Comprehensive Summaries of Uppsala Dissertations
from the Faculty of Science and Technology 856

Studies on the Life Cycles of Akinete Forming Cyanobacteria

BY

IRENE KARLSSON ELFGREN

ACTA UNIVERSITATIS UPSALIENSIS
UPPSALA 2003

Dissertation presented at Uppsala University to be publicly examined in Limnologens föreläsningssal, Norbyvägen 20, Uppsala, Wednesday, June 4, 2003 at 10:00 for the degree of Doctor of Philosophy. The examination will be conducted in English.

Abstract
Karlsson Elfgren, I. 2003. Studies on the Life Cycles of Akinete Forming Cyanobacteria. Acta Universitatis Upsaliensis. *Comprehensive Summaries of Uppsala Dissertations from the Faculty of Science and Technology* 856. 39 pp. Uppsala. ISBN 91-554-5665-0

Cyanobacteria which can form resting cells (in this case akinetes) are common in meso-eutrophic lakes in temperate regions, often dominating the phytoplankton communities during summer. The life cycles of akinete-forming cyanobacteria has been studied with *Gloeotrichia echinulata* as a model organism. *Anabaena* and *Aphanizomenon* were also included in a migration study. The focus of this thesis has been the factors influencing the processes of germination and subsequent growth, the factors influencing migration from the sediment, and the amount of growth occurring in the water.

Germination of *G. echinulata* was strongly favoured by light, and recruitment was highest from organic-rich sediments in shallow, sheltered littoral areas, between 0-3 m. Recruitment of *Anabaena* and *Aphanizomenon* was less light dependent, yet the highest recruitment occurred from shallow sediments (0-2 m). This means that organic-rich sediments (0-3 m) in shallow areas are the most important seed-banks of akinete-forming cyanobacteria. The inocula contributed only to a minor extent to the maximum pelagic populations. 4% for *G. echinulata* in the mesotrophic Lake Erken, and 0.03% for both *Anabaena* and *Aphanizomenon* in the eutrophic Lake Limmaren. This implies that processes of growth and division in the water are important for the maximum size of the pelagic population. Prolonged recruitment from the sediment strongly promoted establishment of the species in the water, especially *G. echinulata*.

Keywords: limnology, akinete, germination, recruitment

Irene Karlsson Elfgren, Department of Evolutionary Biology, Evolutionary Biology, Norbyv. 18D, Uppsala University, SE-75236 Uppsala, Sweden

ISSN 1104-232X
ISBN 91-554-5665-0
urn:nbn:se:uu:diva-3432 (http://urn.kb.se/resolve?urn=urn:nbn:se:uu:diva-3432)

List of Papers

This thesis is based on the following papers, which are referred to in the text by their Roman numerals:

I Karlsson I. 1999. On the germination of the akinete-forming cyanobacterium *Gloeotrichia echinulata*, in Lake Erken, Sweden. Algological Studies 94: 175-180.

II Karlsson I. Benthic growth of *Gloeotrichia echinulata*. Accepted by Hydrobiologia.

III Karlsson-Elfgren I., Rengefors K. & Gustafsson S. Factors regulating recruitment to the water column in the bloom-forming cyanobacterium *G. echinulata*. Submitted to Freshwater Biology.

IV Karlsson-Elfgren I., Rydin E., Hyenstrand P. & Pettersson K. Recruitment and pelagic growth of *Gloeotrichia echinulata*. Submitted to Journal of Phycology.

V Karlsson-Elfgren I., Hyenstrand P. & Rydin E. Pelagic growth and colony division of *Gloeotrichia echinulata* in Lake Erken. Submitted to Journal of Plankton Research.

VI Karlsson-Elfgren I. & Brunberg A-K. Recruitment of *Anabaena* and *Aphanizomenon* from shallow vs deep lake sediments. Submitted to Journal of Plankton Research.

Papers I and II were reprinted by permission from the publishers.

Contents

Abbreviations

Introduction

Life strategies of cyanobacteria

The cyanobacteria comprise a very diverse group of organisms. They can be found all over the world: in the sea, damp soil, glaciers, deserts and hot springs, for instance. Most of them, however, live in freshwater (Van Den Hoek *et al.* 1995, Adhikary 1996), where they can be found in both benthic and pelagic habitats. In the latter they can become extremely dominant, forming dense blooms. Pelagic cyanobacteria can be divided into groups based on several characters; e.g. the ability to fix N_2, to regulate buoyancy, or to form akinetes or other resting propagules. One such classification can be based on differences in life strategy, dividing the cyanobacteria into (1) species which form neither gas vesicles nor specialised resting cells (e.g. certain Chroococcales and Oscillatoriales), (2) species which do form gas vesicles, but do not form specialised resting cells, (e.g. other Chroococcales and Oscillatoriales), and (3) species which form both gas vesicles and specialised resting cells (certain Nostocales such as *Gloeotrichia echinulata*, *Anabaena* spp., and *Aphanizomenon* spp.). The organisms found in groups 2 and 3 form gas vesicles, and are therefore able to migrate actively through the water column. This thesis is focused on group 3, in which benthic resting cells (in this case akinetes) occur. Having gas vesicles, these cyanobacteria may actively migrate from the sediment into the water column. This group is interesting because it consists of species that in a short period of time can influence the phytoplankton composition. Moreover, these cyanobacteria may also influence nutrient transport and dynamics in the lakes where they occur (Barbiero & Welch 1992, Hansson 1996).

These planktonic Nostocales have complex life cycles, which I will describe, using *Gloeotrichia echinulata*, one of the species discussed in this thesis, as an example (Figure 1).

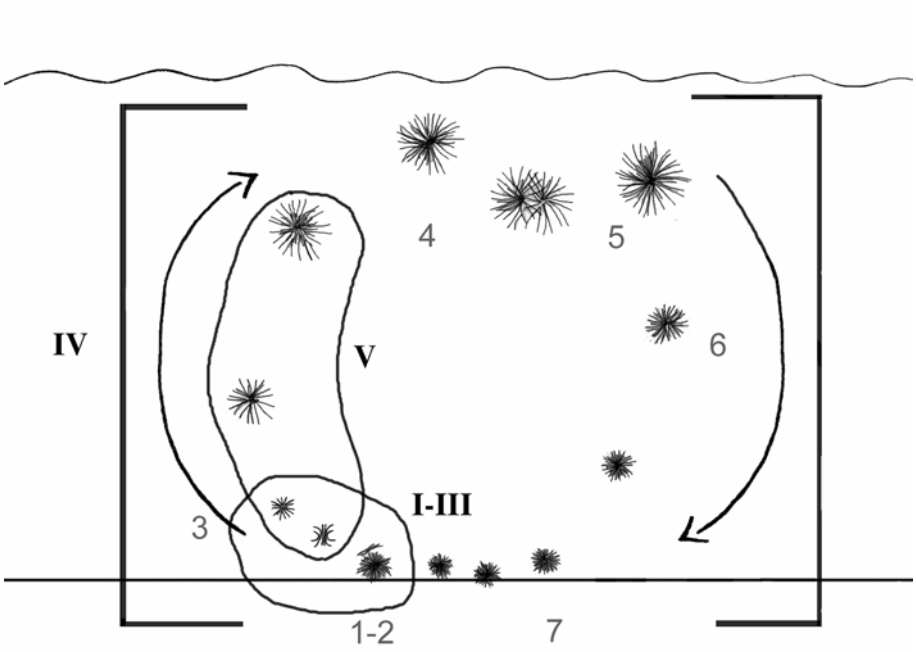

Figure 1. The life cycle of *G. echinulata* consists of several different phases: 1) germination on the sediment, 2) a growth period on the sediment, 3) formation of gas vesicles and migration up into the water, 4) growth and division in the water column, 5) formation of akinetes at the base of the filaments, 6) loss of the outer parts of the vegetative filaments and sinking out of the water, and 7) a period of resting and maturation of the akinetes (within the akinete colonies) on the sediment, perhaps including nutrient uptake. The roman numerals refer to the papers included in this thesis that study the different life stages of *G. echinulata*.

G. echinulata is filamentous and colony-forming, with filaments arranged radially in a sphere. During germination, the akinete produces a short filament or "germling", and then several filaments clump together to form filament bundles. In the next stage of development the filaments start to curve, and two heterocytes are formed in the middle of the filament. The connection between the two heterocytes breaks, and in a typical colony the filaments become arranged radially with the heterocytes in the middle. In the next stage of development a sheath of mucous is formed around the filaments closest to the heterocyte, and the vegetative cells furthest from the middle of the colony start to acquire a tapered appearance (Wesenberg-Lund 1904). *G. echinulata* is common in moderatly eutrophic lakes in the temperate zone, which are shallow and well mixed or are subject to periods of turbulent mixing (Barbiero & Welch 1992, Pierson *et al.* 1992).

