# ECOLOGICAL OBSERVATIONS ON THE PLANKTONIC CYANOPHYTE *GLEOTRICHIA ECHINULATA*[1]

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ABSTRACT

*Gleotrichia echinulata* was planktonic in Green Lake (Seattle, Washington) during summer, making its initial appearance between May and early July and disappearing during September. It apparently spent 8 to 10 months of the year on the bottom where colonies developed from spores deposited by the preceding year's bloom. The depth of spore deposition may be important in determining the success of spore maturation, and solar radiation may be a primary factor in inducing the annual return of this alga to the plankton. The maximum growth rate in 1966 was about 0.124 colony doublings per day. The vertical distribution of the colonies was controlled primarily by wind-induced currents. The colonies had no measurable effect on light penetration even at a maximum density of over 400 colonies per liter. Laboratory studies indicated that *G. echinulata* can fix nitrogen. Only one herbivore in Green Lake, *Lindia euchromatica*, is known to feed on this species.

## INTRODUCTION

*Gleotrichia echinulata* (J. E. Smith) Richt. is widely distributed in freshwater lakes of the northern hemisphere. In Washington it has been reported from Lakes Washington and Stevens (Edmondson, unpublished) and Green Lake (Roelofs 1967). Because of its very large (1–2 mm) and morphologically complex colonies, it is difficult to quantify and hence is often omitted from standard plankton counts or only noted as present. The relative importance of this form may thus have been underestimated for some lakes and its presence not even recorded in others.

This colonial species occurs as sheathed aggregations of filaments (Fig. 1) each having a basal heterocyst and several large, barrellike cells, tapering to long rectangular cells at the apex of the filament. Akinetes (special resting or reproductive spores) develop adjacent to the heterocyst from the first vegetative cell.

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## DESCRIPTION OF GREEN LAKE

The study was conducted at Green Lake (Seattle, Washington) which has the following morphometric characteristics: surface area, 104 ha; shoreline length, 4.7 km; average water depth, 3.8 m; maximum depth, 8.8 m; normal water content, $4.12 \times 10^6$ $m^3$; shoreline development, 1.30; and $Z:Z_m$, 0.43. Four depths (surface, 3 m, 4 m, and immediately off the bottom in the deepest portion) were sampled routinely at a station near the center of the lake. Data presented in Table 1 were determined by averaging values from all depths sampled and are typical of summer values for other years as well. Other occasional determinations indicate that the calcium content is about 8 mg/liter, magnesium about 3 mg/liter, and silicon about 2 mg/liter. The total hardness averages around 32 mg/liter as $CaCO_3$ and total dissolved solids average about 60 mg/liter.

Green Lake is generally well mixed and exhibits no permanent thermocline in summer. Although the lake has frozen over in the past, there was no ice during the winters immediately preceding and following our study.

Green Lake has probably been eutrophic for some 7 millenia and the depth of organic bottom deposits now exceeds that of the overlying water (Sylvester and Anderson 1960, 1964). Nuisance blooms of the





