Blue-Green Algal Mats from Acidified Adirondack Lakes: Mat Structure and pH Response of Algal Isolates

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BLUE-GREEN ALGAL MATS FROM ACIDIFIED ADIRONDACK LAKES:
MAT STRUCTURE AND pH RESPONSE OF ALGAL ISOLATES

A Thesis
Presented to the Faculty of the Department of Biological Sciences of the State University of New York College at Brockport in Partial Fulfillment for the Degree of Master of Science

by
Maureen Ann Leupold
October 1983
# THESIS DEFENSE

FOR

Maureen Longo
Master's Degree Candidate

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ABSTRACT

Seven acidified lakes in the Adirondack mountains of New York, USA were sampled for benthic algae during the summer of 1982. Benthic cyanophyte mats, dominated by *Schizothrix* spp. were found in three of the seven lakes sampled (Big Moose, pH 4.00-4.40; Limekiln, pH 4.60-5.30; Wolf, pH 3.45-3.70). The blue-green algal mats found were structurally similar to living stromatolite analogs found in other extreme environments. Under controlled laboratory conditions, unialgal isolates of *Schizothrix calcicola* (Ag.) Gom., grew best at or near neutrality but could survive and grow slowly at low pH (4.0, 5.0). Increased nutrient levels appeared to have little affect on growth or survival in buffered low pH (4.0) media. Cultures of *S. calcicola* were able to raise the pH of unbuffered media three pH units in less than 72 hours. Clumping and aggregation of filaments was enhanced by lowering the pH (to pH 3.5 in 5.5 hours) of actively growing cultures.
INTRODUCTION

Increased acidity and the concurrent changes in nutrient and metal concentrations caused by acid precipitation affect all trophic levels in sensitive aquatic ecosystems. Acidified lakes have impoverished zooplankton assemblages (Almer et al. 1974, Hendrey and Wright 1976, Roff and Kwiatkowski 1977, Raddum et al. 1980, Yan and Struss 1980, Confer et al. 1983), often dominated by acid tolerant species [e.g. Bosmina, Polyothera, Diaptomus (Confer et al. 1983)]. Similarly, phytoplankton species diversity declines with decreasing pH (Almer et al. 1974, Kwiatkowski and Roff 1976, Hendrey and Wright 1976, Yan 1979). In some acidified lakes, aquatic macrophytes are being replaced by mosses (Almer et al. 1974, Hultberg and Gran 1976, Hendrey and Vertucci 1980) or are being covered by abundant growths of periphytic algae, often dominated by diatoms and filamentous green algae (Lazarek 1982b, Muller 1980). Not only are the benthic fauna reduced or eliminated by the decreased pH (< 6.0) (Okland and Okland 1980) and increased metal concentrations (Raddum 1980) but also by the altered conditions of the lake bottom sediments (Almer et al. 1978). For example, increased rates of sedimentation of organic debris which is evidence of reduced decomposer activity (Hendrey et al. 1976, Traaen 1980), may also exclude certain benthic species (Almer et al. 1978). In general a shift in species composition and
a decline in species diversity occurs. Although many organisms, such as fish (Beamish et al. 1975, Schofield 1976), are eliminated, acidified lakes are often dominated by the few species which are able to exploit the changed conditions.

The development of benthic algal mats in lakes acidified by acid precipitation is also a recent phenomenon. These dense, felt-like algal mats which blanket the bottoms of some acidified lakes, are composed primarily of small filamentous blue-green algae (Oscillariaceae). Although low diversity cyanophyte mats are known to occur in many extreme environments such as Antarctica lakes, thermal pools and alkaline lakes (Parker et al. 1981), the mats described in Lake Colden, New York (Hendrey and Vertucci 1980) and Lake Gårdsjön, Sweden (Lazarek 1980) are the first reports from environments below pH five. Blue-green algae have historically been thought to be excluded from acid conditions (Brock 1973). Thus it is surprising to find them as the dominant benthic organisms in acidified lakes.

In Lake Gårdsjön, algal primary productivity of the mat was 32.8 ± 12.9 mg C m⁻² day⁻¹ (Lazarek 1982). The contribution of blue-green algal mat primary productivity to the total annual primary productivity of acidified lakes has not been estimated, but may be relatively high in these impoverished
The objectives of this study were to document the occurrence of cyanophyte mats in Adirondack Mountain lakes, identify and isolate the major mat-forming species into unialgal cultures and determine the effects of pH on growth of the isolated species under controlled laboratory conditions. We test here the hypothesis that the blue-green algae observed in benthic mats in acidified lakes are acidophlic ecophenes.
METHODS

Fieldwork

Seven lakes were chosen based on previously reported pH values (Pfeiffer and Festa 1980) and observations of benthic algal mat development (Lee, personal communication, Vertucci, personal communication). Wolf Lake, Falls Pond and Cellar Pond are small high elevation lakes, reached only by hiking trails (Table 1). Equipment, including a small inflatable boat, was backpacked into these areas. Big Moose Lake, Dart Lake, Fourth Lake and Limekiln Lake are larger, lower elevation lakes (Table 1) near accessible roadways.

In all the lakes, surface and bottom water samples were obtained with a Van Dorn water sampler. Within eight hours after collection, alkalinity was analysed by potentiometric titration (American Public Health Association 1975) in June and July, and by the Gran titration procedure (Talling 1973) in August.