Recruitment

The process including the first three stages of the life cycle (germination to migration) will be called recruitment in this thesis. In most investigations, germination in *G. echinulata* has been studied indirectly, by correlating environmental factors with the appearance of colonies in the water. Temperature and light conditions at the sediment surface have been the most common factors mentioned in previous studies. An increase in solar radiation was the only tested factor that correlated with an increase in the abundance of *G. echinulata* in Green Lake (Seattle, USA) in a study by Roelofs & Oglesby (1970). At the same site, Barbiero (1993) found that an increase in light at the sediment surface correlated with an increase in colonies in the water three weeks later. The delay in the response to light suggests there is a variable growth period on the sediment between germination and migration. An increase in temperature may shorten this period (provided it is greater than an unknown threshold), as Barbiero (1993) found that the migration period was shorter in a year when the temperature was higher. Barbiero (1991) also suggested that light may act as a trigger mechanism. In Lake Erken, south-eastern Sweden, blooms of *G. echinulata* often occur during July and August, coinciding with a gradual deepening of the epilimnion to ca 10 m (Pettersson *et al*. 1990; Pierson *et al*. 1992; Pettersson *et al*. 1993). This suggests that either germination or the growth rate on the sediment may be temperature-dependent. Germination is probably not directly influenced by depth, but is correlated with other factors such as light and temperature. In a shallow Danish lake, *G. echinulata* became dominant during the course of a summer following an increase in transparency from 0.5 to more than 2 m that coincided with a period of low dissolved oxygen concentrations (Jacobsen 1994). In this case it was probably the increase in light rather than the decrease in dissolved oxygen that affected recruitment, because in two other studies (Perakis *et al*. 1996; Barbiero 1993) dissolved oxygen concentrations were high during periods of recruitment. However, the most important influences on recruitment have not been unambiguously identified as yet.

The contribution of recruitment from the sediment to the pelagic population has been estimated to be very high for *G. echinulata*. For instance, two independent studies (Barbiero & Welch 1992; Istvánovics *et al*. 1993) reported that ca 40% of the weekly increase in the planktonic population was derived from the sediment. These findings were based on results from migration traps in Green Lake (Barbiero, 1992) and measurements of the phosphorous content of the colonies (Istvánovics *et al*., 1993; Forsell & Pettersson 1995) in Lake Erken. According to Perakis et al. (1996), the planktonic population of *G. echinulata* in Green Lake was

largely dependent on sustained recruitment in response to adequate light and temperature regimes at the sediment surface. Newly recruited colonies had higher cellular phosphorus contents than planktonic colonies, indicating that phosphorus was transported from the sediment to the water column, as also shown by Pettersson et al. (1993) in Lake Erken. Estimation of growth and division is difficult in a population that consists of a mixture of older and recently migrated colonies, especially since the recruitment period may be long, continuing at least between June and September (Barbiero & Welch 1992; Forsell 1993). Some attempts have been made to estimate growth rates using the phosphorus content of the colonies, and in one case measured epilimnetic increases in *G. echinulata* biomass during periods of high wind far exceeded potential growth-related increases, suggesting that wind-induced mixing could intensify recruitment from the sediments to the epilimnion (Istvánovics *et al*. 1993). The requirements for growth in the water could also include the availability of an organic compound produced by microorganisms, since addition of garden soil induced colonies to grow and divide in filtered lake water as opposed to autoclaved media (Rodhe 1948). To evaluate this it would be necessary to follow individual colonies in the water from migration to senescence.

Akinete formation

Akinete formation seems to depend on species-specific combinations of factors. Sporulation of *G. echinulata* in Green Lake only occurred during the last few weeks of planktonic existence (Barbiero 1993). In laboratory studies, akinete formation of *G. echinulata* has mostly been found towards the end, or after, the exponential growth phase (Nichols & Adams 1982; Wyman & Fay 1986), but it has also been shown that logarithmically growing cultures may form akinetes (Roelofs & Oglesby 1970). Suggested factors that may initiate akinete development in *Gloeotrichia spp* include, *inter alia*, colony size, light and nutrient limitation. According to Wyman & Fay (1986), light is the key trigger for differentiation, and light quality rather than light quantity is the most critical factor. Akinete differentiation was also found to be stimulated by nitrogen limitation, and it occurred earlier when colonies were cultured in green rather than white light. As green light is the dominant spectral component during bloom conditions this could also explain the observation of Rother & Fay (1977), that akinete differentiation in field populations is frequently associated with the development of surface blooms. Deficiencies in Mg, Ca, Fe and S led to a decrease in the number of akinetes in *Gloeotrichia ghosei*, while increasing numbers of akinetes were found during phosphorus deficiency in a study by Sinclair & Whitton

(1977). After akinetes have been formed, the outer parts of the filaments are lost, together with a large part of the gas vesicles. This response, coupled with the presence of the relatively dense akinetes, makes the colonies sink out of the water column. Thick layers of colonies can also be found on the shoreline during blooms, indicating that a large part of the akinetes are deposited on shallow sediments (Forsell 1998). Thus, aggregates of akinetes and remains of vegetative filaments kept together by thick mucous can be found on the sediment, and in this thesis they are called akinete colonies. The process of akinete formation will not be further discussed in this thesis.

Akinete forming cyanobacteria

In addition to the studies of *G. echinulata*, an investigation on the recruitment of *Anabaena* spp, and *Aphanizomenon flos-aquae* is included in this thesis. All three of these species are very common in meso-eutrophic lakes in temperate regions, often dominating the phytoplankton communities during the summer (e.g. Rosén 1981). Comparing the life cycle of *G. echinulata* with those of *Anabaena* spp, and *Aphanizomenon flos-aquae* there are both similarities and differences. They show similar (although probably not identical) requirements for germination, which is favoured by light, oxic water, high temperature, and increasing day length. Evidence suggesting that there is a growth period before migration has been found in some cases (Barbiero & Kann 1994), and akinete formation seems to take place towards the end of the growth season (Cmiech *et al.* 1984). As far as differences are concerned, the inocula seem to be of much lower importance for *Anabaena* and *Aphanizomenon* than for *G. echinulata*. Inoculation from the sediments appeared to account for at most 8.2% of the biomass of *Aphanizomenon flos-aquae* in an investigation by Barbiero & Kann (1994), and a small pool of vegetative filaments present in the water during winter probably constitutes the majority of the inoculum for the following season's bloom (Baker 1999). Germination may occur soon after akinete formation in some cases (Rother & Fay 1977). In some *Anabaena* species fructose has been shown to induce germination in the dark (Neeley-Fisher *et al.* 1989), but this seems to be an exception. Akinetes of wild populations of *Anabaena* sp. germinated within seven days after they were placed in filtered lake water, and filaments floated to the surface after emergence from the akinete envelope (Cmiech *et al.* 1986). *Anabaena* and *Aphanizomenon* may also have variable floating capacities, and may undergo active diurnal migration cycles in some cases (e.g. Osgood 1988). However, except for the differences in migration, and some variations in the factors inducing life-form changes, the life cycles of these three species are quite similar.

G. echinulata is the least common of the species discussed in this thesis, but it has several advantages as a model species. The colonies are large (average diameter, 2 mm), and easy to concentrate from the lake water. The early life stages are morphologically different from the pelagic colonies. As the akinetes are retained in the akinete colonies they are easy to find and to pick out of the sediment, and the size of akinete colonies and filament bundles also makes it possible to confirm germination with the naked eye or with the aid of a stereo microscope. One interesting question is if the planktonic dominance of an akinete-forming cyanobacterial species is governed by the conditions in the epilimnion, or if the size of the pelagic population is directly related to the size of the inoculum from the sediment. If the latter hypothesis is true, it would imply that the conditions regulating the size of the inoculum and initiation of the migration would be of a greater importance to the population maximum than the conditions in the epilimnion. To determine which of the alternatives predominantly govern the size of pelagic populations of akinete forming cyanobacteria, it should be important to find out more about the ecological behaviour and significance of migrating phytoplankton, and the mechanisms that initiate their migration.

Questions addressed in this thesis:

The life cycle of akinete forming cyanobacteria is the main subject of this thesis and the following questions are addressed:

- Are depth of deposition and time of the year important for the germination frequency in *G. echinulata*? (Paper I)
- How fast does *G. echinulata* develop on the sediment? (Paper II)
- What conditions determine the size of the inoculum/recruitment? (Paper III)
- How much does recruitment contribute to the pelagic population of *G. echinulata*? (Paper IV)
- (How much) does *G. echinulata* grow in the water? (Paper V)
- How large is the recruitment from sediments at different depths during the season for *Anabaena* spp and *Aphanizomenon* spp? (Paper VI)
- Is depth of deposition important for the size of recruitment of akinete forming cyanobacteria? (Paper I and VI)
- Which factors are important for germination of akinetes? (Paper III and VI)

Study sites

Lake Erken is a moderately eutrophic (yearly mean total nitrogen and phosphorus contents, 657 ± 127 µg/l and 27 ± 9.6 µg/l, respectively) lake in south-eastern Sweden (N 59°25´, E 18°15´). It has an area of 24 km^2, a mean depth of 9 m and a maximum depth of 21 m. During an average year, the lake is covered by ice from December to April, and the water is thermally stratified during the summer months (June to September) with spring and autumn mixing periods (Weyhenmeyer 1999).

