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Analysis of the effects of *Gloeotrichia echinulata* on Great Pond and Long Pond, Maine

The development of this paper is in response to landowner concerns associated with the increased abundance of *Gloeotrichia echinulata* in Great Pond and Long Pond in Central Maine. This paper will present a review of the available information on the lakes' ecosystems, as well as the lifecycle and nutritional demands of *G. echinulata* in both its recruitment and growth phases. The goal of this paper is to incorporate all of the available and relevant information on *Gloeotrichia echinulata* so that proper studies and understanding of the organism can be realized for the Belgrade Lakes in Central Maine.

Cyanobacteria are a large and diverse group of organisms that can be found in areas ranging from deserts or glaciers to soil or hot springs. *Gloeotrichia echinulata*, a species under this classification, is commonly found in well mixed mesotrophic and eutrophic lakes at temperate latitudes. Its lifecycle is quite complex having life stages in both benthic (lake bottom) and later pelagic (water column) zones (Karlsson-Elfgren 2003). In the benthos, it begins colonial formation in June and July and assimilates large amounts of phosphorus from nutrient rich sediments. The acquired phosphorus is significantly above its immediate needs, and the colony will store the phosphorus for subsequent growth and divisions once in the water column. These reserves allow *G. echinulata* to thrive under phosphorus limitation in the epilimnion when other phytoplankton cannot (Barbiero and Welch 1992).



Additionally, *G. echinulata* is a nitrogen fixing cyanobacteria which allows it to utilize molecular nitrogen for its cellular machinery where as most other plankton requires ammonium or nitrogen oxides for this same process (Karlsson-Elfgren, Hyendstrand, and Riydin 2005). This pathway is also another way in which *G. echinulata* has evolved to out compete other species for

nutrients.

Gloeotrichia echinulata has the ability to have an immediate and significant impact on its surrounding ecosystem. Under the right conditions it has been observed that populations of *G. echinulata* have progressed from little or none present in the plankton community in one year, to complete dominance in the following season (Jacobson 1994). Due to its dominant characteristics and complex life cycle, the presence of *Gloeotrichia echinulata* has become a cause of concern with regard to the greater ecosystems in Great Pond and Long Pond. This paper has been designed to address key factors involved in *G. echinulata*'s life stages to better understand growth dynamics of this species in the Belgrade Lakes.

Background

The lakes in Maine are a valuable state resource supporting a diversity of wildlife in a spectacular natural setting, attracting tourists from all over the world. Unfortunately,

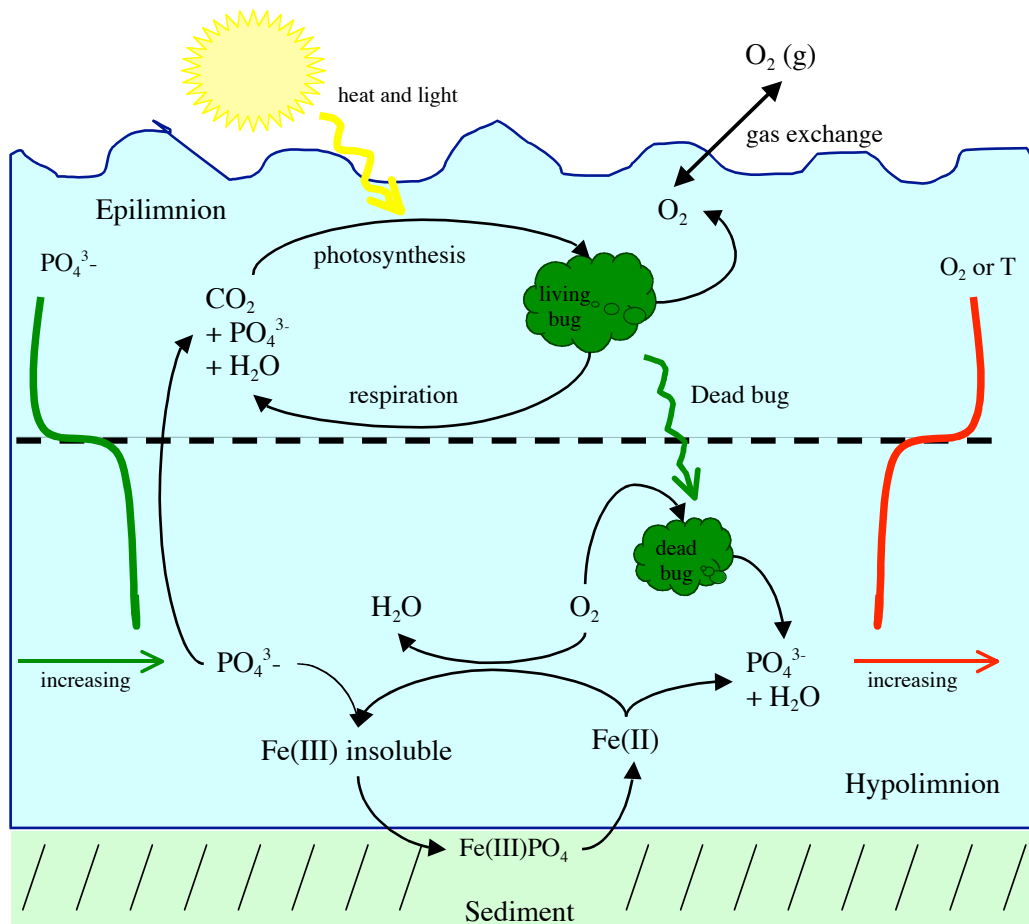
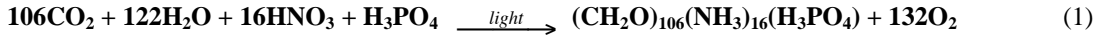


Figure 1. Schematic of phosphorus cycling in a temperate lake.

some of the Maine lakes are suffering from cultural eutrophication: decreased water quality due to excessive growth in phytoplankton species, and free-floating microscopic-sized plants. This excessive growth causes a reduction in lake water clarity and turns the water green or brown. In highly eutrophic lakes the amount of dissolved oxygen in the deep lake will fall because of the high level of organic material forming in the lake and being oxidized at depth. Removal of oxygen in the deep water may cause changes in species diversity in the lake by severely impacting many trout and salmon game fish species that require cold, well oxygenated water.

Elevated concentrations of phosphorus in lake water are often the trigger for algal blooms. Phosphorus is an essential nutrient for plant growth, and is the limiting reagent in most lakes, controlling the rate at which plants grow and the final phytoplankton biomass. The quantitative relationship between biomass formation and phosphate concentrations was first described by Redfield (1936) and has subsequently been used to describe nutrient limitation in a wide range of aquatic environments (Stumm and Morgan, 1996).



Equation 1 is essentially a simplified chemical stoichiometry for photosynthesis, with the reverse reaction representing respiration. In this expression $(\text{CH}_2\text{O})_{106}(\text{NH}_3)_{16}(\text{H}_3\text{PO}_4)$ represents biomass. The coefficients in the expression indicate that 106 moles of carbon dioxide can be converted into plant biomass per mole of phosphate. Thus, small additions of phosphate to a lake ecosystem can produce significant quantities of algal biomass, approximately at 35-fold amplification on a mass basis (mass plankton to mass H_3PO_4).