Temperatures were measured with a thermistor thermometer. In June and July pH readings were determined from collected water samples with a Corning pH meter equipped with a combination electrode. In August pH was obtained in situ.
Benthic algae samples collected with an Ekman Grab sampler were preserved with Acid Lugol's solution. Live material for culturing purposes was stored in translucent plastic bottles for return to the laboratory. The Drouet (1968) classification and nomenclature system was employed for all Oscillatoriaceae identification.

Algal Culture Isolation

Algal enrichment cultures were started using Guillards' Woods Hole MBL medium (Nichols 1973). *Schizothrix calcicola* (Ag.) Gom. was isolated from four lakes into unialgal cultures following the methods of Hoshaw and Rosowski (1973). Attempts to obtain axenic cultures by centrifugation, ultrasound treatment, antibiotics and surfactants were unsuccessful (Hoshaw and Rosowski 1973). The presence of bacteria in the unialgal cultures was continuously monitored by inoculating Difco Nutrient Broth with culture material, streaking plates of Guillards' medium solidified with 1.3% agar and subsequent microscopic examination. Through successive transfers from liquid to solid medium bacterial contamination was reduced but not eliminated in the isolates. Aseptic technique was used throughout to minimize bacterial contamination.

Stock cultures of the *S. calcicola* isolates were kept in a growth chamber at 20°C with a light cycle of 16 hours.
light, 8 hours dark (ca.3000 lux) under cool white fluorescent tubes. Guillards' medium was modified for all experimental work and stock cultures by eliminating Na₂SiO₄ enabling better control of pH after autoclaving. Stocks were routinely transferred each week. All experiments were begun with seven day old cultures in Pyrex erlenmyer flasks. Cell counts were with a hemacytometer (Improved Neubauer Ruling) by the method of Burnham et al. (1973).

Ecophene Experiment

*S. calcicola* isolates from Limekiln Lake, Falls Pond, Big Moose Lake and Wolf Lake were grown in a pH range of 4.0 to 7.0. Experimental cultures (initial density = 5.0 x 10³ cells per ml) contained modified Guillards' medium buffered with 0.2% cyclo acid (cyclopentanetetracarboxylic acid). pH was adjusted (4.0-7.0) in 0.5 increments using NaOH prior to autoclaving. Each pH level was run in triplicate. Experimental conditions included constant light (ca.3250 lux under cool white fluorescent tubes) and temperature (20° C) with shaking at 100 RPM. Flasks were randomized daily to insure no positioning effects. At the end of seven days pH was measured and dry weight measurements of growth were obtained by the membrane filtration method of Sorokin (1973). Control filters (n=10), rinsed with deionized-distilled water, were processed in the same manner as experimental filters (growth=zero).
Dilution Experiments

Unbuffered modified Guillards' medium was prepared at 0.10, 0.25, 0.50 and 1.00 strength and adjusted to pH 4.0 with H$_2$SO$_4$. Limekiln Lake S. calcicola were centrifuged and washed two times with 0.10 strength medium. Each nutrient level was run in quadruplicate, starting with $3.4 \times 10^4$ cells per ml. Growth conditions duplicated the ecophene experiment except the flasks were not shaken. At the end of two weeks pH was measured and cell counts were made to determine growth.

The second dilution experiment differed in that the medium was buffered with 0.2% cyclo acid and dilution strengths were 0.125, 0.250, 0.375 and 0.500. Growth was determined by cell counts on day 10.

Growth Curves

Limekiln Lake isolates of S. calcicola were grown in 0.5 strength modified Guillards' medium with a pH range of 4.0 to 7.0 buffered with 0.2% cyclo acid (adjusted with Tris base to the desired pH level). Washed cells of the Limekiln Lake isolate were inoculated into 30 ml of medium in 50 ml flasks giving an initial cell density of $4.3 \times 10^4$ cells per ml. Growth conditions duplicated the ecophene experiment. For 14 days, triplicate flasks from each pH
level were harvested daily for cell counts of suspended and total algae and pH measurements.

Nutrient Addition

Additional nutrients, equaling the original amount contained in 0.50 strength medium were added to 7 day old cultures of Limekiln Lake *S. calcicola*. Experimental conditions duplicated the growth curve experiment. On days 7 and 14 cell counts from cultures with added nutrients and from control cultures with added deionized-distilled water were made.

Titration Experiment

500 ml of 0.50 strength unbuffered modified Guillards' medium in a liter flask was inoculated with Limekiln Lake *S. calcicola* isolates to a starting cell density of $1.5 \times 10^5$ cells per ml. The culture was shaken at ca. 50 RPM in a growth chamber under constant light (3150 lux) and temperature ($20^\circ$C). pH of the growing culture was continuously monitored with a Chemtrix pH meter and a Beckman recorder. Starting at the peak of population growth, density was monitored (by cell counts of suspended algae) as the pH was lowered with a pH Controller connected to an automatic injection syringe containing 0.02 N $\text{H}_2\text{SO}_4$. The pH was lowered to 3.5 over 5.5 hours.
RESULTS

Algal Mat Development

Wolf Lake contains a benthic algal mat composed primarily of the blue-green alga Schizothrix Friesii (Agardh.) Gomont (Oscillatoriaceae). The mat is dark green, underlying and occasionally growing over submerged macrophytes. Schizothrix Friesii filaments are 3 to 4 μm in diameter with cell lengths of 5 to 9 μm and secrete a distinct sheath. The mat is laminated with live filaments on top of discarded sheath material and dead filaments. Diatoms are frequently dispersed within the mat.

