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THE IMPORTANCE OF SHALLOW SEDIMENTS IN THE RECRUITMENT OF *ANABAENA* AND *APHANIZOMENON* (CYANOPHYCEAE)[1]

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Recruitment of *Anabaena* and *Aphanizomenon* from the sediments to the water column was investigated in shallow (1–2 m) and deep (6–7 m) areas of Lake Limmaren, central Sweden. Recruitment traps attached to the bottom were sampled weekly throughout the summer season (June through September). A comparison between the two sites shows that the largest part of the recruited cells originated from the shallow site, although recruitment occurred at all depths in the lake. There were also differences between the species, regarding the site as well as the timing of the recruitment. The contribution of the inoculum to the pelagic population was calculated to vary between 0.003% and 0.05% for the different species. From these results we conclude that shallow sediments are more important than deep ones for the recruitment and that the inoculum in Lake Limmaren is small but may still be an important factor in the population dynamics.

Key index words: **akinete; cyanobacteria; life cycle; migration; recruitment**

The cyanobacterial genera *Anabaena* and *Aphanizomenon* belong to the order Nostocales and the family Rivulariaceae, which includes filamentous, nitrogen fixing, and akinete forming species (Komárek and Anagnostidis 1989). Akinetes are morphologically and physiologically differentiated cells that arise from vegetative cells and function as resting cells. They are normally larger than the vegetative cells, with thicker cell walls and contain large reserves of building materials such as carbon and nitrogen. These reserves can be seen as glycogen granules, lipid bodies, and cyanophycin granules (Wildman et al. 1975, Cmiech and Leedale 1984). The presence of akinetes was first reported in 1856 (Carter 1856, as referred by Adams and Duggan 1999). Since then, several studies have been performed to characterize the changes taking place in the cell when akinetes are formed (Nichols and Adams 1982, Adams and Duggan 1999).

Akinetes are very tolerant to extreme conditions, such as desiccation and freezing, and they can survive buried in the sediment for many years (Livingstone and Jaworski 1980), although the level of tolerance may vary with species (Reddy 1983, Whitton 1987, Baker and Bellifemine 2000). This "seed bank" may serve as an inoculum for planktonic growth or even contribute significantly to the size of the pelagic population (Barbiero and Welch 1992, Hansson 1996, Head et al. 1999).

The process of recruitment can be divided into three different phases: germination, a potential growth phase on the sediment, and migration to the pelagic. Most studies of the recruitment process have concentrated on germination or migration and some also include conclusions about growth on the sediment before migration (Cmiech et al. 1984, Barbiero and Kann 1994, Karlsson 2003). The focus of the different studies varies according to the methodology applied. The field studies focus on the recruitment, and conclusions about germination are mostly drawn from the environmental conditions prevailing during previous weeks. Laboratory studies focus on different aspects of the germination process but do not reveal much about the actual migration from the sediment.

Akinetes may spend a variable time on the sediment before germination, depending on a number of factors such as depth of deposition, burial in the sediment, and the amount of disturbance of the sediment surface. The akinetes of *Anabaena circinalis* are known to have an active metabolism, which means that temperature, light availability, and oxygen conditions affect the viability of the akinetes (Fay 1988). Low temperature, darkness, and low oxygen levels were positive for the viability, which means that the sediment is an ideal storage place, provided that the akinetes are not buried too deep. This may also indicate that akinetes function both as a short-term (during bloom conditions) and a long-term survival trait (e.g. overwintering). Akinetes of some species may also need a period of maturation before germination may take place (Rother and Fay 1977, Karlsson 1999), whereas others have the capacity to germinate immediately if the conditions are appropriate (Rother and Fay 1977, Lynch and Shapiro 1981, Cmiech and Leedale 1984).