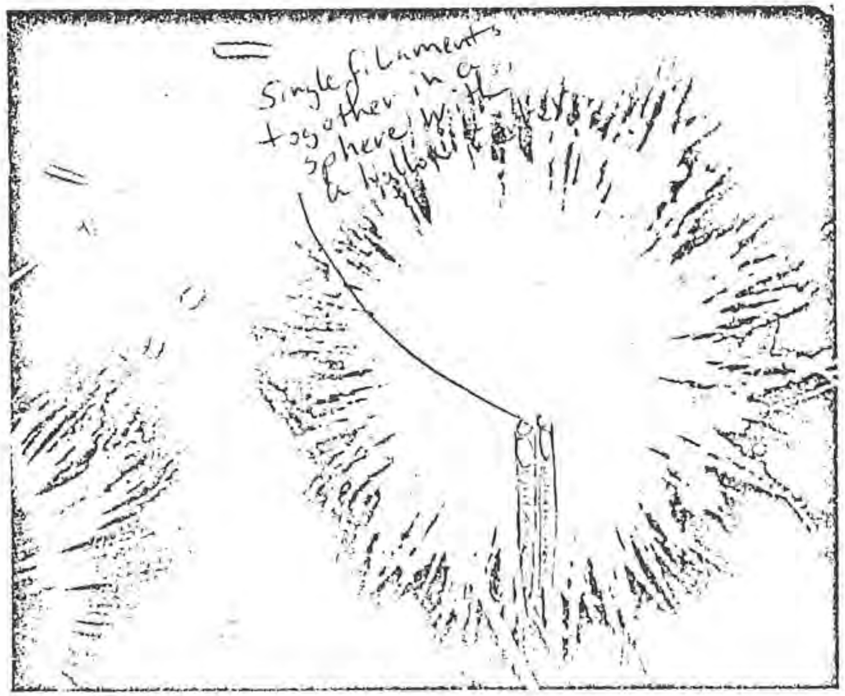

FIG. 1. *Gleotrichia echinulata* colony showing thallus of radially arranged filaments (dark field illumination, 320×).

cyanophytes *Anabaena circinalis*, *A. constricta*, and *G. echinulata* occur in late summer and early autumn. Other genera of prominent algae in the phytoplankton are *Dictyosphaerium*, *Oöcystis*, *Staurastrum*, *Dinobryon*, *Eudorina*, *Melosira*, *Asterionella*, *Fragilaria*, *Pediastrum*, and *Anacystis*.

## LIFE CYCLE OF *G. ECHINULATA*

*Gleotrichia* colonies were found in the phytoplankton during summer months only. They first appeared in early June in 1965, early May in 1966, and early July in 1967. In all 3 years, colonies had disappeared from the water mass by mid-September. A curve showing the change in colony numbers during a portion of summer 1966 (Fig. 2) illustrates the approximate rate of growth of this species in Green Lake. It was estimated that the population increased at a rate of 0.124 colony doublings per day between 20 July and 10 August.

Akinetes were first seen in 1966 on 18 July. They seem to be produced when the colonies reach a certain size (Fritsch 1945). They were present in a limited number of colonies in 1966 before the period of maximum growth, indicating that spore production probably was not due to an unfavorable environment; akinetes were also observed on colonies growing and reproducing rapidly in the laboratory.

After the species had disappeared from the phytoplankton in September 1966, a bottom sample taken in November had no recognizable colonies, but did contain iso-

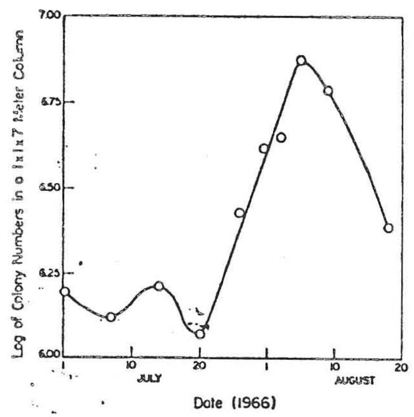


FIG. 2. *Gleotrichia echinulata* growth curve for 1966 in Green Lake. Colony counts were made on single 200-ml samples from depths of 0, 3, 4, and 7.5 m.

lated individual akinetes. In March 1966, developing colonies were found on the lake bottom; they had a stubbed appearance and were yellow-brown to pale green. The filaments were short, being composed of from 4 to 6 cells. Similar developing colonies were found on the bottom in January 1967.

It thus appears that the colonies at the end of one season's bloom deposit spores which then develop on the bottom over winter and that the new colonies enter the plankton when they become sufficiently buoyant. A vertical series of water samples taken on 23 June 1967 contained no *Cleotrichia*. By 3 July, colonies were entering the plankton (Fig. 3). The atypical vertical distribution on this date, with larger numbers at greater depths and none at the surface, may represent this process.