The algal mat in Limekiln Lake is extensive in the littoral zone, covering the sediments, logs, rocks and submerged macrophytes. The growth ranges in color from olive-green to greyish tan. The matrix of the mat is formed by a small blue-green alga, Schizothrix calcicola (Agardh.) Gomont, 1.5 to 2.0 μm in diameter, which secretes a gelatinous sheath. Other cyanophytes, including Schizothrix Friesii, Merismodedia sp., Hapalosiphon sp. and Chrococcus sp., are dispersed throughout the densely entangled filaments of Schizothrix calcicola. Diatoms, desmids and the red alga Batrachospermum sp. are also associated with the mat.

Big Moose Lake contains areas of mat development similar to
Limekiln Lake but not as extensive. Dense growths of the green alga *Mougeotia* sp. occurs as periphyton and metaphyton. *Batrachospermum* sp. is also frequently encountered as periphyton.

No cyanophyte mat development was observed in Cellar Pond, Dart Lake, Falls Pond or Fourth Lake, yet the major mat forming *Schizothrix* species were present in all lake benthos samples. Temperature, pH, and alkalinity of the seven lakes is given in table 2. Of the seven lakes, only Falls Pond had received state sponsored lime applications in 1975 and 1979: private landowner organizations have limed the north bay of Big Moose Lake in the past (Pfeiffer personnel communication, see appendix II). Table 3 is a partial list of the algal genera collected from all the lakes' benthic samples.

Unialgal cultures of *Schizothrix calcicola* were isolated from Big Moose Lake, Limekiln Lake, Falls Pond and Wolf Lake. *Schizothrix Friesii* from Wolf Lake would not grow in defined media under laboratory conditions (see appendix III).

Ecophene Experiment

All isolates grew best at or near neutral pH (6.5 or 7.0) (fig.1). A Newman - Keules multiple range test (p = .05)
(Zar 1974) indicated that generally below pH 6.5, no significant difference in abundance occurred between each pH range for each isolate (fig. 2).

Dilution Experiments

Static cultures of Limekiln Lake *Schizothrix calcicola* in unbuffered media (initial pH 4.00) grew equally well in full and half strength media (fig. 3a). Mean pH (n=4) was 8.50 in half strength and 7.84 in full strength experimental cultures after two week incubation periods. No live algae were found in the 0.10 strength medium (pH after two weeks = 4.05). 15.7% of the initial cell density (5.32 x 10^3 cells per ml) was present in the 0.25 strength medium after 2 weeks' incubation (final pH = 3.80) (fig 3a). Static cultures, incubated for 10 days in buffered (pH 4.0), reduced strength media (0.500, 0.375, 0.250, 0.125), never reached the initial cell density (fig. 3b). However, cell survival occurred at all pH levels (fig. 3b).

Growth Curves

Mean daily cell counts of Limekiln Lake *Schizothrix calcicola* cultures (n=3) buffered in one unit increments from pH 4.0 to 7.0 are given in figure 4. The growth curves at pH 6.0 and pH 7.0 are typical sigmoid curves, displaying exponential growth from days four to seven
A decrease in cell density occurred initially at pH 4.0 by day two followed by a cyclic but increasing growth pattern. At pH 5.0, a slight increase in cell density occurred by day two followed by a decline in cell density by day four (fig. 4b). Cell density increased in a cyclic pattern from day four to fourteen.

**Nutrient Addition**

Adding additional nutrients to seven day old cultures caused no significant difference in growth or cell survival between nutrient levels (fig 5). Cell density remained nearly constant in all nutrient levels over the two week incubation period.

**Titration Experiment**

Limekiln Lake *Schizothrix calcicola* isolates grown in unbuffered medium initially at pH 5.00 changed the pH to over 8.00 in less than 72 hours. By day three the algae had attached to the flask bottom and sides, forming a green film. By day five the pH had reached 10.20 and dense tufts of attached algae had formed on the bottom. When the pH had reached 10.45 on day six, the solution became greener as the attached algae proceeded to disperse into the solution. On day eight no attached algae were visible and the solution (pH = 10.30) was bright green. As the pH of
the solution was lowered with H₂SO₄, the suspended algae gradually flocculated and settled out of solution. Figure 6 is a graph of the percent of suspended algae (100% = abundance of suspended cells per ml before titration) versus decreasing pH. Less than 20% of the algae was still in suspension at pH 4.00. Reattachment to the flask bottom occurred two hours after pH 4.00 had been reached. Sixteen hours after pH 4.00 had been reached the pH had dropped to 3.62 (no additional H₂SO₄ was added) and the algae had formed a loose aggregation, light olive-green to light tan in color. Microscopic examination detected no living cells 24 hours after pH 3.5 was reached.
Discussion

Taxonomy

The systematics of blue-green algae are in revision primarily because morphological characteristics, used in some taxonomic keys (e.g. Prescott 1962, Tiffany and Britton 1952), were observed to vary under different laboratory and field conditions for a given algal isolate. For example, Pearson and Kingsbury (1966) observed that sheath size and consistency, color of trichomes, cell diameter, type of crosswall constriction and macroscopic morphology of a *Lyngbya* isolate varied with culture conditions and at times in identical culture conditions within the same flask. In fact, some *Lyngbya* phenotypes produced in Pearsons and Kingsbury's study would key to *Oscillatoria* or *Phormidium* in Prescott's (1962) taxonomic key.