The principal requirement of akinete germination seems to be exposure to light, although critical intensities can be low for some species, and the appropriate wavelengths may also differ (Van Dok and Hart 1997). Experiments performed by Reddy (1984) showed two different types of akinetes in *Anabaena fertilissima* and *A. arnoldii*, one that contained everything necessary for germination, even in nutrient-deficient growth media, and one that needed a supplement of nutrients to complete germination.

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Active migration from the sediment occurs after germination when the formation of gas vacuoles is completed. Migration may also be facilitated by resuspension events, which may lift the akinetes from the surface and induce germination in the water. Active migration from the sediment surface seems to be governed by high insolation and appropriate oxygen conditions. However, the results regarding the optimal oxygen conditions vary. Some studies have indicated that oxygenated waters seem to promote the recruitment of *Aphanizomenon* spp. (Trimbee and Harris 1984, Barbiero and Kann 1994) and *Anabaena* spp. (Reynolds 1972). In contrast, a compilation of data from several different lakes indicated that recruitment of cyanobacteria in general (except possibly of *Aphanizomenon*) was enhanced by anoxic conditions over lake sediments (Trimbee and Prepas 1988).

Several authors investigated the impact of recruitment on the size of the pelagic population (Trimbee and Harris 1984, Barbiero and Welch 1992, Barbiero and Kann 1994, Hansson et al. 1994, Forsell and Pettersson 1995, Hansson 1996, Perakis et al. 1996, Head et al. 1999). The general conclusion to be drawn from these studies is that the recruitment in most cases only contributes a minor part of the pelagic biomass, although the results vary between different lakes and different species. Still, the migrating cyanobacteria may be important as an inoculum for the pelagic growth or for nutrient cycling (Istvánovics et al. 1993, Pettersson et al. 1993, Perakis et al. 1996).

Most recruitment studies have been performed with samplers modified from sedimentation traps, which are turned upside down, in some cases equipped with nets to prevent grazing losses, and placed on different distances from the sediments. Most authors have assumed that horizontal transportation of migrating cyanobacteria is negligible when using this kind of trap. Hansson (1995) performed tests with shielded traps, which indicated minor influence of horizontal transportation. Others have experienced a certain amount of "contamination" of their traps by plankton from the surrounding water (Forsell and Pettersson 1995, Head et al. 1998).

In this study we followed the migration of buoyant akinete forming cyanobacteria from the sediments of Lake Limmaren, at a shallow and a deep site. The purpose was to elucidate whether there was any difference in the timing and intensity of recruitment from the two sites. The impact of recruitment on the pelagic population was also considered. To avoid problems with horizontal transportation, especially at the shallow site, we used a new design of the traps, which were placed directly on the sediment.

MATERIALS AND METHODS

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 6 years. Thermal stratification normally only occurs for a few days during summer, but this varies depending on the weather conditions. Ice covers the lake during winter, approximately from late December through March. The lake is naturally eutrophic with frequent cyanobacterial blooms during summer, dominated by *Microcystis* spp., *Aphanizomenon flos-aquae*, and *Anabaena* spp.

Recruitment of *Anabaena* and *Aphanizomenon* from the sediments was studied at two sites in the lake, in a shallow bay (approximately 1 m water depth) and in the deepest part of the lake (approximately 7 m depth). To collect cyanobacterial filaments, leaving the sediments, migration traps were used (Brunberg and Blomqvist 2003). The traps were constructed of big transparent plastic enclosures (20-L flasks) that were open at the bottom (Fig. 1). To allow exchange of water but not of the studied cyanobacterial species, two openings were cut on the side of the flask and covered by 40 μm mesh. The traps were attached to the bottom by long spikes penetrating into the sediment and placed in triplicates in the shallow bay and in the deep part of the lake, respectively. The traps in the bay were attached to poles and the deep traps were attached by lines to an anchor, to which a surface buoy was connected. On top of each trap, a 500-mL plastic bottle filled with filtered (40 μm mesh) lake water was attached to collect filaments moving upward. The traps were installed on 31 May and sampled by scuba divers on a weekly basis throughout the summer except for the first week in June and the first 2 weeks in September, when the diving was canceled due to different reasons.