Lake Limmaren is situated 70 km north of Stockholm at 59° 44´N 18° 44´E. It has an area of 6.5 km^2, a mean depth of 4.7 m and a maximum depth of 7.8 m. The water renewal time is about six years. Thermal stratification normally only occurs for a few days at a time during summer, but this varies depending on the weather conditions. The lake is naturally eutrophic with frequent cyanobacterial blooms during summer, dominated by *Microcystis* spp., *Aphanizomenon flos-aquae* and *Anabaena* spp.

Methods

Akinete material for laboratory experiments was taken from surface sediments in Lake Erken. Sediment samples were collected with a core sampler. The cores were sliced in the field and the top 2 cm of each core was brought into the laboratory, where it was stored at 4°C in darkness until the experiments started. Akinete colonies range in colour from green to light beige. The viability of these akinete colonies is uncertain, but assuming that green akinete colonies had been recently deposited on the sediment, they were selectively picked out with a pasteur pipette and used in the experiments. The germination study in 1998 (Paper I) was performed in filtered lake water spiked with nitrogen and phosphorus at 20°C, and a light:dark cycle of 12:12 h.

To test the length of the initial growth period on the sediment, akinete colonies were placed in wellplates with or without a thin layer of sediment (Paper II). The plates were incubated in a light:dark cycle of 16:8 h at a constant 17°C. The post-germination development was followed until the new filaments started to degrade. The morphology of filament bundles was also compared with filament bundles and colonies found in migration traps (at most seven days after migration). The number and average filament length of bundles and colonies in the migration traps was recorded over the summer.

Another germination experiment in 2001 (Paper III) was performed at two temperatures (7 and 17 °C), with and without light, with and without

bioturbation, and with sediment from three depths (1.5, 4.5, and 14 m). Sediment and filtered lake water were added to test tubes and incubated under the conditions described for Paper II. The test lasted 20 days, and every other day 20 ml of water was withdrawn to count recruited filaments. New water was added rapidly, to stir the sediment, or slowly, to avoid disturbing it.

Migration traps were used to follow the recruitment of *G. echinulata*, *Anabaena* and *Aphanizomenon* in the field. The migration traps were constructed of large, transparent plastic enclosures (20 l flasks) that were open at the bottom. In order to allow exchange of water, two openings were cut in the side of each flask, and covered by 40 µm mesh. The traps were attached to the sediment by long spikes penetrating into the sediment (Figure 1 in Paper II). On top of each trap, a 500 ml plastic bottle filled with filtered lake water was attached to collect filaments moving upwards from the sediment. These bottles were changed by divers once a week. In 1999 the migration traps were placed along a 0.5-4.5 m depth gradient in Lake Erken (Papers IV and V), and in triplicate at a deep site and a shallow site in Lake Limmaren (Paper VI). In 2001 the migration traps were placed in triplicate at three depths in Lake Erken (0.5 m, 4.5 m, and 14 m, Paper IV).

To follow the growth and division of *G. echinulata* in the water, two different enclosure experiments were performed in 2000, and one experiment in 2001 (Paper V). In the first experiment, triplicate 41 l mesh bags with a mesh size of 120 µm were used to monitor an inoculum of *G. echinulata* in three consecutive incubation periods. In the second experiment, twelve polythene bags were filled with 300 l surface water and attached to wooden frames. Different combinations of phosphate, nitrate, boron, and trace element solution were added to the enclosures and the abundance of *G. echinulata* was monitored every fourth day. In 2001, single *G. echinulata* colonies that had recently migrated from the sediment were incubated in ten 0.2 l mesh bags with a mesh size of 120 µm. These microcosms were sealed with plastic clips at the top, suspended in the water just beneath the surface and attached to a raft. The development of the *G. echinulata* colonies was monitored regularly during the incubation period without opening the bags.

The pelagic population of *G. echinulata* was followed during three years in Lake Erken. The monitoring program consisted of an integrated sampling scheme, in which samples were collected at 10 stations spaced at 2 m intervals down to 12 m depth, in such a way that each depth was sampled in proportion to its relative contribution to the total lake volume. In 1999 the sampling was performed every third to fourth week, and in 2000 and 2001 once a week from June to September (2000) or May to September (2001).

Summary of the papers

Are depth of deposition and time of the year important for the germination frequency of *G. echinulata*? (Paper I)

Akinete colonies were collected at different sediment depths from the end of March onwards. Germination occurred *in vitro* between April and August, the highest germination frequency occurring in colonies collected from the sediment of the shallowest station. On average, germination occurred in 30% of the akinete colonies, but as many as 70% germinated in the second week of June from the 0.5 m sediment. The germination period in the lake lasted approximately six weeks from June to the end of July. Akinete colonies sampled from the sediment in August and September had not germinated after two weeks in the laboratory, indicating that the pool of viable akinetes was depleted in the sediment, and that newly deposited akinetes needed to mature before germination. This means that both the time of year and depth of deposition is potentially important for the germination frequency of *G. echinulata* in the lake.

How fast does *G. echinulata* develop on the sediment? (Paper II)

The duration of the time period between akinete germination and migration up into the water has not been clarified previously. Germination occurred in one third of the wells, and subsequent growth was recorded. Germination primarily occurred within four days of incubation, although in occasional akinete colonies germination did not start until 12 or 16 days after the beginning of the incubation period. The newly germinated filaments formed bundles on the surface of the akinete colony from which they originated. Several bundles were found on the same akinete colony during the experiment (Figure 2a). The number of akinetes germinating in one akinete

colony varied between five and several hundred. The time before the filaments started to float varied between 2 to 4 days. In the lake, new colonies and filament bundles were found each week in the migration traps until August. These colonies and filament bundles were examined at most a week after migration. Comparing the morphology of filament bundles from the germination experiment and the migration traps, the filament bundles which had started to produce curved filaments were most similar to the filament bundles found in the migration traps, indicating that the latter were newly germinated (Figure 2b). The average filament length of colonies found in the migration traps was very close to the length of filaments found in filament bundles in the laboratory experiment. Taking into account the previously-described mechanisms of colony formation, this implies that the filament length had on average doubled within a week, thereby increasing the volume of the colony eight-fold and resulting in a growth rate of at least 1.14 day^{-1} during that week. These results show that the time needed for akinete germination and the time needed for gas vacuole formation varies between akinete colonies within the population. Growth just after migration seems to be very rapid. Another important result was that the number of akinetes germinating within one akinete colony varied within the population.

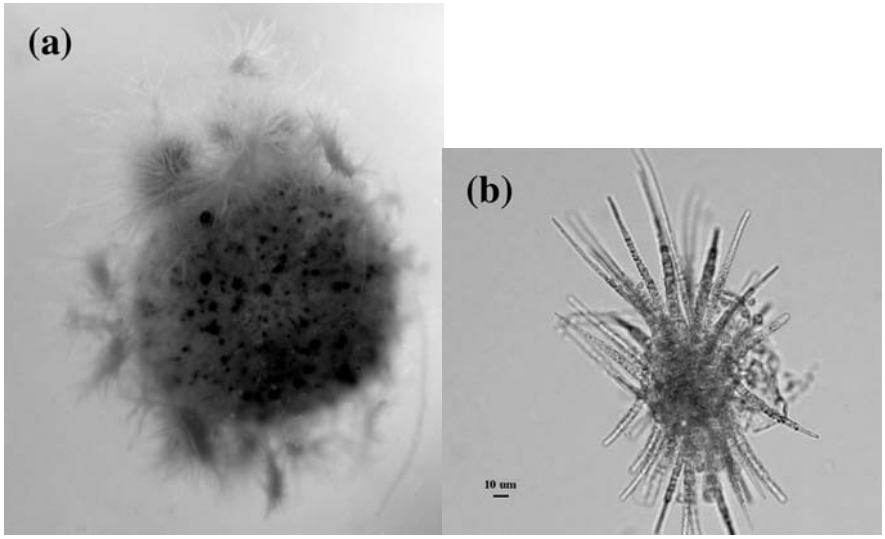

Figure 2. (a) *G. echinulata* akinete colony with filament bundles on the surface three days after germination. (b) *G. echinulata* filament bundle from one of the migration traps in 1999. This structure was similar to the filament bundle which was closest to become defined as a colony during the experiment.

What conditions determine the size of the recruited inoculum of *G. echinulata* ? (Paper III)

To determine the relative importance of a number of factors, such as light, temperature, bioturbation and depth of deposition on recruitment, a full factorial experiment design was set up in the laboratory in 2001. The process of germination was influenced by high temperature and light, while the size of the inoculum was strongly influenced by high temperature and bioturbation. The highest frequency of germination and the highest recruited biomass was found at 17°C in the presence of light and bioturbation (Figure 3). Both the timing and total biomass were positively influenced by high temperature. High temperature may also have increased the effect of bioturbation, making the response to available light at the surface faster at 17 than at 7°C. Colonies and heterocytes were only found in treatments with light and high temperature, and their presence was significantly enhanced by bioturbation. Despite the fact that the deep and shallow sediments contained very similar numbers of akinete colonies, the highest recruitment occurred from shallow sediments, indicating higher viability of akinetes from shallow sediments. All these results confirm the hypothesis that shallow areas with organic rich sediments (0-3 m) are most important for the recruitment of *G. echinulata*.