Using stable morphological characteristics of the protoplast, Drouet (1968) reduced 2400 described species of Oscillatoreaceae to 23 species in six genera. Although Drouet's critics generally agree that a revision was necessary, his work has met criticism because of the lack of genetic and physiological studies to augment Drouet's morphological observations. Stam and Holleman's (1975, 1979) and Stam and Venema's (1977) works suggest the
limitations of Drouet's revision and illustrate the difficulty of using current taxonomic keys for identifying the blue-green algae. They studied 23 strains of *Schizothrix calcicola* (sensu Drouet), mostly from the Indiana Culture Collection, originally identified as nine species of *Phormidium*, *Plectonema*, *Lyngbya* and *Schizothrix*. By DNA hybridization techniques and comparative morphological studies in varying culture conditions, they observed three different taxa which they identified as *Phormidium* spp.

A similar plasticity in sheath consistency, crosswall constriction, protoplast granulation and cell length was observed in blue-green algae isolated from algal mats or sediment samples in this study. Preserved specimens key to *Phormidium*, *Lyngbya* or *Schizothrix* in Prescott's (1962) and Tiffany and Britton's (1952) taxonomic keys depending on the condition of the sheath material. Live specimens from laboratory cultures of the same algae key to *Phormidium minnesotense* (Tilden) Drouet or *Phormidium tenue* (Meneghini) Gomont in Tiffany and Britton's (1952) key or *Phormidium minnesotense* in Prescott's (1962) key. Drouet's (1963) *Schizothrix calcicola* description covers the range of variation observed in the field and in laboratory cultures of the species isolated in this study. Furthermore, when the four strains of *S. calcicola* from the four acidified lakes are grown in the same defined media,
they are identical in morphology and showed a similar pH tolerance (fig. 1). In general, the dominant, but closely related species, forming blue-green algal mats in acidified lakes are all small filamentous Oscillatoriaaceae species which secrete extracellular sheath material (table 4).

Algal Mat Development

An algal mat consists of intertwined filaments and extracellular gelatinous material which forms a more or less cohesive fabric (Golubic 1976). When algal mats spread over loose sediments they can trap and bind particles and physically stabilize the water-sediment interface (Wray 1977, Golubic 1976). As material (silt, sand, detris) is deposited on the mat surface algal filaments penetrate upwards to recolonize the surface, forming layered or laminated structures (Wray 1977). Environmental factors such as light, oxygen supply and ion concentrations can vary along vertical gradients within the developed mats (Golubic 1976). Algal mats can be viewed as miniature ecosystems which modify and stabilize the microenvironment within the mat (Golubic 1976).

These organosedimentary structures can form providing that: (1) the environment is suitable for growth of the mat forming organism; (2) the rate of growth exceeds the rate of consumption by other organisms; (3) the rate of
sedimentation does not exceed recolonization at the fluid-biosediment interface; (4) the mat layers accrete faster than they can be destroyed by boring and burrowing organisms and erosive or other mechanical and chemical forces (Walter 1976). The resulting structures called stromatolites are well represented in the fossil record and are some of the oldest preserved traces of life (>3,000 million years old) (Awramick et al. 1976). Blue-green algae and bacteria are believed to be the dominant organisms which built fossil stromatolites (Awramik et al. 1976). Although relatively rare, modern-day analogs are found throughout the world in a variety of aqueous environments but are generally restricted to areas of extreme light intensity, temperature, alkalinity and/or salinity (Parker et al. 1981). These algal mats are most common in environments of carbonate sedimentation, but are also found in environments of clastic silicate sedimentation (Awramik et al. 1978, Parker et al. 1981).

We are not aware of any reports in the literature identifying the algal mats found in acidified lakes or other acid environments as stromatolite analogs (Walter 1976, Awramik et al. 1978, Parker et al. 1981).

Blue-green algae have historically been thought to prefer neutral or alkaline habitats. Brock (1973) states that blue-green algae are rare or absent below pH 6.0 and do not exist below a pH of 4.0. Yet blue-green algae are well
represented in the floras of a number of acidified lakes, as phytoplankton (Lind and Campbell 1970, Kwiatowski and Roff 1976, Conroy et al. 1976, Hendrey and Wright 1976) and as extensive benthic mat assemblages (Hendrey and Vertucci 1980, Lazarek 1982a, this study). The predominantly blue-green algal mats in acidified lakes are structurally similar to those described as stromatolite analogs.

The existence of extensive blue-green algal mats at low pH is surprising in view of Brock's (1973) work that states blue-greens are rare or absent below pH 6.0. Even laboratory studies of optimum pH ranges (Kratz and Myers 1955, McLachlan and Gorham 1962, Allen 1952) and physiological responses at low pH (Coleman and Colman 1981, Kallas and Castenholz 1982a) of blue-green algal cells indicate little or no survival at low pH (generally <pH 5.0). Low external pH apparently can affect (1) solute transport at the cell wall or membrane (Kallas and Castenholz 1982b) and can (2) lead to an inability to maintain internal pH and thus affect photosynthetic capacity by inactivation of RuBP-carboxylase (Coleman and Colman 1981). Because S,calcicola was abundant in two of our acidified lakes, it suggested that we might be working with an acidophilic blue-green algae. Our laboratory experiments with S,calcicola did not confirm this. Optimum growth occurred near neutrality (fig. 1). However,
survival and slow growth did occur at low pH (figs. 3b, 4b). Batch cultures buffered at low pH (4.0, 5.0), initially decrease in cell density but show a steady increase in cell densities thereafter (fig. 4b). The initial decrease is probably caused by the rapid change from a neutral preexperimental (pH 7.0, full strength medium), to an acid experimental (pH 4.0 or 5.0, reduced strength medium) condition. Nevertheless, *S. calcicola* did grow at a low pH.