The samples were collected by the divers, who replaced the 500-mL bottles with new ones containing filtered lake water. The organisms in the collected bottles were preserved with acidified Lugol's solution (Willén 1962) and stored for counting. At each sampling occasion temperature, light intensity, and the concentration of dissolved oxygen were measured in the bottom water close to the traps. One of the traps in the bay was replaced due to damage in late July. However, the new trap installed was not initially free from pelagic cyanobacteria. The origin of cyanobacteria sampled from this trap could thus not be determined, and only results from the two intact traps at this site could be used from 2 August onward.

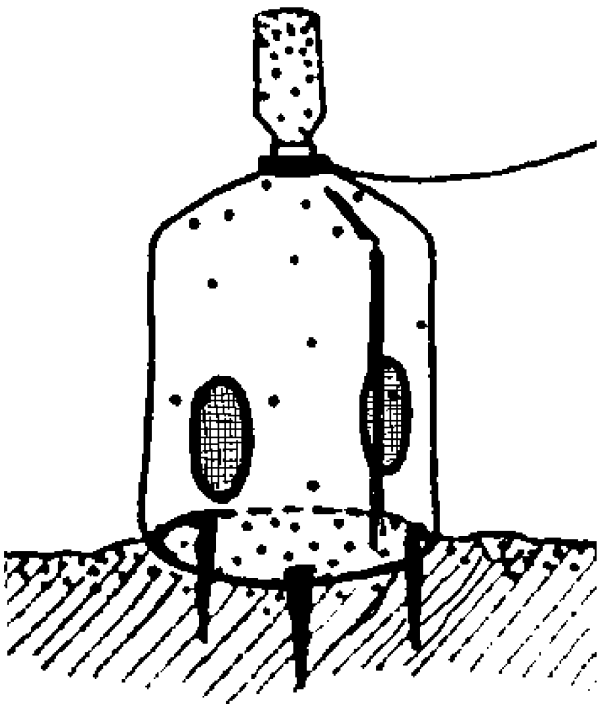

FIG. 1. The migration traps used in Lake Limmaren in 1999.

The samples were counted in an inverted microscope. Species composition of *Anabaena* and *Aphanizomenon* was examined. The number of cells in each filament of *Anabaena* was counted, and the lengths of the *Aphanizomenon* filaments were measured. Differences in abundance between shallow and deep traps at the different dates and over the entire season were tested with Wilcoxon's signed ranks test and regarded as statistically significant at a level of $P < 0.05$.

The pelagic cyanobacterial population in the lake was monitored by integrated sampling according to Blomqvist (2001). Phytoplankton samples were preserved by acidified Lugol's solution and counted using an inverted microscope. Numbers and lengths of filaments of cyanobacteria were also recorded.

RESULTS

Three species of filamentous akinete forming cyanobacteria were caught in the recruitment traps (Fig. 2): *Aphanizomenon flos-aquae* (L.), *Anabaena circinalis* (Rabenhorst), and *Anabaena* sp. The latter species had cells that were 5–10 μm long and 10–15 μm wide. The filaments were straight or very slightly spiraling with no tapering end cells and no visible mucilage. The filaments were predominantly found as single filaments and not aggregated into colonies. This taxon could not be determined to species level because of the lack of akinetes in the preserved material (Whitton and Brook 2002). All three species were recruited from both depths, although the recruitment in all three cases was significantly higher at the shallow site.

Aphanizomenon flos-aquae had its main recruitment period between 21 June and 31 August, although a few filaments were recruited as late as 20 September (1.7×10^6 μm · m^{-2} in the bay and 0.57×10^6 μm · m^{-2} at the deep site; Fig. 2a). Based on the numbers of filaments caught, the recruitment period could be divided into two parts, with similar patterns on both sites, but with lower numbers from the deep site, especially during the second period. The first filaments were found in the pelagic samples on 19 May, but the population increased slowly until the beginning of July and reached its peak on 26 July, 1 week after the first peak of migrating colonies.