Phosphorus enters the water column of lakes from upstream lakes, sewage inputs, rainfall, overland runoff, and from the benthic sediments of the lake. Phosphorus leaves the lake by stream outflow or accumulation in the sediments. The sediments are a significant reservoir of phosphorus; however, most of this phosphorus is locked up in organic material or absorbed on metal oxides leaving only a small amount for plant growth (Burgis). The organic material can become a source of phosphorus if oxidized by bacteria or zooplankton. Absorbed phosphorus in the sediment can also be released into

the water column if active redox processes reduce metal oxides releasing bound phosphate (Amirbahman 2004). The depth at which phosphate enters the lake is also relevant since many Maine lakes are thermally stratified in the summer reducing mixing between the warm surface water, epilimnion, and the cold deep water, hypolimnion. Many of these processes are shown schematically in Figure 1. Dissolved phosphorus in the inorganic form (PO_4^{3-}) is readily available for plants to use for photosynthesis. Particulate phosphorus is mostly in the form of organic material such as plant and animal tissue. Dissolved phosphorus can be converted into particulate phosphorus through primary production occurring in the epilimnion. Particulate phosphorus is often negatively buoyant and will settle out of the epilimnion into the hypolimnion as dead cells and organic detritus. If there is enough oxygen present in the hypolimnion the particulate phosphorus will be converted into dissolved phosphorus through decomposition by aerobic bacteria and reabsorbed on particles (Gachter and Mares, 1985). This process, often called the biological pump, transports phosphorus in the epilimnion to the hypolimnion of the lake independent of physical mixing.

When the concentration of phosphorus in the epilimnion is elevated due to surface water inputs or storm-induced deep water mixing, eutrophication may occur. *G. echinulata* has evolved to short-circuit the regular nutrient cycle of phosphorus by sequestering phosphorus from the sediments and carrying phosphorus in cellular reserves to the epilimnion. We are specifically interested in understanding how *G. echinulata* blooms in Great and Long Ponds are changing the nutrient cycling of phosphorus.

Study Area



The Belgrade Lakes are located in rural Central Maine and include: North Pond, East Pond, Great Pond, Salmon Lake, McGrath Pond, Long Pond, and Snow Pond (or Messalonskee Lake) and each lake is connected by a network of streams that descend ultimately into the Kennebec River. Between each lake is a dam that, biologically speaking, serves as a barrier for upward passage of aquatic species. These lakes are located at an average altitude of 77 meters. All of the lakes freeze annually and on a typical year will be

covered with ice from early December to mid April. Due to freezing and thawing each lake is subject to seasonal turnover as well as periodic wind induced mixing.

Great Pond, with an elevation of 77 meters is the largest of the Belgrade Lakes covering an area of 33,830km². This lake has an average depth of 6.3m and a maximum depth of 21m. The total volume of Great Pond is 2.130x10⁸m³. Based on the volume and in/out flow of water in this lake it takes approximately 2 years for a complete exchange of water (0.5 flushes year⁻¹).

Long Pond covers a total area of 9,210 km² and has a maximum depth of 32 meters. Geographically, Long Pond is a slender lake with a very shallow and narrow section in the middle. Due to its shape an analysis of Long Pond is generally divided into the North and South Basin. The flow of water moves from Great Pond into the North Basin of Long Pond then to the South Basin as it continues on its way to Snow Pond and the Kennebec River. The flushing rates of both the North and South Basins are 3.9 and

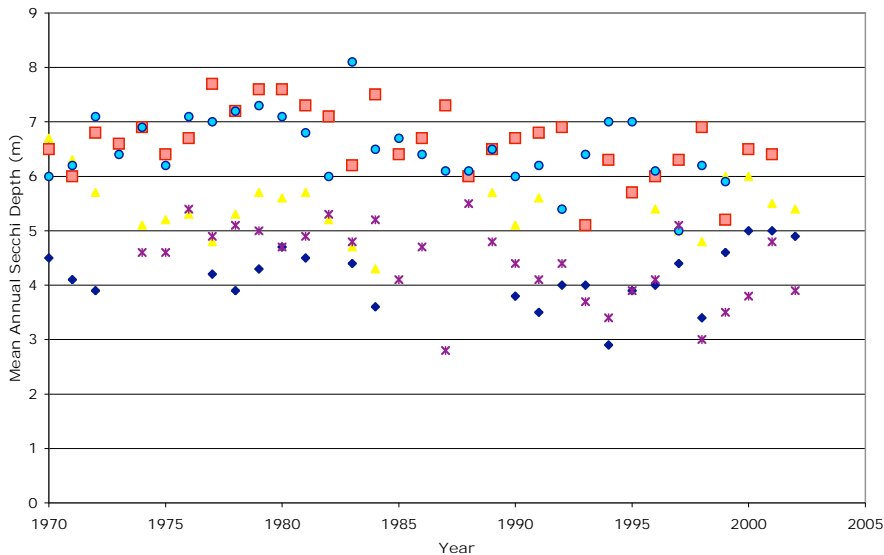


Figure 2. Annual Mean Secchi in the Belgrade Lakes.

3.6 flushes year⁻¹ (Colby College Biology 493 unpublished data 1999). The North Basin has a surface area of 5,097 km² with a maximum depth of 18 meters and an average depth of 7.52 meters. The volume of the North Basin is 3.832x10⁷ m³ while the deeper South Basin has a volume of 3.096x10⁷ m³. The South Basin contains a long deep section on its eastern shore that reaches depths of 32 meters. Although the South Basin has a large

deep section its overall bathymetry is rather shallow leaving the two basins with equal average depths.

Figure 2 shows the historic mean secchi depths for each of the Belgrade lakes over the last thirty years. Great Pond and Long Pond (both basins) have average secchi depths of 6 – 6.5 meters with a trophic index of 35 to 40.

Historically both lakes were renowned for their salmon fisheries but recovery attempts in recent years been abandoned in Great Pond due to declining populations and now the lake is stocked with Brown Trout instead. Introduced illegally, Northern Pike now thrive in these lakes and make up a large portion of the sport fishery. Also present in the lakes are: Small Mouth Bass, Large Mouth Bass, Yellow Perch, White Perch, Black Crappie, and Chain Pickerel (PEARL).