The question arises as to whether *Schizothrix* is a recent addition or was a previous inhabitant of the plankton or sediments of these acidified lakes. This is difficult to answer because of the lack of a previous data base. However, *S. calcicola* is one of the most widely distributed, occurring in both the marine and freshwater plankton and benthos, and hardy of all species of Oscillatoreaceae (Drouet 1963, 1968). In this study, *S. calcicola* was found in benthic samples in all seven lakes (pH range 6.15 to 3.45) but had formed algal mats in only two lakes (table 4). While the development of blue-green algal mats is a recent phenomenon in some acid lakes, the dominating mat species may have been in the lake previously.

We have established that growth of *S. calcicola* can occur at low pH. Do algal mats develop only from established benthic organisms or can mats develop from planktonic forms
of *Schizothrix*. Our laboratory experiments suggest one mechanism of *S. calcicola* mat formation. Suspended filaments of *S. calcicola*, growing at high pH, aggregate and settle out of solution and attach to the flask bottom forming a mat-like structure when the pH of the culture is lowered (fig. 6). Although little or no work on blue-greens' flocculation and coagulation is evident, considerable work on the mechanisms involved in coagulation and flocculation of microorganisms (especially bacteria) is available. Coagulation and flocculation of particles occurs when the repulsive forces which keep particles suspended are overcome or reduced (Singley 1971).

Microorganisms aggregate due to the interaction of external polymers (such as the polysaccharides in blue-green algal sheaths) which may form bridges of polymer chains between cells (Busch and Strumm 1968, Daniels 1980). Many factors influence the bioflocculation process including the growth phase of the microorganism, nutrient concentration and pH (Busch and Strumm 1968, Daniels 1980). A change in pH can reverse the capability of a bacterial cell to adhere to adsorbant particles (sediments, flask bottoms). This adherence or adsorption is generally strongest at pH 3.0 to 6.0 (see Daniels 1980). Clumping and settling of blue-green algae filaments may be enhanced further by the gliding movement of the trichomes within their adhering mucilage sheath (Walsby 1968).
Water Chemistry

Elevated levels of micronutrients have been suggested as a possible factor in blue-green algal mat development in acid lakes (Lazarek, personal communication). With acidification, some macronutrients can become less available. For example phosphorus compounds complex with aluminum, forming precipitates at pH 4.5 to 6.5 (Dickson 1980). Micronutrients (e.g. zinc, manganese, copper, iron) and heavy metals (aluminum, lead, cadmium, mercury, nickel) have greater solubility at low pH (Moss 1980, Wright and Gjessing 1976, Norton et al. 1981, Schindler et al. 1980) and leach from soils, sediments or enter lakes by direct deposition (Haines 1981) becoming more available. Although elevated micronutrient and heavy metal concentrations are toxic to most organisms some organisms require increased nutrient concentrations at low pH (Hutner 1972) possibly due to an increased net surface charge which hinders nutrient uptake (Langworthy 1978). In preliminary experiments on the effect of increased micro and macronutrients at low pH no significant effect on growth was observed.

*S. calcicola* growth is not enhanced by elevated micro and macronutrient levels, is not acidophilic and displays only slow growth at low pH in the laboratory. Yet it dominates the littoral as algal mats in Limekiln and parts of Big
Moose Lakes. The existence of blue-green algae in acid environments may partly be a result of the algal mat system's ability to modify the hydrogen ion concentration within the mat. In our laboratory, cultures of *S. calcicola* raised the pH of unbuffered media over four pH units in two-week old unshaken cultures. Similarly, Wildman *et al.* (1974) observed that *Anabaena cylindrica*, *Anacystis nidulans* and *Nostoc muscorum* adjusted the pH of culture media from stress levels (pH 4.0-6.0) to favorable levels (pH 7.0-10.0) and increased the buffer capacity in one week. In an acid, poorly buffered lake, the ability to raise the pH of the mat environment would be advantageous to growth. There is some field evidence of this. In Lake Gårdsjön, Sweden interstitial mat water was found to be higher (pH 5.5-6.2) than the overlying water (pH 4.3-4.7) depending on the time of day (Lazarek 1982a, Lazarek personal communication).

The algal mat may be the result of community succession in an acid environment with a low sediment rate relative to the recolonization rate of the algae. With gradual acidification of lakes the following may happen: (1) the step-wise elimination of acid-intolerant algae and macrophytes occurs. In general, environmental extremes tend to exclude or restrict competing eucaryotes in stromatolite analogs (Garrett 1970, Brock 1976, Golubic 1976). (2) Grazing pressure and burrowing is probably
reduced as benthic invertebrates decrease in abundance (Raddum 1980, Okland and Okland 1980). Stromatolites reached their greatest diversity and distribution during the late precambrian, before the advent of metazoans: the evolution of grazing, burrowing and competing organisms may have been the controlling factor in the decline of stromatolites from cambrian times to the present (Garrett 1970, Gebelein 1976). (3) The acid conditions of the overlying water further enhance clumping and aggregation of algal filaments and reduces decomposition processes, allowing a buildup of dead filaments and sheath materials. The end result through a community succession process is an algal mat which can be thought of as a physiologic unit (Lazarek 1982), potentially capable of modifying its immediate environment.