Anabaena circinalis had a clearly defined period of recruitment between 21 June and 16 August (Fig. 2b). There were two peaks of migration at the shallow site, the first peak occurring on 12 July and the second on 26 July. At the deep site, on the other hand, there was no or very low recruitment before 19 July, when the maximum value was recorded. The pelagic population of *A. circinalis* started to increase on 2 June and reached its seasonal maximum on 29 June, 2 weeks after migration had started in the traps but 2 weeks before the first peak of migration.

Anabena sp. also had a defined period of recruitment between 21 June and 26 July (Fig. 2c), with occasional single filaments appearing in the traps until 16 August (0.9×10^6 cells · m^{-2}). The maximum recruitment occurred in mid-July. The increase in pelagic abundance started in the beginning of June, with maximum cell numbers occurring on 28 June, only 1 week after migration started. Hence, the maximum recruitment of filaments occurred while the pelagic population was declining.

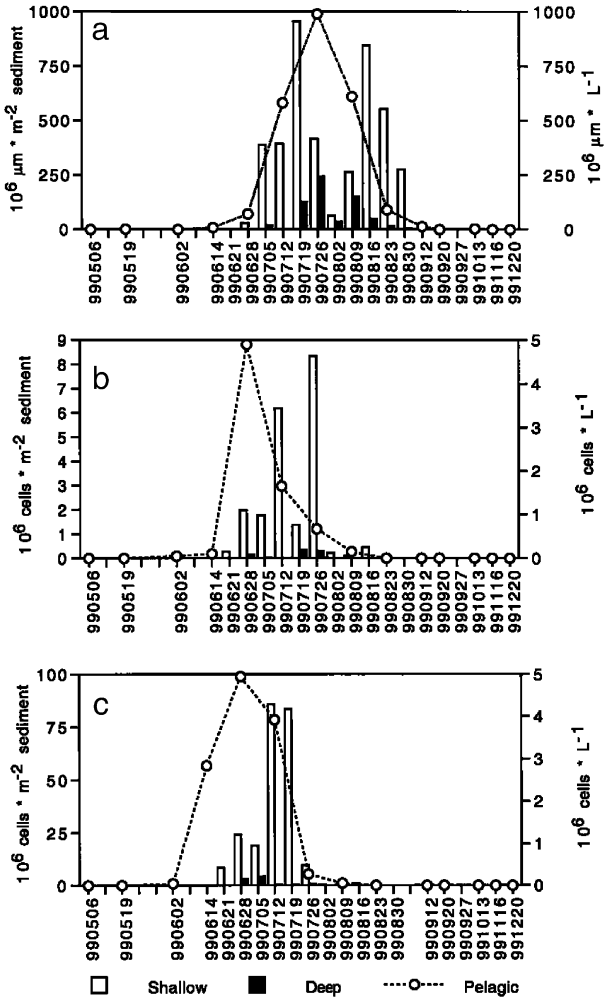

FIG. 2. Recruitment of cyanobacteria from shallow vs. deep sediments (bars, left scale) and pelagic abundance (open circles, right scale) in lake Limmaren during 1999. (a) *Aphanizomenon flos-aquae* (total filament length), (b) *Anabaena circinalis* (number of cells), and (c) *Anabaena* sp. (number of cells). Note that pelagic abundance is shown from April to December, whereas recruitment traps were operating only during the summer period, from June to September.