Life Cycle and Developmental Factors

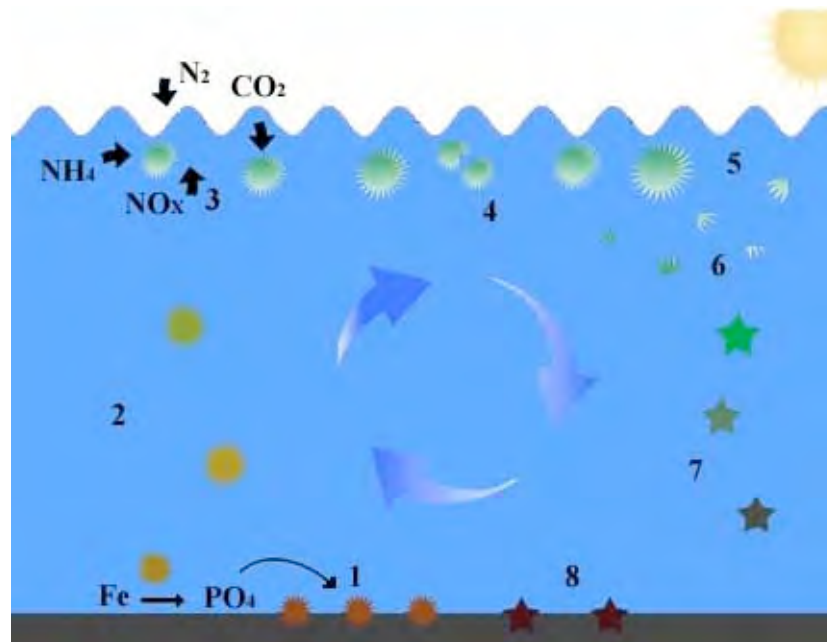


Figure 3. Life Stages of *Gloeotrichia echinulata*

G. echinulata is a photosynthetic organism which has two separate stages within its lifecycle as depicted in Figure 3. Initially, is found as an ‘akinetete package’ or germling on the benthos as spring begins. From here the organism begins to grow and acquire nutrients from the sediments (1). After developing ample nutrients it forms gas vesicles that make it positively buoyant and it begins to migrate up into the water column

(2). Once in the epilimnion it will go through a series of growth (3) and colonial divisions (4). Later, in the summer as phosphorous reserves within the colonies dwindle, akinetes form at the base of its filaments (5). Shortly after, the outer part of the filaments is lost along with the gas vesicles (6) and they begin to fall out of the water column. Eventually the colonies settle onto the sediment where they will lie awaiting the proper conditions in the spring (8) (Karlsson Elfgren 2003).

Recruitment

Recruitment involves the life stages of *G. echinulata* from germination through migration. At the start of recruitment, the akinete spores are found in the benthos of the lake where they begin the process of germination with the formation of filaments that will eventually become filament bundles (Karlsson-Elfgren 2003). At this time their appearance is highly variable but *G. echinulata* will generally appear as colonial spheres with a diameter of approximately 0.3mm and have reddish-brown color. At the core of this spore package are the akinetes along with the remains of the previous year's trichomes (Tymowski and Duthie 2000). In the spring, the akinetes begin to germinate while still in a mucilage covering and then form 3-4 photosynthetic vegetative cells at their periphery along with a spore sheath covering (Barbiero 1993). With the formation of the vegetative cells it can be assumed that the *G. echinulata* colonies have initiated photosynthesis.

With time, two heterocytes form in the center of the filaments and the radiating filaments start to curve. Once the heterocytes have formed the connection between the two heterocytes is broken and the filaments will then begin to radiate from them. Following this new morphology a layer of mucilage is formed that encompasses the heterocytes and the filaments closest to them. As this step occurs it is noted that the vegetative cells furthest from the heterocytes take on an elongated appearance (Karlsson-Elfgren 2003).

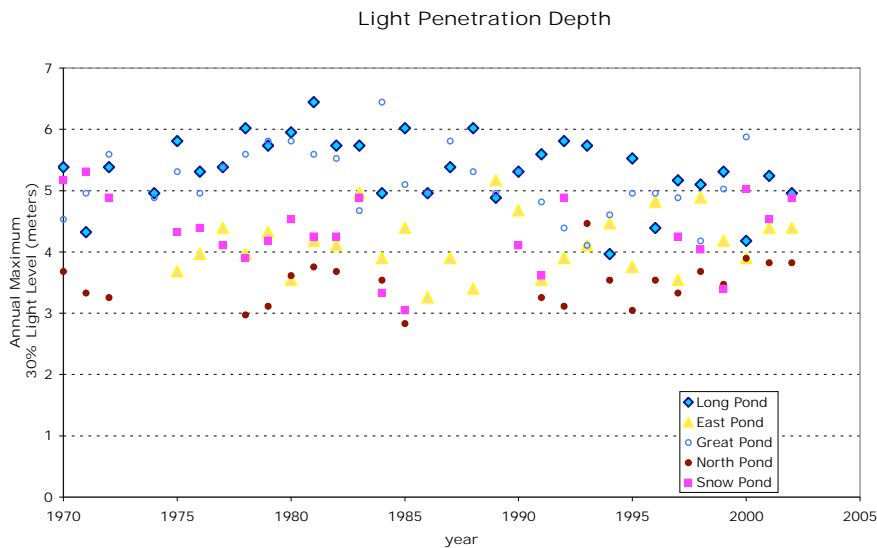
The germination process as reported by Karlsson-Elfgren (2003) initiates in Lake Erken, located in south-eastern Sweden, as early as April and will continue into August with the majority of them forming in less than 3m of depth. In this unstratified lake the highest instance of germination comes from 0.5m with the number of germinating

colonies decreasing as the depth increases (Karlsson 1999). Here very few colonies develop in water deeper than 4.5m and none at all are derived from depths greater than 14m, a depth that corresponds to a level with no available photosynthetically available radiation (PAR) (Karlsson-Elfgren 2003). For each lake the distribution of lake depth (hypsographic profiles) and water temperature will influence germination rates. Clearer waters will tend to have migration from deeper sediments and thus a greater possible bloom due to increased sediment illumination. In 1994, Jacobson observed a marked increase in *G. echinulata* and *Aphanizomenon flos-aquae* with a four fold increase in transparency allowing for a greater amount of the sediment to obtain adequate light and temperature. Estimates of sediment depths where *G. echinulata* will migrate from can be determined by using the secchi depth to determine the light field as a function of depth (Perakis, Welch, and Jacoby 1996)

$$I_z = I_o e^{-nz}$$

$$n = 1.7 / Z_{sd}$$

where I_o is the light intensity at the surface, n is the light extension coefficient, and Z_{sd} is the secchi depth. Using these equations it is possible to calculate the depth of the 30%



light level for each of the Belgrade Lakes. Notice that Long Pond and Great Pond have the greatest light penetration depth, consistent with their deeper secchi depths.

It is widely agreed upon that light is the trigger for germling growth, yet only weak correlations can be made between the appearance of light and the onset of the recruitment process *in situ* (Barbiero 1993). With akinete formation phosphorus uptake begins, a process that is typically energy dependant. Though light is the trigger for phosphorus uptake it is thought not to be the source of energy for this process. The pathway that phosphorus is absorbed into the cells is still under question (Istvanovics et al. 1993).