SNSF Project, Asa, Norway.


Lazarek, S. University of Toronto, Toronto, Canada M5s 1A4.


Lazarek, S. 1982b. Structure and productivity of epiphytic algal communities on Lobelia dormanna L. in


Pfeiffer, M.H. and P.J.Festa. 1980. Acidity status of


Vertucci, F. Cornell University, Ithaca, New York.


TABLE ONE

Location, Elevation and Surface Area of Lakes Sampled in the Adirondack Mountains of New York During the Summer of 1982.

<table>
<thead>
<tr>
<th>Lake</th>
<th>County of N.Y., USA</th>
<th>Elevation in Meters</th>
<th>Surface Area in Hectares</th>
</tr>
</thead>
<tbody>
<tr>
<td>Big Moose Lake</td>
<td>Herkimer</td>
<td>556</td>
<td>514.4</td>
</tr>
<tr>
<td>Cellar Pond</td>
<td>Hamilton</td>
<td>909</td>
<td>2.4</td>
</tr>
<tr>
<td>Dart Lake</td>
<td>Herkimer</td>
<td>535</td>
<td>56.4</td>
</tr>
<tr>
<td>Falls Pond</td>
<td>Hamilton</td>
<td>759</td>
<td>15.2</td>
</tr>
<tr>
<td>Fourth Lake</td>
<td>Herkimer</td>
<td>609</td>
<td>868.4</td>
</tr>
<tr>
<td>Limekiln Lake</td>
<td>Herkimer</td>
<td>575</td>
<td>184.4</td>
</tr>
<tr>
<td>Wolf Lake</td>
<td>Hamilton</td>
<td>793</td>
<td>5.2</td>
</tr>
</tbody>
</table>
TABLE TWO

Temperature, pH and Alkalinity of Adirondack Lakes Sampled.

<table>
<thead>
<tr>
<th>Lakes</th>
<th>pH</th>
<th>Temp (°C)</th>
<th>Alkalinity + (meq/ liter)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Sur</td>
<td>Bot</td>
<td>Sur</td>
</tr>
<tr>
<td>Fourth Lake</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>June 82</td>
<td>6.15</td>
<td>6.15</td>
<td>18.5</td>
</tr>
<tr>
<td>Limekiln Lake</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>22 Oct. 81</td>
<td>5.30</td>
<td>---</td>
<td>4.0</td>
</tr>
<tr>
<td>1 July 82</td>
<td>5.20</td>
<td>5.20</td>
<td>18.0</td>
</tr>
<tr>
<td>20 Aug. 82</td>
<td>4.60</td>
<td>4.60</td>
<td>22.0</td>
</tr>
<tr>
<td>Falls Pond</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>22 June 82</td>
<td>4.50</td>
<td>4.70</td>
<td>20.0</td>
</tr>
<tr>
<td>21 Aug. 82</td>
<td>4.20</td>
<td>4.50</td>
<td>19.4</td>
</tr>
<tr>
<td>Dart Lake</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>29 June 82</td>
<td>4.45</td>
<td>4.60</td>
<td>20.0</td>
</tr>
<tr>
<td>Big Moosé Lake</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>29 June 82</td>
<td>4.10</td>
<td>4.40</td>
<td>19.0</td>
</tr>
<tr>
<td>23 Aug. 82</td>
<td>4.00</td>
<td>4.00</td>
<td>19.0</td>
</tr>
<tr>
<td>Cellar Pond</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>30 June 82</td>
<td>3.80</td>
<td>3.70</td>
<td>17.0</td>
</tr>
<tr>
<td>22 Aug. 82</td>
<td>3.65</td>
<td>3.70</td>
<td>15.2</td>
</tr>
<tr>
<td>Wolf Lake</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>28 June 82</td>
<td>3.50</td>
<td>3.50</td>
<td>23.0</td>
</tr>
<tr>
<td>21 Aug. 82</td>
<td>3.45</td>
<td>3.70</td>
<td>18.5</td>
</tr>
</tbody>
</table>

* negative alkalinity indicates acidity
++ Sur = Surface, Bot = Bottom
* alkalinity measured by potentiometric titration
** alkalinity measured by Gran titration analysis.
### TABLE THREE
Partial List of Algal Genera Identified From Preserved Benthic Samples.