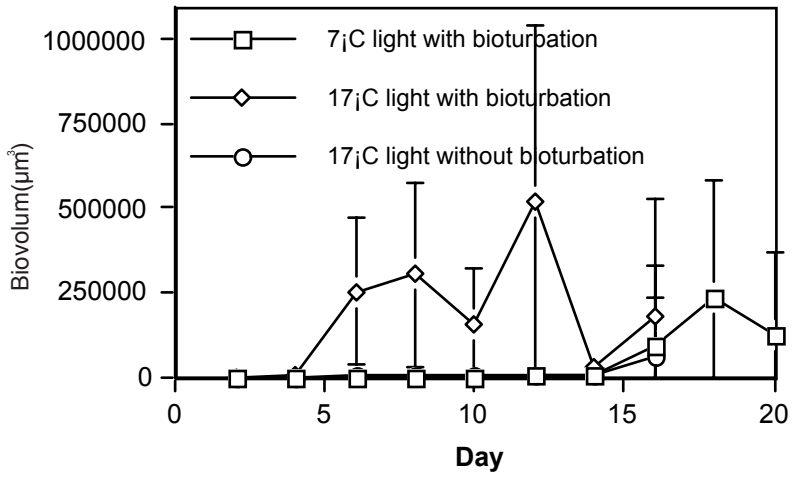

Figure 3. Average recruited biovolume (μm^3) of *G. echinulata* per sampling day in three treatments, error bars represent ± one standard deviation.

How much does recruitment contribute to the pelagic population of *G.echinulata*? (Paper IV)

The recruitment of *G. echinulata* from the sediments was followed during two years, and at the same time the pelagic populations were monitored. The results were used to validate a life-cycle model. Although the migration traps were deployed after migration had started in 1999, the calculated average recruitment rate was the same for the two years: 320 colonies m^{-2} day^{-1} for the sediments between 0 to 6 m (between June 14-September 27 in 1999, and May 15-August 28 in 2001), although the small scale variation was high both in time and space. The highest recruitment rates occurred between 0 to 3 m in both years. Very few colonies were recruited at 4.5 m and none at all at 14 m. The recruitment peaks occurred in late June, while the pelagic maxima occurred in early August in both years, with 24 colonies l^{-1} in 1999 and 30 colonies l^{-1} in 2001. A close correlation between measured and modelled pelagic abundance of *G. echinulata* was possible to obtain for both years of the study. Using iteration and changing the colonial division rate, the best fit was found for an average pelagic residence time of 14 days. In order to fit the modelled number of colonies with the observed abundance, the rate of division had to vary during the summer and gradually decline towards the end of the experimental period. Alternatively, assuming a constant rate of colony division, the pelagic residence time for the colonies had to vary considerably. Even when no loss processes were taken into account, the recruited colonies would represent less than 4% of the maximum pelagic population in both 1999 and 2001 (Figure 4). In conclusion: the pelagic population was dependent on input from the benthos in early summer, but only recruitment (and the calculated maximum growth found in Istvánovics *et al.* 1993) could not explain the rapid population increase observed during the weeks before the pelagic population maxima. This means that the colonies must be able to grow and divide more than has been calculated from internal phosphorus stores.

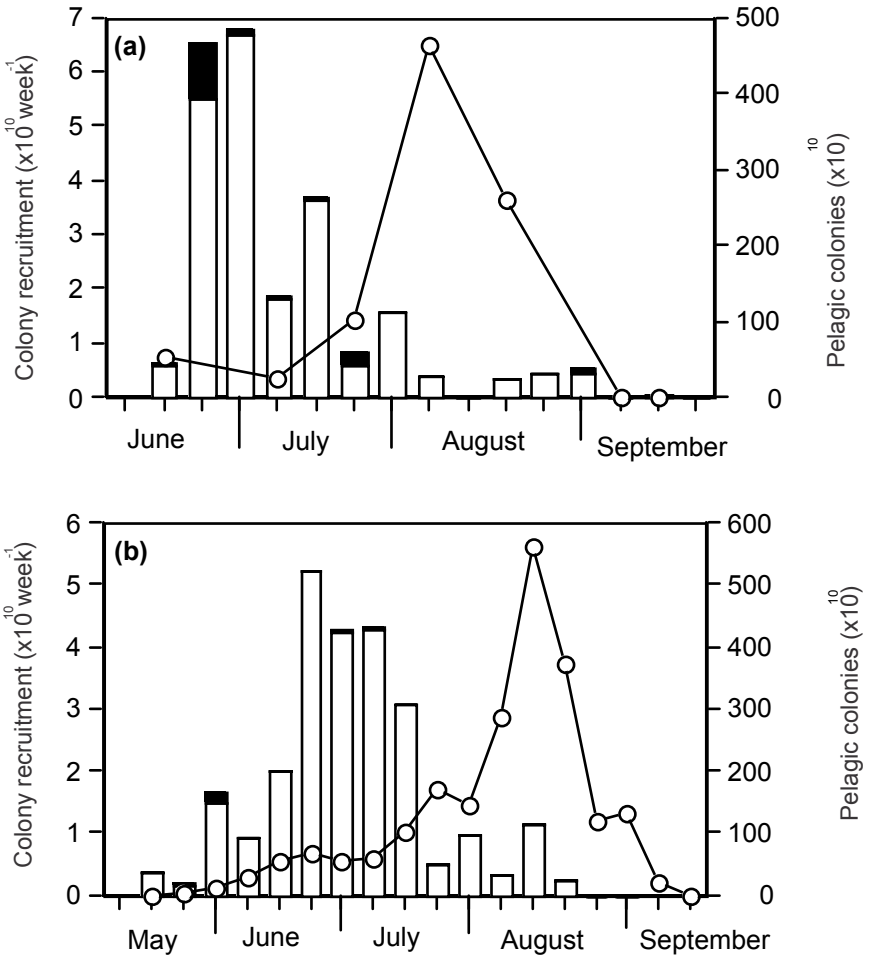

Figure 4. Recruitment and pelagic colony abundance in 1999 (a) and 2001 (b). Lines show pelagic population of *G. echinulata*, with depth integrated sampling every third week from June-September (1999) and May-September (2001) at ten stations. The values are calculated for total number of colonies in the lake down to 12m. White columns shows calculated recruitment between 0-2 m (1999) and 0-3 m (2001), and stacked black columns shows calculated recruitment between 2-4 m (1999), and 3-6 m (2001).

(How much) does *G. echinulata* grow in the water? (Paper V)

To evaluate the rate of colony division of *G. echinulata* in Lake Erken three enclosure experiments were performed in 2000 and 2001, and the pelagic population was followed through depth-integrated sampling. In the first enclosure experiment in 2000, no significant colony division occurred in mesh bags between June 27 and August 7, although the abundance of the pelagic population in the lake increased during the experimental periods. In the second enclosure experiment in 2000 (involving growth in plastic bags with nutrient additions), the only treatment that favoured *G. echinulata* development was addition of phosphate, nitrate and iron. The enclosure experiment in 2001 followed the development of individual colonies in the water, which showed large variations. On average, the colonies divided once every 18 days, but in several bags the inoculated colony had disappeared and in others a maximum of four colonies were present at the end of the experiment.

The development of the pelagic populations differed between the two years. In 2000 a maximum abundance of 90 colonies l^{-1} was recorded, while in 2001 a maximum of 30 colonies l^{-1} was found. The colonies were distributed throughout the whole sampled 12 m layer, although the highest concentrations were found in the top two meters of the water column (Figure 5). 60% of the colonies in 2000 and 70% in 2001 were found in layers deeper than 2 m. The size distribution of pelagic colonies varied between the two years, but the colonies tended to increase in diameter towards the end of summer. The division rate calculated from the increase in pelagic colonies was higher in 2000 than in 2001, indicating that smaller colony sizes occur when the division frequency is high.

Based on these findings it is suggested that circulation of *G. echinulata* colonies by wind induced currents to deeper, nutrient-rich water supports pelagic growth. In support of this hypothesis, a large proportion of the pelagic colonies was found at several metres depth, despite the high floating capacity of the colonies.

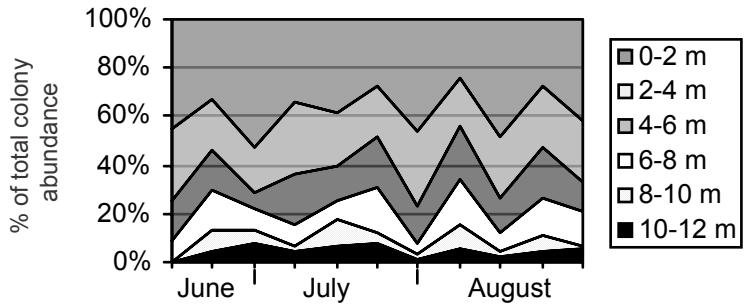

Figure 5. Depth distribution in percent of total number of *G. echinulata* colonies present in 2-m intervals between 0-12 m in 2001. The sampling was performed weekly at ten stations.