In 1990, Barbiero found there to be a three week growth period between the presence of necessary light levels and migrations (Barbiero 1993), where Karlsson-Elfgrén (2003) showed in a laboratory enclosure experiment that *G. echinulata* colonies could germinate within 4 days and buoyancy was observed as soon as 2 days later. Additionally, the distribution of the akinetes in the sediment will have an influence on the extent of the subsequent year's potential growth (Forsell and Pettersson 2000). Prior to migration, *G. echinulata* colonies were discovered to be fairly well distributed over the sediments. The average number of colonies found in Lake Erken in 1991 was 500,000 m⁻². For depths below 10 m there was a sharp reduction in abundance to approximately half the quantity seen elsewhere (Pettersson, Herlitz, Istvanovics 1993). This likely occurs because *G. echinulata* colonies are positively buoyant and therefore are subject to wind induced translocation. Generally the colonies will be moved toward the shallower shoreline areas on the windward side of the lake where they will tend to deposit as they settle out in August and September.

Due to the importance of light and temperature in the development of colonies the bathymetry of a host lake can play a large role in the maximum potential for *G. echinulata* growth. A broad shallow lake will tend to have greater light levels and greater sediment temperatures reaching a higher percent of the benthic inoculum (Head, Jones, and Bailey-Watts 1999). Depth itself probably has less to do with germination than the overall temperature and light availability. We would expect to have a more significant inoculum in a warmer, shallower lake with a greater secchi depth.

Germination of *G. echinulata* is dependant upon light and temperature (optimal 17 degrees C) yet the total size of the inoculum is affected by temperature and bioturbation. A decrease in temperature slows the heterocyst formation by slowing its

overall metabolic activity. With this in mind it can be assumed that a warm spring will allow for faster colony formation and migration, permitting further colonial divisions at the surface and thus a greater late summer bloom (Karlsson-Elfgren, Rengefors, and Gustafsson 2004). In this same laboratory experiment it was also shown that sediment mixing was also a very important factor in migration. Sediments stirred vigorously showed a ten-fold increase in migration (Karlsson-Elfgren, Rengefors, and Gustafsson 2004). Aiding in bioturbation, omnivorous crayfish are a benthic species will stir the benthos of shallow aspects of lakes. This action aids in the migration of *G. echinulata* colonies *in situ*. Also these organisms feed on plankton but not on *G. echinulata* due to its toxic nature. This reduces *G. echinulata*'s competing species further allowing it to flourish (Dorn and Wojdak 2004).

As previously discussed, *G. echinulata* has adapted uniquely to acquire an excess of phosphorus above and beyond its current needs to allow for subsequent colonial divisions and growth once in the epilimnion. Through sampling of *G. echinulata* in Lake Erken it was determined that within each cell there is a minimum P demand of $2.30 \pm 1.18 \times 10^{-6} \text{ g P / mg C}$ (Istvanovics et al. 1993) with an absorption rate of between $0.01 \times 10^{-6} \text{ g P mg}^{-1} \text{ hr}^{-1}$ and $0.02 \times 10^{-6} \text{ g P mg}^{-1} \text{ hr}^{-1}$ which may be symbiotically aided by attached bacteria (Tymowski and Duthie 2000). The P half saturation constant of *G. echinulata* is exceptional and ranges between 25 and $500 \times 10^{-6} \text{ g L}^{-1} \text{ day}^{-1}$ when compared to other algae that will typically have ranges from 1-100 $10^{-6} \text{ g L}^{-1} \text{ day}^{-1}$ (Istvanovics et al. 1993).

Following phosphorus absorption, in order to allow for buoyancy and upward migration, *G. echinulata* begins forming gas. This stage in development is marked by the development of short trichomes radiating from its core of about 5 cells. Formation of gas vacuoles are thought to be genetically correlated rather than relating to a particular phosphorus concentration. Peninsula Lake colonies that rose earlier were shown to have fewer phosphorus stores, likely because they had less time to assimilate phosphorus in the benthos (Tymowski and Duthie 2000). The gas vacuoles allow *G. echinulata* to migrate quickly and position themselves high in the epilimnion allowing it to out-compete other species for light and CO₂. In 1992, colonies collected prior to July 27th from surface water on Lake Erken had a mean floating rate of $34 \pm 12 \text{ m day}^{-1}$ while colonies collected on August 10th carried a more significant mean floating rate of $67 \pm 16 \text{ m day}^{-1}$.

¹, both showing excessive buoyancy. Migrating colonies have floating rates even higher where their floating rates average 104 +/- 15 m day⁻¹ (Rodrigo et al. 1998). This buoyancy allows *G. echinulata* to remain higher and closer to light in the euphotic zone during periods of significant wind induced turbination. These buoyancy rates are very different from other phytoplankton species that will generally have finite buoyancies that allow them to hover at specific depths where they will be able to gather light as well as necessary nutrients.

G. echinulata colonies take on a yellow to pale green appearance as they migrate up through the water column becoming more photosynthetically active as the light levels increase. At its core each colony contains a terminal heterocyst, or a germinated akinete contained in a spore sheath, as well as approximately 12 vegetative cells. The exterior of this region contains 10-15 gas vacuole cells of uniform size that are linked together. At this time staining of the polyphosphates within the colonies shows that they are concentrated with phosphorus toward the basal region of the trichome and appear in greater quantities than do older planktonic *G. echinulata* (Barbiero 1993). At this point *G. echinulata* colonies though high in phosphates have limited carbohydrates. Once at the top of the water column the colonies will begin to utilize phosphates and will be creating carbohydrates through photosynthesis (Rodrigo et al. 1998). Migrating colonies were found to contain a C:P ratio of 50:1 (by weight), as the season progressed the phosphorus concentration was reduced to 150:1 (Pettersson, Herlitz and Istvanovics 1993).

As previously discussed, while *G. echinulata* migrates to the epilimnion to access greater PAR for photosynthesis it carries with it phosphorus reserves assimilated from the benthos. In 1991, Lake Erken showed an increase in phosphorus as a result of *G. echinulata* as the summer progressed. When sampling first began in mid June only 1.1% of the epilimnetic phosphorus was due to *G. echinulata*. As the summer progressed migration continued with 53% of the epilimnetic phosphorus being derived from *Gloeotrichia echinulata* (Pettersson, Herlitz, and Istvanovics 1993).

With respect to timing, in 1990 Barbiero found that in Green Lake the presence of higher temperatures lead to a shorter migration period (Barbiero 1993). Also Forsell and Pettersson (1995) found that the greatest migration correlated with a disruption in the

stratification of Green Lake in mid August. Phosphorus translocation due to migration accounted for phosphorus flux to the water column of $2.25 \text{ mg m}^{-2} \text{ day}^{-1}$ in Green Lake (Barbiero and Welch 1992). As would be expected, Pettersson et al. (1993) noted that the newly migrated colonies contained the highest concentration of phosphorus compared to colonies in the benthic and the pelagic zones.

Pelagic Growth

On the surface of lakes *G. echinulata* colonies are easy to identify and appear as



bright green dots about 1-2mm in diameter.