<table>
<thead>
<tr>
<th>Genera</th>
<th>Lakes</th>
<th>FL</th>
<th>LL</th>
<th>FP</th>
<th>DL</th>
<th>BML</th>
<th>CP</th>
<th>WL</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Cyanophyta</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Schizothrix</em></td>
<td></td>
<td>O</td>
<td>A</td>
<td>F</td>
<td>F</td>
<td>A</td>
<td>O</td>
<td>A</td>
</tr>
<tr>
<td><em>Hapalosiphon</em></td>
<td></td>
<td>-</td>
<td>O</td>
<td>-</td>
<td>A</td>
<td>O</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td><em>Chroococcus</em></td>
<td></td>
<td>-</td>
<td>F</td>
<td>F</td>
<td>-</td>
<td>F</td>
<td>F</td>
<td>-</td>
</tr>
<tr>
<td><em>Merismopedia</em></td>
<td></td>
<td>-</td>
<td>F</td>
<td>O</td>
<td>F</td>
<td>F</td>
<td>F</td>
<td>-</td>
</tr>
<tr>
<td><em>Microcystis</em></td>
<td></td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>O</td>
</tr>
<tr>
<td><strong>Chlorophyta</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Mougeotia</em></td>
<td></td>
<td>-</td>
<td>-</td>
<td>F</td>
<td>-</td>
<td>A</td>
<td>O</td>
<td>-</td>
</tr>
<tr>
<td><em>Microspora</em></td>
<td></td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>A</td>
<td>-</td>
</tr>
<tr>
<td><em>Bulbochaete</em></td>
<td></td>
<td>F</td>
<td>O</td>
<td>-</td>
<td>-</td>
<td>O</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td><em>Spirogyra</em></td>
<td></td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>F</td>
<td>-</td>
</tr>
<tr>
<td><em>Penium</em></td>
<td></td>
<td>-</td>
<td>F</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>O</td>
<td>F</td>
</tr>
<tr>
<td><strong>Diatoms</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Batrachospernum</em></td>
<td></td>
<td>A</td>
<td>F</td>
<td>A</td>
<td>F</td>
<td>A</td>
<td>A</td>
<td>F</td>
</tr>
<tr>
<td><strong>Fourth Lake</strong></td>
<td>FL</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>Limekiln Lake</strong></td>
<td>LL</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>Falls Pond</strong></td>
<td>FP</td>
<td>A</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>Dart Lake</strong></td>
<td>DL</td>
<td>F</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>Big Moose Lake</strong></td>
<td>BML</td>
<td>O</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>Cellar Pond</strong></td>
<td>CP</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>Wolf Lake</strong></td>
<td>WL</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

*Fourth Lake = FL, Limekiln Lake = LL, Falls Pond = FP, Dart Lake = DL, Big Moose Lake = BML, Cellar Pond = CP, Wolf Lake = WL*

*O = Occasional, A = Abundant, F = Frequent, - = None observed*
### TABLE FOUR

**Dominant Blue-green Algae in Mat Systems in Acidified Lakes.**

<table>
<thead>
<tr>
<th>Algae</th>
<th>pH</th>
<th>Lake</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Phormidium tenue</em> (=<em>Schizothrix calcicola</em>)</td>
<td>4.8</td>
<td>Colden, USA. (Hendrey and Vertucci 1980)</td>
</tr>
<tr>
<td><em>Lyngbya bourrellyana</em> (=<em>Phormidium ambiguim</em>)</td>
<td>4.3</td>
<td>Gardsjon, Sweden (Lazarek 1982)</td>
</tr>
<tr>
<td><em>Schizothrix calcicola</em> (=<em>Phormidium minnesotense</em>)</td>
<td>4.1</td>
<td>Big Moose, USA</td>
</tr>
<tr>
<td></td>
<td>5.2</td>
<td>Limekiln Lake, USA (This Study)</td>
</tr>
<tr>
<td><em>Schizothrix Friesii</em> (=<em>Phormidium indunatum</em>)</td>
<td>3.5</td>
<td>Wolf, USA (This Study)</td>
</tr>
</tbody>
</table>
Fig. 1. Growth versus pH of <i>Shizothrix calceolus</i> isolates from Limekiln Lake (LL), Falls Pond (FP), Big Moose Lake (BML), and Wolf Lake (WL). Plot of means (n = 3). Pooled standard deviation: LL = .75, FP = .69, BML = .86, WL = .86 mg/50 ml.
FIGURE 2
Results of the Newman-Keules Multiple Range Test

**Schizothrix calcicola**

<table>
<thead>
<tr>
<th>pH Level</th>
<th>Limekiln Lake</th>
<th>Falls Pond</th>
<th>Big Moose Lake</th>
<th>Wolf Lake</th>
</tr>
</thead>
<tbody>
<tr>
<td>Control</td>
<td>4.0 4.5 5.0 5.5 6.0 7.0</td>
<td>6.5</td>
<td>4.0 4.5 5.0 5.5 6.0 6.5 7.0</td>
<td>Control</td>
</tr>
<tr>
<td></td>
<td>4.0 4.5 5.0 5.5 6.0 6.5 7.0</td>
<td>6.5</td>
<td>4.0 4.5 5.0 5.5 6.0 6.5 7.0</td>
<td>Control</td>
</tr>
</tbody>
</table>

---

| Range with no significant difference in growth. (measured by dry weight) |
| Control = zero growth |
Growth of \textit{Schizothrix calcicola} (Limekiln Lake isolate) in reduced strength unbuffered (Fig. 3a) and buffered (Fig. 3b) medium. Pooled standard deviation Fig. 3a = $1.24 \times 10^5$ cells/ml, Fig. 3b = $1.37 \times 10^4$ cells/ml. Replicates = 4.
Figure 3

**a.**

![Graph showing media strength and initial cell density.](image)

**b.**

![Graph showing cell density in different media strengths.](image)
FIGURE 4

Growth curves of *Schizothrix calcicola* in pH 6.0 and 7.0 (Fig. 4a) and pH 4.0 and 5.0 (Fig. 4b) buffered media. Values represent mean cell count (n = 3). A Limekiln Lake isolate was used. Pooled standard deviation: pH 7.0 = 2.49 x 10^6 cells/ml, pH 6.0 = 3.45 x 10^6 cells/ml, pH 5.0 = 2.00 x 10^6 cells/ml and pH 4.0 = 1.5 x 10^6 cells/ml.
FIGURE 4

(a) Graph showing cells per ml x 10^7 vs. Day for pH 6 and pH 7.

