH µM
END CELL
N
L 198
C 96
Cu 327
C
L
Cu
6.0
5.0
4.0
3.0
2.0
1.0
0
0
8
16
LENGTH µM

FIGURE 48. Scattergrams of length to width ratios of vegetative and end cells in the Carman Bay population


CARMAN FALL
VEGETATIVE CELL
(ACROSS) AA
1.00
3.00
5.00
7.00
9.00
11.00
13.00
5.00
4.50
4.00
3.50
3.00
2.50
2.00
1.50
1.00
0.50
0.0
LENGH / WIDTH
A. sleenkiell
0.0
2.00
4.00
6.00
8.00
10.00
12.00
WIDTH

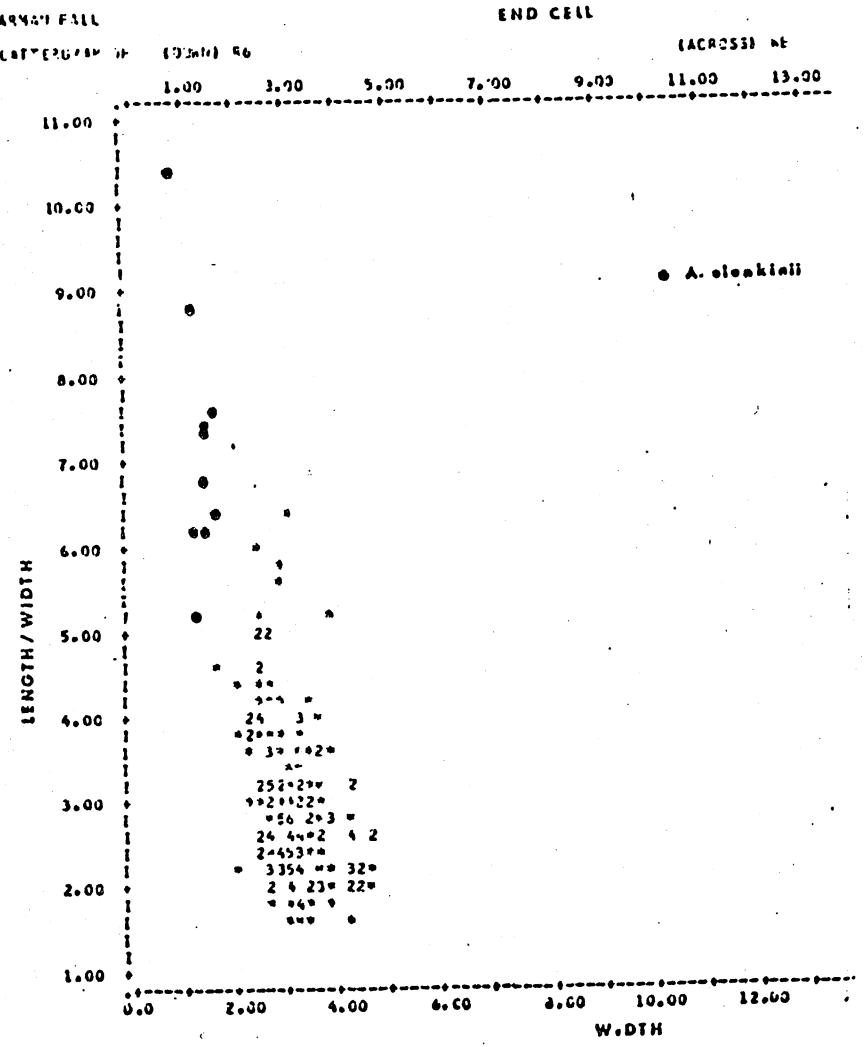

CARMAN FALL
END CELL
(ACROSS) AE
1.00
3.00
5.00
7.00
9.00
11.00
13.00
11.00
10.00
9.00
8.00
7.00
6.00
5.00
4.00
3.00
2.00
1.00
LENGTH / WIDTH
A. sleenkiell
0.0
2.00
4.00
6.00
8.00
10.00
12.00
WIDTH

FIGURE 49. Unusual morphological variations in *Aphanizomenon* filaments

10 µ