Light penetration down to the sediments at the deep station was very poor. Of the 14 sampling occasions, measurable light intensities were only recorded three times, and then at very low levels (< 1 μmol photons · m^{-2} · s^{-1}). A generalization of the compensation level for photosynthesis (1% of incoming light) (Rodhe 1965) was used to calculate the compensation depth in the lake to about 3 m depth. At the shallow site, a maximum light intensity at the bottom of 140 μmol photons · m^{-2} · s^{-1} was recorded in June. During July and August, light intensities varied between 1 and 40 μmol photons · m^{-2} · s^{-1} at the different sampling occasions. The 1% level of light penetration was always deeper than the actual water depth. Hence, we conclude that light intensities high enough to sustain photosynthetic

activity were present at the surface sediments of the shallow bay throughout the summer. The water temperature close to the bottom did not differ between the sites and varied between 14 and 21° C, with maximum occurring in July. No anoxic conditions occurred in the water column, although low concentrations (about 2 mg $O_2 \cdot L^{-1}$) were recorded occasionally at both sites in August.

DISCUSSION

This study shows that recruitment of filamentous cyanobacteria may take place at all depths in Lake Limmaren, although shallow sediments seem to be the more important recruitment site. Recruitment of the three species investigated occurred to a much higher extent in the shallow bay. The sediments shallower than 2 m have been largely ignored in many investigations, but our study indicates that a substantial part of the total recruitment may originate from this part of a lake. Several factors may contribute to this. First, the concentration of akinetes might be higher in shallow than in deep sediments. This was the case for *Gloeotrichia* akinetes in the nearby Lake Erken (Forsell 1998). However, data from Lake Limmaren show that the survival of other cyanobacteria within the sediments do not differ substantially between shallow and deep areas, and even vegetative *Microcystis* colonies are abundant in large amounts at both sites included in this investigation (Brunberg and Blomqvist 2003).

Nevertheless, earlier studies showed that akinetes seem to be more resistant to extreme conditions like desiccation and freezing than vegetative filaments (Whitton 1987, Forsell 1998), although exceptions are known (Baker and Bellifemine 2000). This makes the very shallow sediments a potential source for recruitment, because the conditions present on the sediment (i.e. high temperatures early in the season and more light than at deeper sites) should be favorable for germination earlier after ice-out than in deeper parts of the lake. Generally, the optimum temperature for germination corresponds to the optimum temperature for cell growth and varies between species (Baker and Bellifemine 2000). In *Anabaena circinalis* optimum temperature for growth, as well as for germination, was found to be 22–24° C. However, germination occurred at diminishing rates down to 15° C and up to 30° C (Fay 1988). This could be one explanation for different germination rates at different depths in lakes, especially in spring and early summer when the shallow sediments are exposed to higher temperatures. In Lake Limmaren, maximum recruitment rates coincided with maximum water temperature of approximately 18–21° C during July and early August. However, the differences between shallow and deep areas cannot be explained by this factor, because the water temperature was similar at both sampling sites.

According to some earlier studies, high insolation and oxic conditions close to the sediment favor the recruitment of *Anabaena* and *Aphanizomenon* (Reynolds 1972, Trimbee and Harris 1984, Barbiero and Kann 1994). Yet other studies indicated that with the possible exception of *Aphanizomenon*, the recruitment of cyanobacteria in general was favored by anoxic conditions over lake sediments (Trimbee and Prepas 1988). These ambiguous results can be compared with the results found in this study, which indicate that light is not an absolute prerequisite in direct connection with recruitment, especially not for *Aphanizomenon*, and that substantial recruitment may occur despite oxic conditions close to the sediment surface. Hence, the question of exact mechanisms for germination and subsequent recruitment still needs further studies to be answered.