Once the colonies reach the epilimnion internal phosphorus reserves are utilized for growth of the trichomes (Barbiero 1993). In the recently migrated colonies trichomes will appear as an aggregation of 4-6 cells in a line with the furthest cell on each trichome being a gas

vacuole. Also visible at this time is the development of the heterocysts in the basal region of the trichomes. At this time the amount of available phosphorus becomes very important because it represents the maximum possible bloom that can occur that year by the number of possible colonial divisions

While in the pelagic growth phase, and under the proper conditions, *G. echinulata* has the ability to dominate a phytoplankton community. During 1991, in Lake Erken the population maximum occurred on August 16th and accounted for 62% of the chlorophyll A and particulate carbon present (Istvanovics et al. 1993). Having 62% of chlorophyll A in the lake originating from *G. echinulata* implies that it is dominating the phytoplankton community, yet this is probably an underestimate of biomass because large *G. echinulata* colonies have less chlorophyll A per mass of carbon compared to smaller organisms. Due to their large size, significant numbers, and optimal buoyancy *G. echinulata* will shade other organisms floating at depth, significantly impairing concomitant phytoplankton growth (Pierson, Colom and Rdorigo 1994).

From data also collected in 1991 on Lake Erken the maximum growth rate was calculated to be 0.371 ± 0.035 divisions day^{-1} . Due to the increased presence of *G.*

echinulata the total phosphorus in the lake doubled between July 23 and August 20 and on any one particular day *G. echinulata* abundance increased at a rate of $0.47 \times 10^{-6} \text{ g day}^{-1}$. At this same time period phosphorus concentrations were increasing by $2.4 \text{ mg m}^{-2} \text{ day}^{-1}$, equivalent to 2/3 of the total internal phosphorus loading of the lake (Istvanovics et al. 1993). The average phosphorus quantities for each colony were 114ng with a total population of 350,000 colonies m^{-2} in August.

Maximum *G. echinulata* populations were found in mid-August in Lake Erken by Istvanovics et al. (1993) in conjunction with maximum total phosphorus (TP) levels of 28 ppb, while Barbiero and Welch (1992) observed a more significant maximum of 45 ppb in early August on Green Lake. Increases in TP are principally a result of increases in particulate phosphorus (PP) and soluble unreactive phosphorus (SUP) (Barbiero and Welch 1992). The phosphorus maximum reported in Green Lake in 1989 came from a total of 2,561 colonies L^{-1} that resulted from an average migration of 1.95×10^5 colonies $\text{m}^{-2} \text{ day}^{-1}$ (Barbiero and Welch 1992). In 1990 the migration rate and pelagic population maximums were significantly less than that in 1989 and were 34.84 colonies $\text{m}^{-2} \text{ day}^{-1}$, totaling a maximum of 651 colonies L^{-1} (Barbiero and Welch 1992). By estimating migrating *G. echinulata* catches and estimating epilimnic populations Barbiero and Welch (1992) found that in Green Lake 40% of the pelagic population was from the sediments and the remaining 60% had formed as a result of epilimnic colonial division which is made possible by excess phosphorus stores in the *G. echinulata*.

In contrast to Green Lake, results obtained from Lake Erken in 1999 indicate that 2.6% and in 2001 3.4% of the pelagic maximum had originated from migrating colonies. Also noted in this study the majority of migration took place between June 14 and July 26 yet proceeded as late as September 20th. For this particular study the most productive recruitment depth was 1.5m (generally ranging from 1-3m) and only few colonies migrated from depths below 3m. In these years the pelagic abundance of colonies peaked at 24 and 30 colonies L^{-1} (Karlson Elfgren, Rydin, Hyenstrand and Pettersson 2003). This lake in particular tends to have a much smaller migrating inoculum that is derived from the benthos compared to the amassed populations observed at the water's surface due to pelagic growth and divisions.

In Lake Erken, the small percent of recruited colonies in the pelagic zone refute the notion that *G. echinulata* cannot assimilate epilimnetic phosphorus because nutrient reserves from the benthos could not account for the vast number of colonial divisions observed (Karlson Elfgren, Rydin, Hyenstrand and Pettersson 2003). For this particular process the literature on the pelagic reproduction and possible phosphorus uptake is often conflicting. Karlsson-Elfgren, Hyenstrand, and Riden (2005) show that with the increased presence of iron and phosphorus more divisions can occur, implying that the colonies must be absorbing phosphorus. Conversely, Istvanovics (1993) showed that in the presence of excess isotopically labeled phosphorus there was no uptake. The former implies that in the right circumstance there is an opportunity for rampant growth while the later explanation shows that benthic acquired reserves will limit pelagic blooms to a threshold established by their maximum benthic phosphorus assimilation. On Peninsula Lake in Ontario, Canada pelagic colonies were noted to absorb phosphorus at a rate that was 1,000 to 10,000 times slower than was observed on the sediments (Tymowski and Duthie 2000). In Green Lake colonial division was held to a minimum as 50% of the total pelagic population with the rest of the biomass migrating from the sediment surface (Forsell and Pettersson 1995).

Another study supporting the notion that *G. echinulata* can absorb phosphorus was done in 2000 on Lake Erken using 300L plastic bags filled with lake water, each inoculated with 40 newly migrated *Gloeotrichia echinulata* colonies. Specific nutrients were added to these bags and their pelagic reproduction was monitored. By day 16, 11 of the 12 enclosures had less than 3 colonies L⁻¹, including the control. The bag with added phosphate, nitrogen and iron contained a total of 600 colonies L⁻¹, requiring a doubling period of less than 4 days throughout the entire course of the experiment (Karlsson-Elfgren, Hyenstrand, and Rydin 2005).

Iron is a necessary component for photosynthesis and therefore can be a limiting factor for photosynthetic organisms. Specific to cyanobacteria, iron is also essential in nitrogen fixation (Hyenstrand, Rydin and Gunnerhed 1999). Under anoxic conditions iron becomes soluble in water as it is converted from Fe³⁺ to Fe²⁺, yet anoxia is generally only observed in the late summer when *G. echinulata* had already reached its pelagic maximum and is declining in numbers. In three enclosure experiments introduction of

Fe²⁺ was found to enhance growth and production of *G. echinulata* as well as chlorophyll a production (Hyenstrand, Rydin and Gunnerhed 1999). Because *G. echinulata* tends to be more prevalent in lakes subject to periodic mixing it can be assumed that the recirculation events may replenish iron deficiencies leading to an enhancement of pelagic colonies above the level at which they would otherwise be sustained (Hyenstrand, Rydin and Gunnerhed 1999).

A separate study was performed with the addition of iron and boron to *Gloeotrichia echinulata* in enclosure experiments on Lake Erken (Hyenstrand et al. 2001). In mesh bags containing phosphate and nitrate, but no iron and boron, colonies did not develop while the colonies outside the bags grew at a rate of 0.15 doublings day⁻¹. In the bags supplied with phosphate, nitrate and iron colonies proliferated at a rate of 0.19 doublings day⁻¹. For bags receiving all four nutritional additions the growth rate was 0.26 doublings day⁻¹ (Hyenstrand et al. 2001). It seems very apparent that iron is a limiting factor in growth, division, and chlorophyll A production for *G. echinulata*. Hyenstrand et al. (2001) postulated from their results that boron has the ability to stabilize the heterocyte envelope. Furthermore, O₂ created from photosynthesis is assumed to inhibit nitrogen fixation yet the presence of boron helps to extricate O₂ from the colony thus accelerating N₂ fixation.