How large is the recruitment from sediments at different depths during the season for *Anabaena* spp and *Aphanizomenon* spp? (Paper VI)

In order to find out which factors are important for recruitment of two other akinete forming species, *Anabaena*, and *Aphanizomenon,* and from which water depth recruitment primarily occured, a migration study was performed in Lake Limmaren. In this study the differences in recruitment between *Anabaena* spp, and *Aphanizomenon* sp. were assessed at two sites, at 1-2 m, and 6-7 m water depth. The photic depth (1% light level) was calculated to be 3 m, so the shallow sediment always lay within the photic zone, and the deep site only had measurable light intensities three times during the summer. The water temperature did not differ between the sites and no anoxic conditions were recorded in the water column. Recruitment occurred at both sites, but most of the recruited cells originated from the shallow site. Neither *Aphanizomenon flos-aquae* nor *Anabaena* sp. showed any difference in phenology between the two sites, although *A. circinalis* started recruitment later at the deep site (Figure 6). This means that recruitment of filamentous cyanobacteria may take place at all depths in Lake Limmaren, although recruitment of all three species investigated was significantly higher at the shallow site. Of the three species, *A. flos-aquae* was the only one for which a population peak in the pelagic zone occurred after the peak of migration was detected in the traps. Sediments below 2 m have been largely ignored in earlier studies, but this study indicates that a large part of

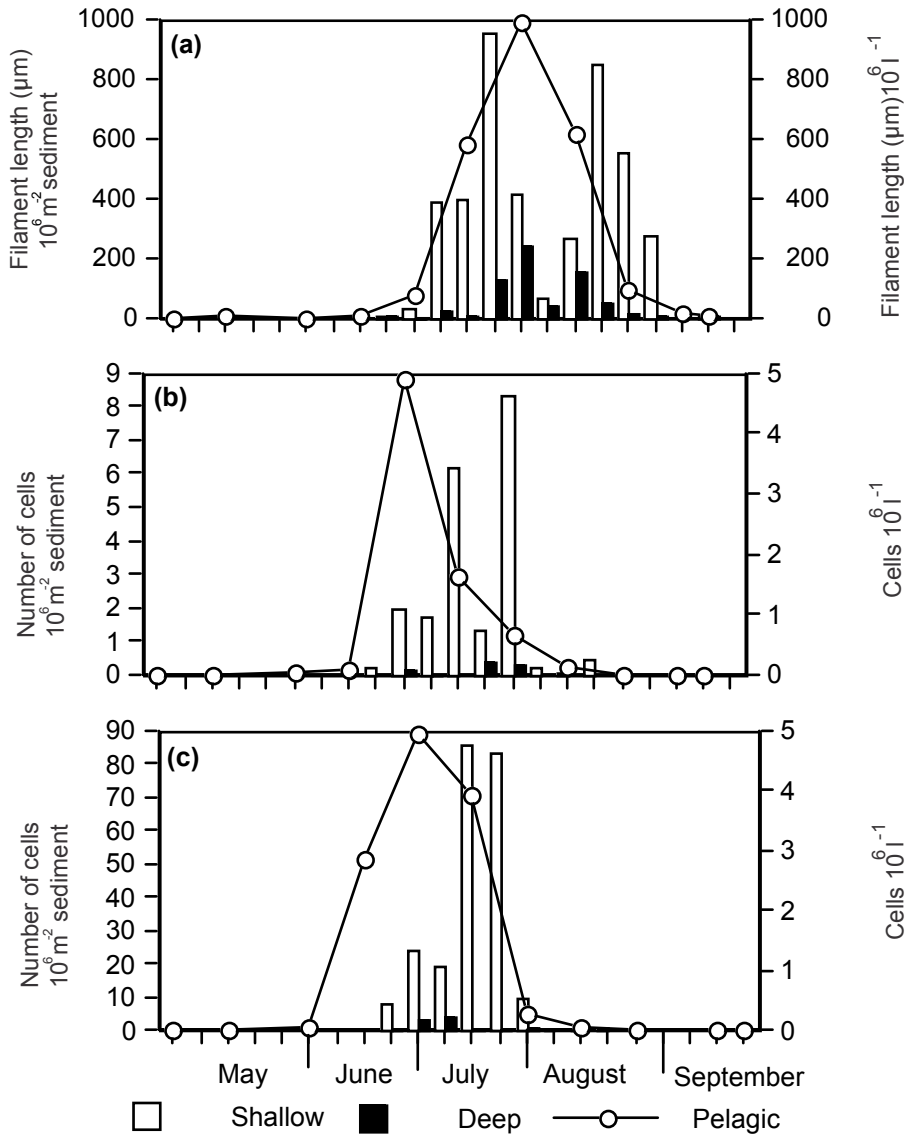

Figure 6. Population dynamics of *Aphanizomenon flos-aquae* (a), *Anabaena circinalis* (b), and *Anabaena* sp (c) in Lake Limmaren during 1999. Line with circles show abundance in the water (integrated sample from 0 to 7 m). Columns show recruitment rate from the sediment, with white columns representing the shallow site (1 m), and black columns representing the deep site (7 m).

the total recruitment from the sediment may occur from this part of a lake. Nevertheless, the calculated contribution of the inoculum (total recruitment up until maximum recorded pelagic concentrations) only amounted to 0.03% of the maximum pelagic population. From these results we conclude that shallow sediments are most important for the recruitment, and that the inoculum in Lake Limmaren is small, but may still be a factor to take into account when evaluating phytoplankton population dynamics.

General discussion

Depth of deposition and length of the lag phase before germination in *G. echinulata*

The findings in this thesis support the hypotheses that the depth where the akinete colonies are deposited is important for the recruitment of *G. echinulata*, and that the shallow sediments (< 3 m) are especially favourable. This is interesting as earlier recruitment studies have generally focused on depths between 2-10 m, e.g. (Barbiero & Welch 1992, Barbiero & Kann 1994, Hansson *et al.* 1994, Head *et al.* 1999). Roelofs & Oglesby (1970) concluded that light is probably the triggering factor for recruitment, while temperature influences the metabolic activity, and thus the lenght of the lag phase between the triggering event and germination. This is also true for the growth of filaments and the formation of bundles once the newly germinated filaments have left the old akinete colony. The influence of temperature was especially clear in the studies described in Paper III, where the recruitment started later at 7°C than at 17°C. However, the onset of germination and the number of germinated akinetes per akinete colony also differed amongst colonies cultured at the same temperature (Paper II). This shows that the status of the akinetes varies within the available seedbank, there are differences in the status of the akinetes. Whether this reflects a difference in maturation of the akinetes, or in the age of the akinetes after deposition, is not known. Akinetes sampled from the sediment at regular intervals from August 1998 throughout the following autumn and winter did not germinate in the laboratory until April 1999, when newly sampled akinetes also started to germinate (unpublished results). This indicates that in Lake Erken the process of germination may be day-length dependent, or that a period of maturation is needed to ensure that germination does not take place in the autumn. Furthermore, no germination occurred between September and April in the laboratory tests, although the same photoperiod was used throughout the year, indicating that a maturation period is needed. After the akinetes have matured they may germinate in the laboratory, even if no germination is observed in the lake. The lack of germination in the lake in

this case was probably due to the temperature being too low, as the light regime in shallowsediments after ice-out was favourable. In contrast, Roelofs & Oglesby (1970) found small stubby colonies on the sediments in Green Lake in January and March, although no colonies appeared in the water column until early July. It is not known whether this was an effect of light or temperature limitation, or due to some other factor.

Growth patterns before and just after migration

The development after germination on the sediment is another important stage in the life cycle of *G. echinulata*. The minimum lag phase between germination and migration could not be definitively established in the study described in Paper II. However, it seems clear that at a temperature of 17°C, between 2 and 5 days was sufficient for the organism to form gas vesicles and float up into the water. The sediment temperature did not fall below 16°C at the sites of the migration traps, and filament bundles found in the migration traps in 1999 were similar morphologically to those found in the laboratory four days after germination. This implies that the process of gas vesicle formation takes less than a week at 17°C, but may vary between individual filaments.

As the colonies and filament bundles found in the migration traps had approximately the same average filament length (radius), it was concluded that the rate of filament growth after colony formation must be higher than previously assumed. The average growth rate in the water has been estimated to be 0.124 day^{-1} (Roelofs & Oglesby 1970). However, colonies that double in filament length in a single week, as seen in our studies, must increase in volume 8-fold during that week, corresponding to a growth rate of 1.14 day^{-1}. This is much faster than the growth rate (approximately 0.25 day-1) found in enclosure experiments with added nutrients and iron (Hyenstrand *et al.* 2000). This implies that recruitment is especially important in early summer.

What factors differ between depths and may influence recruitment?