The maximum abundance of pelagic *A. flos-aquae* in Lake Limmaren during 1999 was recorded on 26 July, when 989×10^6 cells $\cdot L^{-1}$ were found. Multiplying with the lake volume (27.3 Mm^3) gives a total abundance of 2.7×10^{19} cells in the lake. Assuming that our recruitment data are representative for shallow and deep areas in general and using the 3-m depth level ($\approx$1% light level) as the border between these areas, the total recruitment of *A. flos-aquae* in Lake Limmaren up until the maximum pelagic population was recorded may be estimated to be 4.9×10^{15} cells, of which 85% originate from bottoms of $\leq$ 3 m depth. Despite the fact that the recruitment most likely is overestimated in our calculation (we assume that soft sediments accumulating akinetes are distributed over the entire lake), this benthic inoculum constitutes only 0.02% of the maximum pelagic population. A corresponding calculation for *Anabaena circinalis* gives a recruitment of 3.9×10^{12} cells, of which 94% originated from bottoms of $\leq$ 3 m depth. The contribution of recruitment to the maximum summer population found at 28 June was 0.003%. *Anabaena* sp. had a recruitment of 6.2×10^{13} cells, of which 91% originated from bottoms of $\leq$ 3 m depth. The recruitment compared with the maximum summer population found at 28 June was 0.05%.

The calculations above show that, in general, the shallow sediments seem to be important for recruitment, especially for the two *Anabaena* species. However, during the period from when traps were deployed in the lake and until the maximum pelagic populations were found, the migrated cells directly contributed a very small part of the populations of the three species studied. The percentage of recruitment was low also compared with most earlier investigations, which generally report a contribution of a few percent to pelagic cyanobacteria (Trimbee and Harris 1984, Barbiero and Welch 1992). Barbiero and Welch (1992) found an average contribution of 0.62% for both *Anabaena* and *Aphanizomenon* in Green Lake, Oregon (mean depth, 3.9 m; maximum depth, 8.8 m). Their traps were deployed between 3 and 6 m and 6 and 8.8 m, assuming that recruitment from sediments of less than 3 m depth was negligible. Barbiero and Kann (1994), on the other hand, found higher values (8%) of contribution from the sediment in the shallow (mean depth, 2.4 m), hypereutrophic Agency Lake, Oregon using shielded traps.

Both lakes were largely unstratified, although the shallower lake probably was more completely mixed.

A varying degree of contamination to recruitment traps, originating from lateral transport of phytoplankton, has been experienced in different lake studies, ranging from negligible to considerable (Hansson 1996, Head et al. 1998). The amount of this disturbance probably depends at least to some extent on lake morphometry and the depth of the sampling site. The lakes where migration traps have been used show a range of different morphometry, nutrient status, and mixing regimes. Sampling depths have ranged from 2 to 23 m in different studies, with most traps deployed between 2 and 10 m.

The design of the traps used in this experiment makes it possible to avoid the problem of horizontal transportation and thus may give more reasonable estimates of inoculation. On the other hand, by providing shelter the traps may to some extent exclude the occurrence of resuspension, which may result in a lower total migration in the traps than in the rest of the lake. Resuspension may be an important criterion for recruitment of akinetes (Reynolds 1972, Trimbee and Harris 1984), and some studies indicate that recruitment of resting cells is favored by resuspension or bioturbation (Baker 1999, Kremp 2001, Karlsson-Elfgren et al. 2004). Our traps had net-covered openings to promote water exchange, but resuspension was probably reduced compared with the surrounding bottom areas. On the other hand, gas-vacuolated organisms like *Aphanizomenon* and *Anabaena* might be less dependent on resuspension events for recruitment than other plankton such as dinoflagellates and diatoms. In addition, less restricted resuspension would probably also increase the difference in recruitment between the two stations, because resuspension is higher in the shallow bay than in the rest of the lake, thus giving us the same overall result, that recruitment is higher from the shallow sediments.