As noted earlier, *G. echinulata* is a nitrogen fixing organism which means it can use molecular nitrogen, available from the atmosphere, to meet its nitrogen demands. Conversely, most other aquatic fauna can only use nitrogen in the form of nitrate, nitrite, or ammonium, often limited in the epilimnion. Results reported by Szasz and Pettersson (2000) in a study using the isotope ¹⁵N indicate that although *G. echinulata* can fix nitrogen it prefers to use available NH₄⁺, NO₂⁻, or NO₃⁻ when they are available. Earlier in the season when these concentrations are higher, nitrogen from fixation only accounted for 15-30% of the nitrogen uptake (Szasz and Pettersson 2000). As the season progresses and *G. echinulata* begins to dominate the phytoplankton community it will use much of the available NH₄⁺ and NO₂⁻, and NO₃⁻ leaving very little for other phytoplankton. Some phytoplankton competing for these finite resources will die out while *G. echinulata* will still thrive because of its ability to fix N₂ to meet its nitrogen demands. Often with the

increasing presence of *G. echinulata* it has been observed that the water clarity has been improved (Annadotter et al. 1999) due to the decline of other phytoplankton.

Noges et al. (2004) have studied the ecology of Lake Pepsi on the boarder of Hungary and Russia for several decades. They observed significant changes in nutrient loading due socioeconomic changes in Russia. Previously, with an excess of agricultural and fertilizer runoff there was a much higher N/P ratio (nitrogen in fertilizers being in the form of ammonium) which led to a diverse spectrum of zooplankton and phytoplankton. With the collapse of communism, the farming industry in the area declined reducing the nitrogen input to the lake. With reduced nitrogen *G. echinulata*, who is able to utilize atmospheric nitrogen, doubled its abundance to over 50% in some years (Noges et al. 2004). As noted by Noges et al. (2004), this is consistent with the results of Smith et al. (1995), who showed that cyanobacteria thrive in lakes with greater than 10 ppb P and less than 100 ppb N in the form of ammonium and nitrate (Noges et al. 2004). To limit the extent of cyanobacterial dominance phosphorus concentrations need to be below 5 ppb P, yet even if this minimum is attained cyanobacteria have been able to dominate in some lakes (Dokulil and Teubner 2000).

Sporulation and Over Wintering

In the last few weeks of pelagic existence most colonies have fully formed akinetes and spore sheaths. As phosphorus reserves become scarcer their trichomes become hair like (Barbiero 1993). Proakinetes and hardening of the basil region can first be noted in early August. Akinete formation is triggered by light but several other factors can play a role in the extent of their formation which might include colony size, light and the presence of nutrients. With regards to akinete differentiation nitrogen depletion can be an accelerator and the presence of green light will cause an earlier change. Additionally, with decreased concentrations of Mg, Ca, Fe, and S the number of akinetes formed is diminished. Conversely, they also noted an increased number of akinetes formed as phosphorus concentrations were depleted (Karlsson-Elfgren 2003). On Green Lakes it was noted that this process had begun by August 23rd and August 8th in 1989 and 1990 respectively. These dates can be correlated with a population maximum occurring on August 16th and August 8th in those years (Barbiero 1993).

Once the akinetes have been created, the outer portion of the trichomes and gas vesicles are shed, thus the germlings sink to the bottom where they will winter (Karlsson-Elfgrén 2003). Mechanistically, this occurs as photosynthesis decreases, photosynthate accumulates in the cells and protein synthesis decreases. With these changes turgor pressure increases in the cells and the gas vacuoles will collapse (Rodrigo et al. 1998). The downward migrating akinete packages hold carbon and nitrogen reserves that are stored as glycogen and cyanophycin granules, yet the cells have depleted quantities of phosphorus (Tymowski and Duthie 2000).

There are several theories regarding the form that *G. echinulata* over winters in but the most widely accepted hypothesis is that they survive as an 'Akinete Package'. This form consists of, "a spherical arrangement of akinetes and spore sheath material, embedded in a dense covering of extra-cellular material," (Barbiero 1993). At this point the colonies have lost their vegetative cells and the old colony remains in a layer of mucilage (Forsell and Petersson 1995).

As previously discussed, during their pelagic existence *G. echinulata* is subject to wind induced drifting causing an accumulation of the colonies in the windward coves and shallow section of lakes. As a result, the majority of sedimenting colonies will tend to fall in these areas. In 1998, Forsell reported that on Lake Erken, although depth less than 2 meters accounts for a mere 10% of the lake bottom, 48% of the resting akinete colonies can be found in this depth zone (Forsell 1998). Forsell also reported that the highest concentrations of *G. echinulata* can be found on the shore with concentrations as high as 7,800 akinete colonies m⁻². Colonies located in the littoral zone were found to be able to survive for six months in the air or covered with ice. Although these colonies have a survival rate of only 8/1000 colonies, their numbers can be a significant source of the next year's total inoculum. Surviving under these conditions demonstrates the resilience of the species and thus its ability to thrive.

The over wintering *G. echinulata* spores allow for a dramatic increase in the following year because each colony can have as many as 1,000 filaments, most of which can contain akinetes. Since each new colony only needs about 10 akinetes to form, favorable light and temperature conditions can result in exponential annual growth (Forsell and Petersson 1995).

Resting cells on the sediments are subjected to many factors that can influence fecundity. While mature they contain chemicals that deter predators, but as resting cells they are susceptible to predation from zooplankton and grazing of benthic fauna. Also, with disruption of sediments many akinete packages can become covered by sediments and will not receive the necessary light to allow germination to occur (Karlson-Elfgren 2003).

Externalities

Dokulil and Teubner (2000) describe cyanobacterial dominance as, “the ultimate phase of eutrophication.” Significant blooms of *G. echinulata* can have a large effect on recreational, consumptive, and industrial uses on a particular body of water. Their benthic recruitment and phosphorus assimilation may have profound effects on a lake’s ecosystem but predicting the extent of change associated with this organism is still an active area of research. As *G. echinulata* migrates from the benthos to the surface it takes with it stores of phosphorus essentially short-circuiting conventional biological nutrient cycles. With dramatic blooms the shift of these nutrients can have a drastic effect on the lake’s ecosystem. Forsell and Pettersson (1995) found that in Green Lake, Seattle *G. echinulata* accounted for 2/3 of the lakes phosphorus loading into the water column equivalent to a flux of 0.4-0.6 mg of P m⁻² day⁻¹. In 1991 at Lake Erken, Sweden an astounding flux of 2.4 mg P m⁻² day⁻² was reported, representing 2/3 of the total phosphorus loading for the lake (Forsell and Pettersson 1995). These increases in total phosphorus is due to increases *G. echinulata* biomass and also organic phosphorus released to the lake (Istvanovics et al. 1993). Whether or not organic phosphorus can be utilized by other phytoplankton for subsequent blooms in the Belgrade Lakes is unknown. If this does prove to be a phosphorus source for other phytoplankton it is of significant concern since *G. echinulata* will essentially resuspend phosphorus that has been removed from the lake in previous years.