The number of recruited colonies decreased gradually with increasing depth, with the highest recruitment occurring at 1.5 m, and none at all at 14 m. As akinete colonies found at 14 m germinated in the laboratory, it seems that the conditions present at 14 m prevent recruitment, and that the conditions at 4.5

m significantly impair recruitment. Clearly, therefore, factors that differ between the different depths influence recruitment.

Comparing different factors of potentially high importance to recruitment, such as temperature, light, type of resuspension, and nutrient status between 0.5 and 14 m, we find that the thermocline is usually established at 4 m and gradually deepens during the summer. When the thermocline is established, the temperature is similar at all depths (12-14°C), including 14 m, but temperature increases significantly more slowly 14 m, and rarely exceeds 17°C. This means that the temperature is very similar at 0.5 and 4.5 m (i.e. within Svanberga Bay) except during the early summer when shallow sediments are heated more rapidly on sunny days. Considering the results from germination experiments, this temperature should be sufficient to induce germination. The light availability, on the other hand, differs significantly between the depths, with no available PAR at 14 m, and low levels available at 4.5 m.

Resuspension due to physical action is most likely also very similar at the investigated depths as they contained accumulation sediments. Bioturbation may differ, depending on the type of benthic fauna present in the sediment, but within Svanberga Bay, the composition of the benthic fauna is very similar, with soft sediments dominated by *Asellus aquaticus*. This species is very efficient at turning over sediments, and has been shown to positively influence recruitment of *Anabaena* and *Microcystis* (Ståhl-Delbanco & Hansson 2002). At 14 m the benthic fauna consists entirely of Chironomids and Oligochaetes, which also mix the sediment, but at a slower rate. This means that bioturbation may have an effect on the turnover rate of akinete colonies in the sediment, and the faster turnover time by *A. aquaticus* may result in faster recruitment of viable akinete colonies in the very shallow sediments, where the light climate is better suited for germination, compared to sediments deeper than 3 m.

The nutrient status of the sediment may vary with depth, but as the same proportion of germination in akinete colonies was observed in laboratory experiments regardless of whether lake water, lake water spiked with nutrients, or lake water and sediment was used, this factor does not seem to influence the rate of germination. In conclusion, the factors that differed significantly between 1.5 and 14 m were the rate of sediment turnover, the temperature after the thermocline had been established, and light availability. The differences between 1.5 and 4.5 m were smaller, consisting of a small temperature difference in early summer, and much greater differences in light availability. Collectively, these findings suggest that light availability is probably the most important factor for recruitment of *G. echinulata* in Lake Erken.

Considering the situation in Lake Limmaren, we found that recruitment occurred at all depths, even though the light availability was extremely low for sediments deeper than 3 m. Temperature differences were small, although temperatures could have been significantly higher in the very shallow sediments than in the rest of the lake. Light does not seem to be essential for the recruitment of *Anabaena* and *Aphanizomenon*, but the shallow sediments, which had a favourable light regime, produced a major proportion of the recruited cells. This means that for *Anabaena* and *Aphanizomenon* light may not be as strongly correlated to recruitment as for *G. echinulata*, but light availability appears to be important for the scale of recruitment for all the studied species.

Does recruitment of akinete forming cyanobacteria have a direct influence on the size of the pelagic population?

Measured recruitment of *Anabaena* and *Aphanizomenon* in Lake Limmaren had a very small influence on the size of the pelagic population, accounting for just ca 0.03%, of the total, and only *Aphanizomenon flos-aquae* displayed a peak in recruitment before its maximal population size was reached in the water, according to our measurements (Paper VI). Recruitment could occur in all parts of the lake, but the majority of the recruited cells originated at the shallow site. The only species to show a difference in timing between the two sites was *A. circinalis*, for which recruitment started later at the deep site. Similarly, Head et al. (1999) found that recruitment was not a significant source of biomass for *Anabaena* and *Aphanizomenon*, and concluded that low numbers of filaments observed during the winter constituted the primary source of inocula for the summer populations. In Lake Limmaren no filaments have been observed during the winter, but if very low numbers are present in the water they would easily be missed in standard sampling. This means that unlike *G. echinulata* there is no doubt that once filaments of *Anabaena* and *Aphanizomenon* have migrated up into the water column they grow and divide very quickly.

The cumulative contribution of recruitment in *G. echinulata* (up until the pelagic population peaked) from sediments between 0-6 m deep represented less than 4% of the maximum pelagic population (Paper V). The recruitment pattern did not follow the development of the pelagic population closely, and the peak in migration occurred six weeks before the observed pelagic maximum. This made the calculated contribution to the weekly pelagic increase in colonies highly variable (ranging between 0.02 and 120%) and the resulting data were not considered sufficiently reliable for calculating

average figures. At the time when maximum recruitment was detected, it accounted for 17% of the pelagic population, indicating that recruitment of *G. echinulata* may have a direct influence on the size of the pelagic population early in the summer, but the size of the maximum pelagic population is not directly influenced by recruitment. In contrast, according to calculations based on the phosphorus contents of colonies in studies by Istvánovics et al. (1993) and Forsell & Pettersson (1995), newly migrated colonies accounted for 40% of the total number of colonies, on average, on each sampling occasion. Thus, if colonies are able to grow and divide more rapidly than the cited calculations suggest (as indicated by the growth rate of newly migrated colonies found in my studies) these figures should be re-evaluated.

Growth and division in the water

The extent to which *G. echinulata* grows and divides in the water is a complex issue. The calculated number of recruited colonies does not seem to be sufficient to explain the peak of the pelagic populations of *G. echinulata* in Lake Erken, according to calculations based on their internal phosphorus stores. These reserves have been calculated to suffice for 3-4 doublings of the biomass by Istvánovics et al. (1993), and 1.7 to 2.2 doublings by Tymowski & Duthie (2000). As the average size of pelagic colonies is fairly constant over the summer, with a tendency to increase shortly before the colonies disappear from the water, we assume that one colony division corresponds to one doubling of the biomass. The model simulations (Paper IV) indicate that it is possible for the colonies to grow and divide more than has been inferred from measurments of their internal phosphorus contents.

There are no obvious explanations for the discrepancy between the calculated and observed pelagic maxima, but it could be due to a large recruitment event occurring just before the pelagic maximum. In Lake Erken, pelagic maxima of *G. echinulata* typically coincide with a lowering of the thermocline to 10 m, increasing the sediment area in contact with epilimetic waters (Pettersson *et al.* 1993). If movements of the thermocline induce resuspension and transport of akinete colonies to shallow sediments, this may indeed cause a recruitment event that would not have been detected by the migration traps. However, resuspension would not be enough by itself to induce germination unless the akinetes were suspended within the photic zone long enough to induce germination and development of gas vesicles in the new filaments. Alternative explanations include the possibility that under certain conditions colonies may take up phosphorus from the water, or that the process of nitrogen fixation may be affected by the presence of iron in

the water. In several enclosure experiments performed in Lake Erken, Hyenstrand et al. (2000) found that the abundance of *G. echinulata* increased exponentially if iron was added to enclosures containing phosphate and inorganic nitrogen, but without iron the number of colonies decreased. Complementary additions of boron resulted in an even higher rate of colony division (Hyenstrand *et al.* 2001). This was also the case in an experiment reported in Paper V, with the additional result that the presence of a trace element solution decreased the number of *G. echinulata* colonies in the bags.

During enclosure experiments in mesh bags, newly migrated colonies showed very low rates of division at the same time as the pelagic population increased in the lake. In addition, monitoring of individual colonies also showed that there were large variations in growth and division, although all colonies included were gathered within a day after migration when the experiment started. The main difference between the colonies in the mesh bags and those in the lake was in their position in the water. Pelagic colonies were found down to 12 m (Paper V), whereas the mesh bags were placed just under the water surface in a sheltered bay. The low rates of division in the bags may have been due to light inhibition, as the colonies were trapped close to the surface. On the other hand, as the colonies are large, the cells in the middle of the colonies were probably protected against excess light, as indicated by an experiment in which oxygen was still being produced by colonies that had been exposed to strong light for several hours (unpublished results). Alternatively, circulation to deeper waters may give individual colonies access to uppwelling nutrients, e.g. iron, from the hypolimnion. In addition, the presence or absence of combined nitrogen, and trace elements may affect the status of other organisms, such as heterotrophic bacteria, which could produce an organic factor necessary for growth in *G. echinulata*. The organism´s possible dependence on an organic factor for growth was suggested in a study by Rodhe (1948), in which colonies grew in filtered lake water if non-autoclaved garden soil was added, but not if autoclaved substrate was added.

My results differ from what has been found in lakes in other parts of the world. Lake Erken is one of the northernmost sites where *G. echinulata* has been found (Wesenberg-Lund 1904), and it is possible that the northern latitude has an influence on some of the processes in the life cycle. The germination pattern, for example, may be different in lakes with higher average temperatures and no ice cover during winter.

In conclusion, it is clear that growth and division must occur in the water to explain the observed pelagic increase. Furthermore, a stationary position close to the surface was not conducive to growth, indicating that mixing within the epilimnion is essential for epilimnetic growth in *G. echinulata*.