Akinetes in mature colonies have what appear to be oil droplets inside the cells. It seems probable that these represent a food reserve that provides energy for resting metabolism of the spores. If, at the onset of summer, food reserves are insufficient to allow for new colony formation, then the depth of spore deposition, water transparency, and the amount of solar radiation available for photosynthesis may be critical. Circumstantial evidence supporting this is the rarity of *G. echinulata* in Lake Washington as compared with Green Lake; although the waters are chemically similar, Lake Washington has a steep-sided basin with only about 17% of its area consisting of waters 10 m or less in depth. More direct evidence is provided by comparison of the chemical and physical conditions in Green Lake during 1965–1967 for the periods when *Cleotrichia* first made its appearance in the plankton. All the parameters listed in Table 2 represent averages, and no marked increases or decreases oc-

TABLE 1. *Some physical and chemical characteristics of Green Lake, Seattle, May–September 1966*

| Measurement | No. of observations | Avg value | Range of values |
|---|---|---|---|
| Temp (°C) | 25 vertical profiles | — | surface, 14.3–22.5<br>7.6 m, 12.2–19.5 |
| Conductivity (μmhos/cm at 25C) | 86 | 86.9 | 59–116 |
| Secchi disc transparency (m) | 24 | 3.0 | 1.1–4.3 |
| Turbidity (mg/liter $SiO_2$) | 91 | 4.4 | 0–44 |
| Color (color units) | 86 | 17.5 | 5–70 |
| pH | 103 | 7.7 | 6.6–9.0 |
| Dissolved oxygen (mg/liter) | 106 | 8.6 | 0.75–11.0 |
| Dissolved oxygen (% saturation) | 99 | 89.5 | 8–122 |
| Total alkalinity (mg/liter as $CaCO_3$) | 100 | 32.6 | 20–50 |
| Nitrate-N (μg/liter) | 89 | 23.0 | 0–91 |
| Orthophosphate-P (μg/liter) | 85 | 8.6 | 0–34.3 |
| Total-P (μg/liter) | 74 | 30.7 | 3.3–75.0 |
| Chlorophyll *a* (μg/liter) | 79 | 3.89 | 0.55–23.21 |



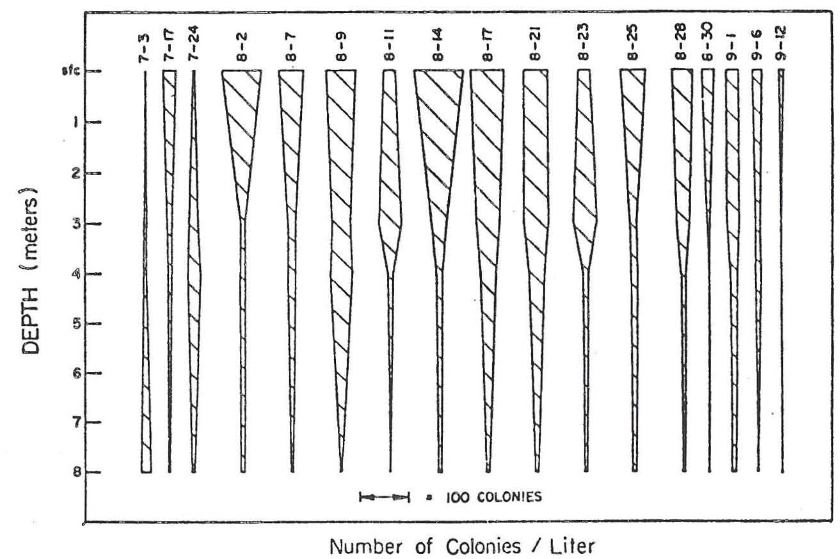


FIG. 3. Number of *Gleotrichia echinulata* colonies per liter versus depth in Green Lake, 1967. Sampling dates are given at the top of each figure.

curred immediately before and during the periods of interest. Nitrate-N, chlorophyll *a*, transparency, and temperature all show rather wide, and apparently uncorrelated, variations between the 3 years. Phosphate-P was present at the same concentration each year at the time of *Gleotrichia*'s emergence into the plankton and also during the entire early summer. Only solar radiation seems to offer an obvious correlation with the advent of *Gleotrichia* in the water mass (Table 3). The values for 1–7 June 1965 and 1–7 May 1966 are much above seasonal norms for the Seattle area and in both cases, are considerably greater than for the preceding weeks. On the other hand, in 1967, when *G. echinulata* did not appear in the plankton until early July, weekly averages of solar radiation exhibited a pattern of gradual increase up to this time, with no pronounced bursts of energy like those characterizing the periods when the alga became planktonic in 1965 and 1966.