The light conditions recorded during the sampling period indicate that very small amounts of light may be enough to initiate germination and recruitment. Hence, as far as the light conditions are considered, recruitment may well have started earlier in spring, possibly even under the ice cover (ice-out occurred toward the end of March), promoted by higher insolation to the bottom before plankton densities decreased the water transparency. Another indication of this is that both the *Anabaena* species had their maximum abundances in the pelagic population before the peak in migration was detected by the traps, which might be explained by recruitment earlier in the season before the traps were deployed (31 May). However, this potential early recruitment was at least not large enough to show up in the pelagic sampling program during April and May. To be detected in the pelagic sampling, a minimum of 1000 cells $\cdot$ L^{-1} need to be present. This represents an average recruitment of 4.6×10^6 cells $\cdot$ m^{-2} in the whole lake and can be compared with the first recruitment that we recorded in June, 0.26×10^6 cells $\cdot$ m^{-2} for *A. circinalis* and 8.38×10^6 cells $\cdot$ m^{-2} for *Anabaena* sp. Hence, regardless of the source of the first pelagic colonies of the season (vegetatively overwintered in the water, actively migrated from the sediments, or recruited during resuspension events), the growth dynamics of these species in the lake water must have been very rapid.

Because the percentage of pelagic abundance contributed by active migration seems to be very small, the question arises yet again regarding the ecological role of this process in the population dynamics of cyanobacteria. One alternative could be that the newly germinated filaments take up phosphorus from the sediment before migrating (Barbiero and Welch 1992, Brunberg and Boström 1992, Pettersson et al. 1993) and in that way maintain the pelagic population. It may also be a long-term mechanism providing a seed bank for times when vegetative filaments are lost through outflow from the lake. Recruitment may potentially prolong the pelagic presence of the species through input of newly migrated filaments or ensure that there is an inoculum for a bloom whenever favorable conditions occur during the summer season. This is supported by our results showing that all three species continued to migrate throughout the decline of the pelagic population.

In conclusion, migration of cyanobacteria from sediments, albeit quantitatively small, may still play an important role in their population dynamics. The shallow sediments should not be overlooked in future studies of this phenomenon.

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Adams, D. G. & Duggan, P. S. 1999. Tansley review no. 107. Heterocyst and akinete differentiation in cyanobacteria. *New Phytol.* 144:3–33.

Baker, P. D. 1999. Role of akinetes in the development of cyanobacterial populations in the lower Murray River, Australia. *Mar. Freshwater Res.* 50:265–79.

Baker, P. D. & Bellifemine, D. 2000. Environmental influences on akinete germination of *Anabaena circinalis* and implications for management of cyanobacterial blooms. *Hydrobiologia* 427: 65–73.

Barbiero, R. P. & Kann, J. 1994. The importance of benthic recruitment to the population development of *Aphanizomenon flos-aquae* and internal loading in a shallow lake. *J. Plankton Res.* 16:1581–8.

Barbiero, R. P. & Welch, E. B. 1992. Contribution of benthic blue-green algal recruitment to lake populations and phosphorous translocation. *Freshwater Biol.* 27:249–60.

Blomqvist, P. 2001. A proposed standard method for composite sampling of water chemistry and plankton in small lakes. *Environ. Ecol. Stat.* 8:121–34.

Brunberg, A.-K. & Blomqvist, P. 2003. Recruitment of *Microcystis* (Cyanophyceae) from lake sediments—the importance of littoral inocula. *J. Phycol.* 39:58–63.

Brunberg, A.-K. & Boström, B. 1992. Coupling between benthic biomass of *Microcystis* and phosphorus release from the sediments of a highly eutrophic lake. *Hydrobiologia* 235/236: 375–85.

Cmiech, H. A. & Leedale, G. F. 1984. Morphological and ultrastuctural variability of planktonic Cyanophyceae in relation to seasonal periodicity. *Br. Phycol. J.* 19:259–75.

Cmiech, H. A., Reynolds, C. S. & Leedale, G. F. 1984. Seasonal periodicity, heterocyst differentiation and sporulation of planktonic Cyanophyceae in a shallow lake, with special reference to *Anabaena solitaria*. *Br. Phycol. J.* 19:245–57.

Fay, P. 1988. Viability of akinetes of the planktonic cyanobacterium *Anabaena circinalis*. *Proc. R. Soc. Lond. B* 234:283–301.