Dominance of cyanobacteria, the importance of resting stages

Resting on the sediment has disadvantages as well as advantages. While cells that overwinter as plankton can exploit favourable conditions immediately, resting cells must first be triggered to germinate and then recolonise the water column. This introduces a problem of timing: if resting cells germinate too early the population may die out, but germinate too late will reduce the number of possible divisions, and thus fecundity. Another disadvantage associated with the benthic stage is that the sediment does not offer an ideal habitat, as resting cells are prone to parasitism (see, for instnce Chang 1983; Persson 2000), or to grazing by benthic fauna. Resting cells also risk becoming buried too deep in the sediments or translocated by the currents to sediments that are unfavourable for germination. The formation of the resting stage is also very costly to the individual. Energy investments are required for the physiological processes involved in constructing the resting cell and for building up nutrient reserves. In addition, a resting stage results in a number of ”lost” divisions during the dormancy period. However, as cyanobacteria with resting stages are often dominant in aquatic systems, especially during warm, stratified conditions, there must also be advantages. Several theories have been put forward to explain the dominance of cyanobacteria, and it seems unlikely that a single factor is responsible for cyanobacterial success. Rather, a number of factors working synergistically are likely to determine whether a bloom is formed or not. These factors include the ability to fix molecular nitrogen, resistance to zooplankton grazing, buoyancy, and a competitive advantage at low light intensities (see the review by Hyenstrand 1999). The ability to form resting stages may also contribute to cyanobacterial success. Phytoplankton with life history strategies involving benthic stages may influence a range of processes in the pelagic zone, including nutrient transport and phytoplankton succession dynamics.

Conclusion

My results show that germination of *G. echinulata* is strongly favoured by light (Paper III), and that recruitment was highest from organic-rich sediments in shallow, sheltered littoral areas, between 0-3 m deep (Paper IV). Recruitment of *Anabaena* and *Aphanizomenon* was less light dependent, yet the highest recruitment occurred from shallow sediments (0-2 m) Paper VI). This means that organic-rich sediments (0-3 m) in shallow areas are the most important seed-banks of akinete-forming cyanobacteria. The inocula

contributed only to a minor extent to the maximum pelagic populations: 4% for *G. echinulata* in the mesotrophic Lake Erken, and 0.03% for both *Anabaena* and *Aphanizomenon* in the eutrophic Lake Limmaren. This implies that processes of growth and division in the water are important for the maximum size of the pelagic population. Prolonged recruitment from the sediment strongly promoted establishment of the species in the water, especially *G. echinulata*.

Svensk sammanfattning (Summary in Swedish)

Cyanobakterier, eller blågröna alger som de också kallas, är en organismgrupp vars arter återfinns över hela jorden. De kan hittas i hav, jord, ökensand, snö och varma källor, men de flesta arterna finns ändå i sötvatten. Under sommaren brukar man höra talas om en del av de här arterna, de kan nämligen bilda så kallade vattenblomningar, särskilt när vädret är varmt och vindstilla. Cyanobacterier kan vara både stora och väldigt små, och ha många olika former. En särskild grupp av trådformiga cyanobakterier är de, som bildar ett slags vilceller vilka kallas för akineter. De här vilcellerna gör att de kan vila på sjöbottnen när förhållandena i vattnet inte är gynnsamma för tillväxt och därmed utgöra en sorts "fröbank". På våra breddgrader är det ogynnsamt att växa i vattnet t.ex. på vintern i en sjö täckt av is och snö, där vattnet är mörkt och kallt.

Syftet med den här avhandlingen var att studera livscyklerna hos de akinetbildande cyanobakterierna för att komma fram till vilka faktorer som påverkar övergången från vilcell till filament, vilka faktorer som påverkar migrationen upp i vattnet samt hur tillväxten i vattnet fungerar. Livscyklerna hos de här arterna är ganska komplicerade, och jag har använt mig av en art, *Gloeotrichia echinulata* (igelkottsalg på svenska), som modell för att ta reda på vilka faktorer som styr de olika stadierna (Figur 1). Den här arten är vanlig i sjön Erken, som är en naturligt näringsrik sjö ca 8 mil nordost om Stockholm. Gloeotrichia kan hittas i Erkens vatten från juni till september, och bildar ofta omfattande vattenblomningar med maximum i början av augusti. Två andra arter studerades också i den närbelägna sjön Limmaren. De frågor som ställdes var:

- Vilka faktorer som styr grodden, och varifrån migrerar organismerna?
- Hur lång tid det tar efter grodden innan kolonier har bildats som flyter upp i vattnet, och gror alla akineter samtidigt?
- Har antalet akineter som gror har en direkt påverkan på hur många kolonier som hittas i vattnet eller har tillväxt i vattnet större betydelse?

För att pröva vilka faktorer som styr grodden av vilceller gjordes olika laboratorieförsök. Resultaten visade att tiden på året, depositionsdjup, temperatur, ljus och omrörning alla påverkade om vilcellerna grodde eller inte. Jag kunde få akinetkolonierna att gro på laboratoriet mellan april och augusti, medan de i sjön grodde mellan juni och slutet av juli. Att nybildade vilceller inte kunde fås att gro under hösten och vintern tyder på att de behöver en mognadsperiod innan de gror, antagligen för att undvika att gro lagom till vintern. Vilceller inplockade från grunda bottnar (0—3 m) uppvisade i större utsträckning grodd än akinetkolonier från 14 m djup. Det tyder främst på att de vilceller som hittas på djupa bottnar är äldre än de som hittas på grunda bottnar. Grodden kom igång betydligt fortare med ljus och vid 17°C än 7°C, och resulterade också i fler grodda vilceller. I mörker grodde väldigt få vilceller över huvud taget. Däremot var det en stor variation av hur många vilceller som grodde även inom samma temperatur, vilket visar att det kan vara stor skillnad i livsduglighet mellan vilceller, eller stor variation av hur många som bildas i en koloni. Omrörning påverkade också antalet grodda vilceller positivt. Alla dessa faktorer tyder på att det främst är grunda bottnar som har betydelse för storleken på grodden, eftersom de värms upp fort i början av sommaren, har god tillgång till ljus, och rörs om både av fysiska orsaker och pågrund av bottenlevande djur.

I ett annat labförsök följde vi vad som händer efter grodden och kunde konstatera att variationen kan vara stor, både hur många vilceller som gror, och hur lång tid det tar innan buntar av filament eller färdiga kolonier flyter upp i vattnet. I genomsnitt tog det fyra dar innan filamentbuntarna började flyta. Vilcellerna verkade ialla fall gro inom 4 dagar i samma gamla koloni.

För att följa migrationen av nybildade kolonier i sjön gjorde vi ett försök med migrationsfällor där vi stängde in en bit av botten och samlade upp allt som rörde sej upp i vattnet från botten. Där kunde vi också se att vattendjupet har en viss betydlese, och att den största rekryteringen skedde i slutet av juni, dvs mer än en månad innan den största mängden kolonier uppmättes i vattnet. När vi följde kolonierna i vattnet kunde vi också konstatera att trots att antalet kolonier ökade i sjö hände det inte så mycket i våra påsar, trots att de borde ha samma förutsättningar. Den enda skillnaden var att de instängda kolonierna inte kunde cirkulera i vattnet, utan fick hålla sej strax under vattenytan. Det kan antingen tyda på att de fick för mycket ljus nära ytan, eller att cirkulationen gör att de får tillgång till något som gör att de kan växa bättre. När vi jämförde bidraget från migration från bottnarna med antalet kolonier i sjön såg vi att det var en ganska liten andel som var nymigrerade. I början av sommaren var migrationen viktig, men under juli skulle kolonierna behöva dela på sej mer än vad man räknat ut att de kan baserat på näringsinnehåll.

Sammanfattningsvis visar den här avhandlingen att bottnar grundare än 3 m har stor betydelse för grodden hos akinetbildande cyanobakterier, främst pågrund av god ljustillgång. Tillväxtprocesser i vattnet har också stor betydelse för hur stor blomingen kommer att bli under sommaren, men tillförseln av nya kolonier från botten är mycket viktig för hur många kolonier man hittar i sjön under början av sommaren.