(b) Graph showing cells per ml x 10^4 vs. Day for pH 5 and pH 4.
Figure 5. Growth of *Schizothrix calcicola* (Limekiln Lake) in half strength buffered (pH 4.0) media with and without added nutrients. Bars represent standard deviation of n = 4 replicates.
FIGURE 6

Plot of percent suspended algae (*Schizothrix calcicola* Limekiln Lake isolate) versus decreasing pH. 100% = suspended algae before titration. Plot of mean percentage of cell counts/ml. Bars represent standard deviation (n = 3).
Picture of algal mat in Limekiln Lake taken from boat through ca. 0.5 meters of water, August 1982.
July 25, 1983

Ms. Maureen A. Leupold
Dept. of Biological Sciences
SUNY College at Brockport
Lennon Hall
Brockport, New York 14420

Dear Ms. Leupold:

Your recent correspondence to Walter Kretser concerning the New York State liming program has been relayed to this office for reply. The only lake in your listing of seven study lakes which has received state sponsored lime treatments is Falls Pond. This received five tons of hydrated lime in 1975 and 20 tons of agricultural limestone in 1978.

However, private landowner organizations are also in the volunteer liming business and, thus, the North Bay of Big Moose Lake has received several lime treatments in the past. I am not personally aware of any liming project at Fourth Lake but it is possible that some individuals are engaged in neutralization efforts. At the present time we do not have any direct control over private liming, although we are attempting to formalize volunteer liming through the Adirondack Conservation Council Volunteer Liming Task Force.

Sincerely,

Martin H. Pfeiffer
Lake Acidification Studies
Project Leader

MHP/TEF
Maureen A. Leupold  
State University of New York  
College at Brockport  
BROCKPORT, N.York 14420

Dear Maureen,

Thank you for your letter and the abstract from Proceedings of the Rochester Academy of Science. I was very glad to hear about your studies. Your letter arrived when I was completing my Ph.D. thesis at the University of Lund. The thesis will be disputed on the 10th of May, 1983. In the summary of the thesis, I refer to your short note about blue-green algal mats in the Adirondacks, to support an idea that the formation of blue-green algal mats is not an unusual response to acidification.

In 1981, during a stay at the Brookhaven Nat. Laboratory, I visited several places in Adirondacks with the help of the Acid Group but I was not able to collect any samples of benthic blue-green algae. The short note by Hendrey & Vertucci (1980) confirmed my observations. I have samples from a few other places in Sweden where such algal mats occur – the principal algal species all belong to Oscillatoriaceae.

You wrote that your algae did not grow in the buffered media. Well, this is exactly what I experienced while trying to grow my algae on the Cambridge cyanophycean agar (CCAP Culture Collection, Cambridge).
I could not successfully keep algae growing just by changing the pH of the media (range 4.2–7.0). I became convinced that some other environmental factors (perhaps some microelements) are necessary for the growth of these algae. In fact, I have obtained continuous growth of my algae, retaining their mat structure, in big Petri dishes. The dishes were filled with the sediment from L. Gårdsjön and lake water was periodically added.

In the lake, the pH within the mat was around 5–6, measured with a pH-electrode. The electrode could not be used satisfactorily in the field, and I preferred (for the purpose of the publication) to measure the pH of the water gently pressed out from the mat. The pH was estimated on an electronic pH-meter (PHM 64) and varied between 5.5–6.2, compared to 4.2–4.7 in the lake water.

I would very much like to meet you to compare and discuss our findings. I will be travelling to Toronto via N.York (G.F.K.) at the end of May. I will be staying at the University of Toronto for about 2 years. My address will be: Institute for Environmental Studies

University of Toronto
TORONTO, Canada M5s 1A4

Unfortunately, I don't have any spare copies of the reprints you requested. If you don't mind I will send you instead a copy of my Ph.D. thesis which includes the paper published in WASP.

I hope to hear from you again, and wish you a successful limnological season. I apologize for the delay in answering your letter but I was in Italy when your letter arrived.

Yours sincerely,

S. Lazarek
Algal Mat in Wolf Lake

_Schizothrix Friesii_, the dominant mat forming blue-green algae in Wolf Lake, failed to grow in defined media [Chu # 10, Guillards, Bristols (Nichols 1973)] or soil water medium. Liquid and soil (1.3% agar) substrates were used along with a range of medium dilutions and pH levels. Yet, abundant growth was obtained in a natural sample kept on a window sill in unfiltered Wolf Lake water. It is possible that _S. Friesii_ has specific macro and micronutrient requirements that were not provided in the culture media used. Wolf Lake is very acid (pH ranges 3.45 to 3.70) yet _S. Friesii_ is thriving there. The environmental requirements of this species should be investigated further since reports of blue-green algae from extremely acid environments are rare.
Suggestion for Future Study

Future studies should address the chemical composition of lake waters where mats have developed. It is possible that blue-green algae have greater resistance to elevated trace metal concentrations. For instance, Oscillatoriaceae species often dominate zinc enriched environments above pH 5.0 (Shehata and Whitton 1980). The microenvironment within mats should be measured in situ for chemical and pH gradients. The bacteria and invertebrate fauna of mat communities should be described.

Reference