While the transport of phosphorus into the water column could increase blooms the often complete domination of the phytoplankton community by *G. echinulata* from July to mid August leads to a reduction in the biodiversity of lake while *Gloeotrichia* is present. Utilizing nitrate, nitrite, ammonium and iron in a period of time where there is

little available phosphorus in the epilimnion decreases the chance for other species of plankton to survive.

G. echinulata echinulata can represent a substantial cumulative biomass that can have a large affect on the oxygen supply of a lake. In the pelagic zone *G. echinulata* colonies exist at the surface undergoing photosynthesis. The oxygen produced here will remain in the water or diffuse into the atmosphere. The loss of other phytoplankton at varying depths as a result of the factors discussed earlier will limit the amount of CO₂ converted to O₂ at more significant depths. In July and August water temperatures in lakes are starting to reach their annual maximums, which in the case of some species of trout and salmon will exceed their tolerance level. These fish will proceed to deeper, cooler water in search of oxygen rich water. Due to loss of phytoplankton at depths there will be less available O₂. Additionally when the *G. echinulata* have begun their downward migration at the end of the summer they begin to breakdown. Breakdown of these carbon compounds requires O₂. This event can be so significant that it can lead to anoxia below certain depths making it impossible for certain species of fish to thrive. Though not necessarily correlated to *G. echinulata*, the decomposition of algae in the benthos is the assumed cause of the decline of Land Locked Salmon in the Belgrade Lakes.

Many species of Cyanobacteria have evolved to protect themselves from predation by producing certain kinds of toxins. These chemicals deter zooplankton as well as fish species that graze on phytoplankton. Human toxicity to *G. echinulata* can range from reported skin irritation from contact, to liver damage as a result of continued ingestion. Further the water may take on an odor as well as a fowl taste (Dokulil and Teubner 2000). A study performed in St. Petersburg, Russia analyzing the affects of several species of cyanobacteria on mice reported an LD₅₀ of 12.0 mg kg⁻¹ and MTD of 6.0 mg kg⁻¹ for *G. echinulata* (Gromov et al. 1996).

Lake recovery mechanisms

Gloeotrichia echinulata's recruitment of phosphorus from the benthos is the primary cause of concern because it transports sediment phosphorus from an area of high concentration into the water column where its increased concentrations can have a profound effect on the aquatic ecosystem. Although *G. echinulata* plays a roll in the transport of phosphorus there are several other mechanisms that allow for movement of nutrients, thus recovery measures generally aim to address all factors. Other mechanisms that can increase phosphate concentrations in a lake are bacterially mediated phosphorus release, bioturbation, changes in pH or redox potentials, as well as runoff and other inputs that are both natural and manmade (DeGasperi, Spyridakis and Welch 1993).

Measures to reduce phosphate concentration typically starts by removing and reducing point sources that will leach phosphates into the water. Effluents from wastewater treatment plants and other industrial sources can often be a major contributor to external loading of a lake. Other origins of phosphates can be fertilizers runoff to the lake. The treatment of such problems begins first by limiting their use and reducing emissions. Buffers such as manmade wetlands that act as a sink work well at reducing effluent waste. Wastewater contains inorganic phosphorus which is readily assimilated by plankton and of utmost priority to reduce (Annadotter et al. 1999). Fortunately in the case of the Belgrade Lakes there are no wastewater treatment plants but the culmination of septic systems and leach fields from the high number of homes and seasonal cottages can play a roll in phosphorus loading and should be properly buffered and monitored.

Internal loading of an oligotrophic and eutrophic lake is the dominant source of suspended phosphorus in a lake on any particular year. Still, external sources must be reduced because if not flushed they will increase future maximum concentrations for subsequent years. The most widely used mechanism for reducing internal phosphorus loading is to add aluminum sulfate to lakes that will bind the phosphorus so that it cannot be released from the sediments. Alum treatments can be effective for up to nine years (DeGasperi, Spyridakis, and Welch 1993). These treatments have been shown to work well in shallow lakes but are ineffective with a pH that varies far from neutral. In an acidic or basic environment the aluminum changes properties to become water soluble and releases its bound phosphate in the process. Using sediments from Green Lake,

laboratory waters treated with alum released only 3% of normal phosphorus quantities, relative to the control (DeGasperi, Spyridakis, and Welch 1993). This experiment was followed by 8.6 mg Al L⁻¹ treatment from October 23rd – 30th in 1991 on Green Lake. Following this addition water clarity was increased and sediment phosphorus release was reduced to 1/3 of pretreatment values. For *G. echinulata*, the results were hard to distinguish because of varied temperatures. Following alum additions the average migration decreased by 93% while there was a two fold increase in other cyanobacterial blooms (Sonnichsen, Jacoby, and Welch 1997). Though this seems significant this variation falls within natural fluctuations and it is thought that the addition of alum was not the cause. Their findings indicate that temperature and light variances are overall more indicative of population size than alum treatments (Perakis, Welch, and Jacoby 1996; Sonnichsen, Jacoby, and Welch 1997). Therefore, Aluminum floc treatment has not been shown to prevent the assimilation of phosphorus for *G. echinulata*.

In Lake Finjasnon, of Southern Sweden, Annadotter et al. (1999) observed reduced *G. echinulata* blooms through drastically different methods of sediment dredging and later trawling. Dredging was the initial measure taken to reduce internal phosphorus reserves. Two meters of sediments were removed by suction dredging over a 6.6 km² expanse. This method showed only a 15 to 30% reduction in phosphorus loading. After dredging biomanipulation was tried in Lake Finjasnon. Prior to treatment planktonivorous species composed 72% of the populations. The goal of the bioremediation was to bring the planktivorous and piscivorous fish to a 1:1 ratio. Planktonivorous fish generally will avoid *Gloetricha* because of its toxicity and will preferentially reduce its competing phytoplankton, thus allowing for greater blooms (Annadotter et al. 1999). These investigators used fish trawls to remove some of the planktonivorous fish. After two years of trawling the target ratio was reached and a significant increase in diversity was seen in the phytoplankton community. With this change the secchi depth doubled and total summer phytoplankton biomass was reduced (Annadotter et al. 1999). This program shows that positive results can be experienced without introducing chemicals and dredging sediments.

Conclusion

Gloeotrichia echinulata's lifecycle is very complex relative to other plankton. Though significant studies have been performed on *Gloeotrichia* many of the factors involved in its lifecycle are still under question. A case by case analysis of this organism shows significant variation from year to year and lake to lake. Recovery mechanisms aimed at reducing the process of eutrophication, presumably caused by *G. echinulata*, have on the whole had limited effects. In some cases water quality has improved as colonies have been reduced but these examples are generally on small bodies of water compared to Great or Long Pond.

Possible remediation efforts on Great or Long Pond are not possible without first understanding the nutrient dynamic of *Gloeotrichia* in these specific ecosystems. At this point in time the goal for future studies of *G. echinulata* in the Belgrade Lakes is to better understand the lifecycle and nutrient cycling of the species as it exists in this habitat. With this information it is hoped that its future impact in these lakes as well as others can be limited.