## COLONY DEPTH DISTRIBUTION AND LIGHT PENETRATION

Wind mixing of Green Lake is important in keeping the colonies distributed throughout the water column. They float at the surface following periods of little or no wind. They also collect at the surface of a water sample shortly after it is taken. This probably is not due to a change in colony density or to temperature differ-

TABLE 2. *Approximate values of chemical and physical parameters at the times when* Gleotrichia echinulata *was first observed in the plankton during 1965, 1966, and 1967*

| | Early Jun 1965 | Early May 1966 | Early Jul 1967 |
|---|---|---|---|
| $NO_3$-N (μg/liter) | 30 | 40 | 10 |
| $PO_4^{3-}$-P (μg/liter) | 10 | 10 | 10 |
| Chlorophyll *a* (μg/liter) | 5 | 10 | 3 |
| Secchi disc transparency (m) | 3.5 | 2 | 3.5 |
| Temp (°C) | 18 | 15 | 22 |

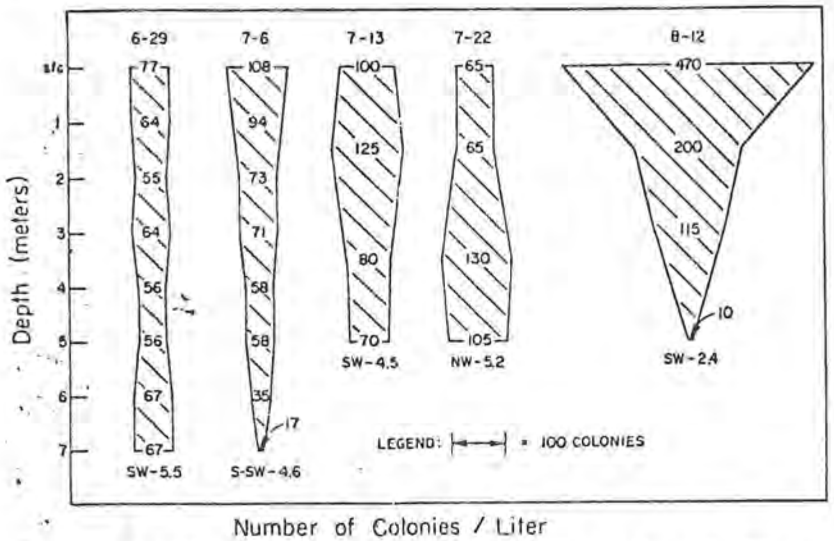


FIG. 4. Number of *Gleotrichia echinulata* colonies per liter versus depth in Green Lake, 1966. Sampling dates are given at the top of each figure and prevailing windspeed and direction, averaged for 4 days before the sample date, are presented at the bottom.

ences, since colonies float at the surface of culture vessels in the laboratory when they are not shaken, even though the temperature remains constant. Ruttner (1963) showed the effect of wind mixing on the vertical distribution of *G. echinulata* in Gr. Plöner See; a similar phenomenon was demonstrated by Roelofs (1967).

Profiles of light penetration were made throughout summer. Colony density of *Gleotrichia* had no observable effect on light penetration in Green Lake. The per cent of surface illumination penetrating to 1 m was the same (about 43%) on 6 July 1966 as it was on 12 August although the colony concentrations were 108 ± 23 and 470 ± 163.5/liter respectively (95% confidence limits). The deepest Secchi disc reading of the summer (4.3 m) was recorded in early August when the *Gleotrichia* population was at its peak. As *Gleotrichia* decreased during August, *A. circinalis* increased rapidly to a maximum density, estimated at 160,000 cells/ml, on 4 October. Transparency decreased sharply with the increase in *A. circinalis* (Oglesby 1969). A similar pattern was observed in 1967 when blooms of *A. constricta* and, subsequently, *A. circinalis* again replaced *Gleotrichia* as the dominant forms of phytoplankton.