Acknowledgements

I dedicate this thesis to my parents who have proved so many times that nothing is really impossible, and who have supported my choices even though I have not always been able to explain what I wanted to do

A thesis is in no way the product of one isolated person. Many people are involved more or less directly in the finished product. The decision to take up research at all, and the subject chosen, often depend on random events and the influence of specific people. My interest in Limnology was first stirred during the LMN1 course which proved to be the most interesting course I had so far taken at Uppsala University. Inspired by this to do a master´s project in Limnology, I had the luck to get Karin Rengefors as my supervisor; she then encouraged me to continue and go on to do a Ph.D. Thank you for the discussions on both the pleasures and pains of writing a thesis. This made me more prepared for the periods when endless hours produced very little text. Thank you also for both friendship and collaboration in studies. I want to go on to thank my supervisors: Kurt Pettersson, for accepting me as a Ph.D. student, finding an interesting project, and giving me lots of room to try my ideas, with occasional reality checks, and my co supervisor Peter Blomqvist for teaching me most of the things I know about phytoplankton and the principles of writing scientific papers. I have collaborated with a number of people in my studies: Anna Brunberg, Emil Rydin, and Per Hyenstrand. Thank you for numerous discussions on methods, statistics, and seemingly endless rounds of comments on the papers. I have spent many summer days those last five years at Lake Erken, and that time would not have been nearly as enjoyable without all the people there. First of all, the staff, Helena Enderskog, Anna Ericsson and Ulf Lindqvist, then my fellow Ph.D. students working at the field station, Maria Kahlert, Niklas Strömbäck, Thorsten Blenckner, Antonia Liess, and Andras Talos. Thank you for arranging barbecues at night, and for many interesting discussions. A nu mber of young students at Forskarskolan have also been there, thank you Sophie and Magdalena for making me define my projects more clearly and helping me perform some of the sampling. Rebecka Fransson also shared one of the longest summers at Erken, thank you for being good company. I also want to thank Maria Kahlert and Tommy Odelström for help with diving during the migration trap

experiment. It could not have been done without you. Not least, I want to thank all the people at the Limnology department, especially my fellow Ph.D. students, for providing a great working environment. I have now definitely arranged my last Edla party, but I plan on coming to the next one! Thank you, Ulrika Stensdotter-Blomberg, for being a friend as well as a colleague; Stina Drakare, for advice on the procedures during the last phase of thesis writing, and my room mates, Silke Langenheder and Sebastian Sobek, for a good working atmosphere. I also want to thank Stefan Djurström for making a lot of the equipment I have used in my experiments. During this time I have also had the opportunity to teach (thank you Anders Broberg) and participate as a representative in the docent committe, and in various other contexts. However, I have not spent my entire waking time at the limnology department. I have a large number of friends who have supported me through these years. The entire family Haldin-Norberg, who made me feel very welcome in Uppsala when I first arrived, and who during hard times nevertheless always had some time to spare for me. The choir at Uppsala Cathedral, the medievalist society SCA where I joined a dance group more than ten years ago and met a number of people I now count as my closest friends, Kristina Hildebrand, Jon and Lina Thorvaldson, Roger Hult, Anna Sahlén, Cecilia Anéer, Sven and Malin Nilsson-Norén, Pär Leijonhufvud and Karin Nilsson with their daughter Ylva, and many others. A number of people besides those mentioned above have helped me relax and think of other things for a while when the thesis seemed to demand more or less all my waking time: among those I especially want to thank Savina Fornsäter and Mats Johansson, and my in-laws Eva and Peter Axlund and their family.

My family have supported me through these years, despite the fact that the field season often coincides with tasks at the farm. My parents and grandparents have been a great help, making me find myself, and remember who I am during times when there has not been room for a lot of things except work. My sister, Catrin, has been a great friend, not least in making my wedding dress last summer. Finally, I want to thank my husband, Johan Elfgren, for the love and support you have given me, and for becoming increasingly better at mindreading during the final hectic months of preparations for this thesis.

References

Adhikary, SP (1996) Ecology of freshwater and terrestrial cyanobacteria. Journal of Scientific & Industrial Research 55 753-762

Baker, PD (1999) Role of akinetes in the development of cyanobacterial populations in the lower Murray River, Australia. Marine Freshwater Research 50 265-279

Barbiero, RP (1991) The contribution of benthic stages of blue-green algae to the development of planktonic populations, with special reference to Gloeotrichia echinulata. Seattle, WA, University of Washington, Ph.D. thesis,

Barbiero, RP (1993) A contribution to the life history of the planktonic cyanophyte, Gloeotrichia echinulata. Archiv fur Hydrobiologie 127 87-100

Barbiero, RP & Kann, J (1994) The importance of benthic recruitment to the population development of Aphanisomenon flos-aquae and internal loading in a shallow lake. Journal of Plankton Research 16 1581-1588

Barbiero, RP & Welch, EB (1992) Contribution of benthic blue-green algal recruitment to lake populations and phosphorous translocation. Freshwater Biology 27 249-260

Cmiech, HA, Leedale, GF & Reynolds, CS (1986) Morphological and ultrastructural variability of planktonic cyanophyceae in relation to seasonal periodicity. II. Anabaena solitaria: Vegetative cells, heterocysts, akinetes. British Phycological Journal 21 81-92

Cmiech, HA, Reynolds, CS & Leedale, GF (1984) Seasonal periodicity, heterocyst differentiation and sporulation of planktonic Cyanophyceae in a shallow lake, with special reference to Anabaena solitaria. British Phycological Journal 19 245-257

Forsell, L (1998) Migration from the littoral zone as an inoculum for phytoplankton. Archiv fur Hydrobiologie Special Issues: Advances in Limnology 51 21-27

Forsell, L & Pettersson, K (1995) On the seasonal migration of the cyanobacterium Gloeotrichia echinulata in Lake Erken, Sweden, and its influence on the pelagic population. Marine and Freshwater Research 46 287-93

Hansson, L-A (1996) Behavioural response in plants: adjustment in algal recruitment induced by herbivores. Proceedings of the Royal Society of London (B) Biological Sciences 263 1241-1244

Hansson, L-A, Rudstam, LG, Johnson, TB, Soranno, PA & Allen, Y (1994) Patterns in algal recruitment from sediment to water in a dimictic, eutrophic lake. Canadian Journal of Fisheries and Aquatic Sciences 51 2825-2833

Head, RM, Jones, RI & Bailey-Watts, AE (1999) An assessment of the influence of recruitment from the sediment on the development of planktonic populations of cyanobacteria in a temperate mesotrophic lake. Freshwater Biology 41 759-769

Hyenstrand, P (1999) Factors influencing the success of pelagic cyanobacteria. Dept. of Limnology, Uppsala, Uppsala University, Ph.D.,

Hyenstrand, P, Rydin, E & Gunnerhed, M (2000) Response of pelagic cyanobacteria to iron additions -enclosure experiments from Lake Erken. Journal of Plankton Research 22 1113-1126

Hyenstrand, P, Rydin, E, Gunnerhed, M, Linder, J & Blomqvist, P (2001) Response of the cyanobacterium Gloeotrichia echinulata to iron and boron additions - an experiment from Lake Erken. Freshwater Biology 46 735-741

Istvánovics, V, Pettersson, K, Rodrigo, MM, Pierson, D, Padisák, J & Colom, W (1993) Gloeotrichia echinulata, a colonial cyanobacterium with a unique phosphorous uptake and life strategy. Journal of Plankton Research 15 531-552

Neeley-Fisher, D, White, W & Fisher, R (1989) Fructose-induced dark germination of Anabaena akinetes. Currents in Microbiology 19 139-142

Osgood, RA (1988) A hypohesis on the role of Aphanizomenon in translocating phosphorous. Hydrobiologia 169 69-76

Perakis, SS, Welch, EB & Jacoby, JM (1996) Sediment-to-water blue-green algal recruitment in response to alum and environmental factors. Hydrobiologia 318 165-177

Persson, A (2000) Possible predation of cysts—a gap in the knowledge of
dinoflagellate ecology? Journal of Plankton Research 22 803-809

Pettersson, K, Herlitz, E & Istvánovics, V (1993) The role of Gloeotrichia echinulata in the transfer of phosphorus from sediment to water in Lake Erken. Hydrobiologia 253 123-129

Pierson, DC, Pettersson, K & Istvánovics, V (1992) Temporal changes in biomass specific photosynthesis during the summer: regulation by environmental factors and the importance of phytoplankton succession. Hydrobiologia 243/244 119-135

Roelofs, TD & Oglesby, RT (1970) Ecological observations on the planktonic cyanophyte Gloeotrichia echinulata. Limnology & Oceanography 15 224-229

Rosén, G (1981) Tusen sjöar -växtplanktons miljökrav. Stockholm, Naturvårdsverket. 119.

Rother, JA & Fay, P (1977) Sporulation and development of planktonik blue-green algae in two Salopian meres, London, Royal Society.

Ståhl-Delbanco, A & Hansson, L-A (2002) Effects of bioturbation on recruitment of algal cells from the ‘‘seed bank’’ of lake sediments. Limnology & Oceanography 47 1836-1843

Tymowski, RG & Duthie, HC (2000) Life strategy and phosphorus relations of the cyanobacterium Gloeotrichia echinulata in an oligotrophic Precambrian Shield lake. Archiv fur hydrobiologie 148 321-332

Van Den Hoek, C, Mann, DG & Jahns, HM (1995) Algae, An introduction to phycology. Cambridge, Cambridge University Press.

Wesenberg-Lund, C (1904) Studier over de danske söers plankton. I.Tekst. Copenhagen, Gyldendals boghandel.

Weyhenmeyer, G (1999) Lake Erken -Meteorological, physical, chemical and biological data and a list of publication from 1933 to 1998. Scripta Limnologica Upsaliensis B:16 51

Wyman, M & Fay, P (1986) Interaction between light quality and nitrogen availability in the differentiation of akinetes in the planktonic cyanobacterium Gloeotrichia echinulata. British Phycological Journal 21 147-153