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Appendix

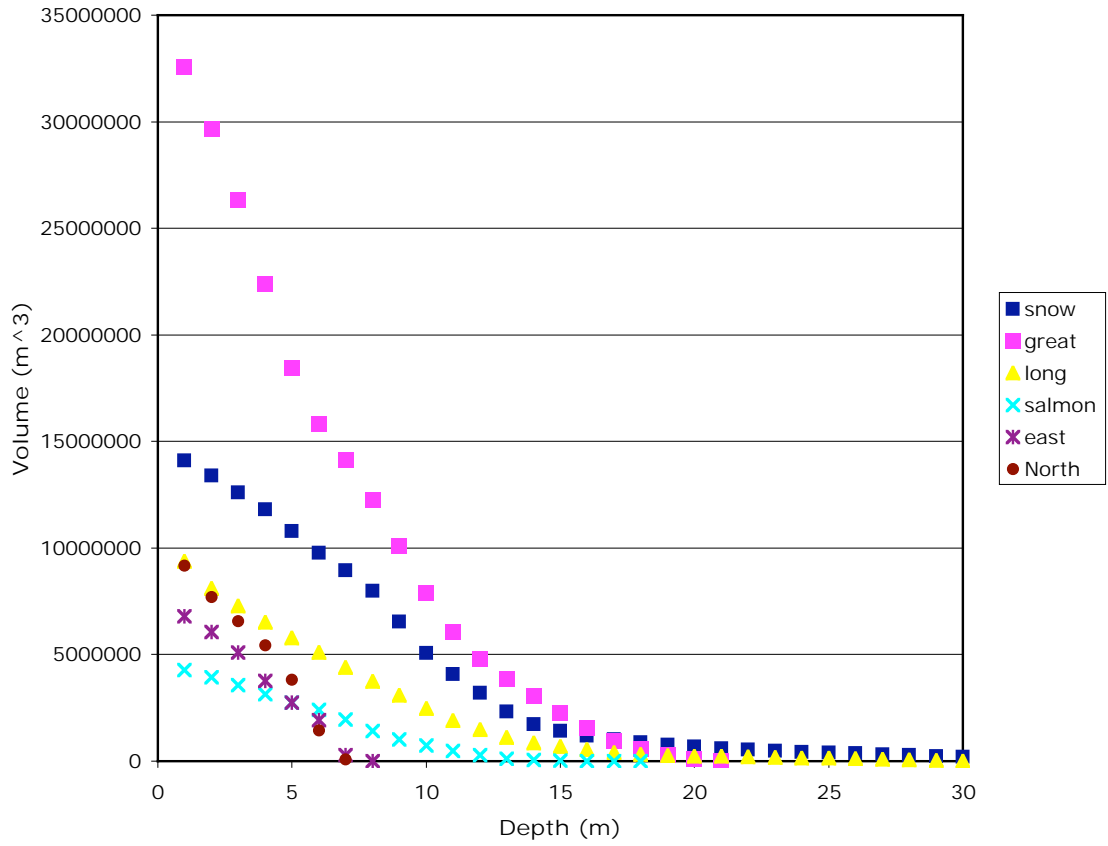
Estimated P flux to the Belgrade Lakes Due to *G. echinulata*

	Great	Long N	Long S	East	North	Snow	
Thermocline depth		10	10	10	5	5	10
Epilimnion volume (liters)	1.90E+11	3.36E+10	2.54E+10	2.44E+10	3.27E+10	1.01E+11	
Light Penetration Depth		5	5.5	5.5	3	2.5	4
Illuminated surface area (m ²)	1.70E+07	2.34E+06	2.11E+06	2.66E+06	3.54E+06	2.96E+06	
Total P flux mg	3.83E+09	5.27E+08	4.74E+08	5.98E+08	7.97E+08	6.65E+08	
Added P (PPB) to epilimnion over summer.		20	16	19	25	24	7

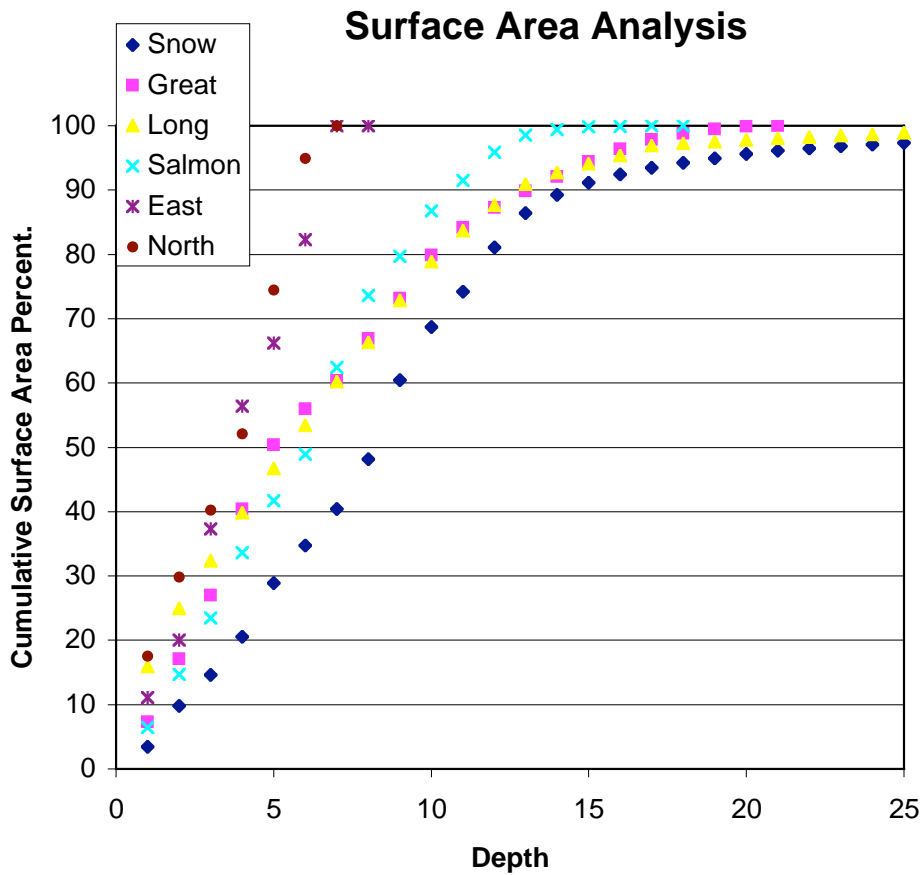
Total P flux is calculated assuming a P flux of 5 mg/m²/day due to *Gloeotricia* recruitment times the illuminated surface area of the lake and a recruitment time of 45 days. These are very rough calculations.

Hydrographic Data

Hypographic Data (1 meter intervals)



Volume of 1 meter depth intervals of each lake. If you look at this plot sideways you get a picture of the average depth profile of each lake.



Surface area analysis of each lake. Using Snow Pond as an example, at a depth of 5 meters, the cumulative surface area is 25%. This means that 25% of the lake is shallower than 5 meters and 75% is deeper than 5 meters. Gloeotrichia growth is favored in lakes with lots of shallow water. The figure below is an expansion of the figure above.