High Lake Clarity

### ANNUAL VARIATIONS IN THE NUMBERS OF *GLEOTRICHIA* COLONIES

A comparison of Figs. 3 and 4 shows that during 1967 numbers of colonies were consistently lower than in the previous year with no periods of rapid increase. Data are not sufficient to show a firm causal relationship but increased washout rates and decreased levels of primary nutrients (Oglesby 1969) were factors possibly contributing to the lower 1967 standing crop of *Gleotrichia*.

### NITROGEN FIXATION

*Gleotrichia echinulata* is probably a nitrogen fixer (Zehnder 1963); culture of the



TABLE 3. *Averages of daily total (direct and diffuse on a horizontal surface) radiation in g cal/cm² measured with an Eppley pyrheliometer at the University of Washington, about 5 km from Green Lake*

| | 1965 | 1966 | 1967 |
|---|---|---|---|
| April | | | |
| 1– 7 | 300.9 | 384.2 | 419.7 |
| 8–14 | 320.9 | 224.3 | 308.8 |
| 15–22 | 346.6 | 387.6 | 274.8* |
| 23–30 | 445.6 | 347.0 | 363.1 |
| May | | | |
| 1– 7 | 386.4 | 548.2 | 317.2 |
| 8–14 | 541.2 | 370.1 | 254.1 |
| 15–22 | 441.6 | 436.8 | 520.7 |
| 23–31 | 413.6 | 573.1† | 439.9 |
| June | | | |
| 1– 7 | 697.2 | 407.1 | 463.6 |
| 8–14 | 429.7 | 518.7 | 465.8 |
| 15–22 | 553.9 | 570.9 | 536.0 |
| 23–30 | 556.1 | 469.5 | 594.0 |
| July | | | |
| 1– 7 | 576.9 | 523.7‡ | 600.7 |

* No data 15, 16, and 17 April.
† No data 28, 29, 30, and 31 May.
‡ 6 and 7 July only.

species in our laboratory gave further indications of this ability. The alga grew well in a Chu No. 10 medium containing no nitrogen, colony numbers increasing 15-fold in one 13-day period. These cultures were not bacteria-free and also contained a small filamentous alga (*Oscillatoria* or *Phormidium*); nitrogen fixation by the latter was ruled out since it was unable to grow alone in a nitrogen-free medium. Cultures were kept in an Eberbach waterbath-shaker at a shaking rate of 30 cpm. Continuous lighting was provided by two fluorescent lights (Gro-Lux) suspended 33 cm above the waterbath and providing 1,722–1,938 lux at the surface of the water. Temperature of the waterbath was not regulated and varied with that of the room (20–23C).

The ability to fix nitrogen may be important to *Gleotrichia* in Green Lake since the nitrate-N levels in the lake fall below detectable limits (phenyldisulfonic acid method) during some months when the species is present (Oglesby 1969); ammonia-N is also undetectable during this period.

### *GLEOTRICHIA* AS AN ELEMENT IN THE FOOD CHAIN

The only Green Lake herbivore seen feeding on *Gleotrichia* was the rotifer *Lindia euchromatica*, a species whose life cycle is centered around this alga (Edmondson 1938). Although it was at times very abundant on individual colonies, we observed *L. euchromatica* on relatively few occasions and then only in late summer. The size of the colonies of *Gleotrichia* (up to 2-mm diam) is thought to restrict their use by copepods and cladocerans, the primary Green Lake herbivores.

Colonies were found in rainbow trout (*Salmo gairdneri*) stomach samples taken in August. They were easily recognized, even in the lower intestines of the fish. These colonies probably were ingested accidentally while the fish were feeding, since *Gleotrichia* was abundant in the lake at this time (200–400 colonies per liter).

Use of the colonies by the usual plankton herbivores is minimal, so this species may be useful in studying growth kinetics of algal populations in the natural environment.

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