Forsell, L. 1998. Migration from the littoral zone as an inoculum for phytoplankton. *Arch. Hydrobiol. Spec. Iss. Adv. Limnol.* 51: 21–3.

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. *Mar. Freshwater Res.* 46:287–93.

Hansson, L.-A. 1995. Diurnal recruitment patterns in algae: effects of light cycles and stratified conditions. *J. Phycol.* 31:540–6.

Hansson, L.-A. 1996. Algal recruitment from lake sediments in relation to grazing, sinking, and dominance patterns in the phytoplankton community. *Limnol. Oceanogr.* 41:1312–23.

Hansson, L.-A., Rudstam, L. G., Johnson, T. B., Soranno, P. A. & Allen, Y. 1994. Patterns in algal recruitment from sediment to water in a dimictic, eutrophic lake. *Can. J. Fish. Aquat. Sci.* 51:2825–33.

Head, R. M., Jones, R. I. & Bailey-Watts, A. E. 1998. Akinete germination and recruitment of planktonic cyanobacteria from lake sediments. *Verh. Int. Verein. Limnol.* 26:1711–5.

Head, R. M., Jones, R. I. & Bailey-Watts, A. E. 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 Biol.* 41:759–69.

Istvánovics, V., Pettersson, K., Rodrigo, M. M., Pierson, D., Padisák, J. & Colom, W. 1993. *Gloeotrichia echinulata*, a colonial cyanobacterium with a unique phosphorous uptake and life strategy. *J. Plankton Res.* 15:531–52.

Karlsson, I. 1999. On the germination of the akinete-forming cyanobacterium *Gloeotrichia echinulata,* in Lake Erken, Sweden. *Algol. Stud.* 94:175–80.

Karlsson, I. 2003. Benthic growth of *Gloeotrichia echinulata*. *Hydrobiologia* 506:189–93.

Karlsson-Elfgren, I., Rengefors, K. & Gustafsson, S. 2004. Factors regulating recruitment to the water column in the bloom-forming cyanobacterium *Gloeotrichia echinulata*. *Freshwater Biol.* 49:265–73.

Komárek, J. & Anagnostidis, K. 1989. Classification systems of Cyanophytes 4—Nostocales. 4. The family Rivulariaceae. *Arch. Hydrobiol.* 82(suppl.):289–92.

Kremp, A. 2001. Effects of cyst resuspension on germination and seeding of two bloom-forming dinoflagellates in the Baltic Sea. *Mar. Ecol. Prog. Ser.* 216:57–66.

Livingstone, D. & Jaworski, G. H. M. 1980. The viability of akinetes of blue-green algae recovered from the sediments of Rostherne Meer. *Br. Phycol. J.* 15:357–64.

Lynch, M. & Shapiro, J. 1981. Predation, enrichment and phytoplankton community structure. *Limnol. Oceanogr.* 26:86–102.

Nichols, J. M. & Adams, D. G. 1982. Akinetes. *In* Carr, N. G. & Whitton, B. A. [Eds.] *The Biology of Cyanobacteria*. Blackwell scientific Press, Oxford, pp. 387–412.

Perakis, S. S., Welch, E. B. & Jacoby, J. M. 1996. Sediment-to-water blue-green algal recruitment in response to alum and environmental factors. *Hydrobiologia* 318:165–77.

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* 253:123–9.

Reddy, P. M. 1983. Effects of temperature pre-treatment, desiccation and aging on the viability of spores of halophilic blue-green algae. *Hydrobiologia* 106:235–40.

Reddy, P. M. 1984. Effect of distilled water pre-treatment, nitrate and phosphate on germination of spores of two blue-green algae. *Arch. Hydrobiol.* 100:261–5.

Reynolds, C. S. 1972. Growth, gas vacuolation and buoyancy in a natural population of a planktonic blue-green alga. *Freshwater Biol.* 2:87–106.

Rodhe, W. 1965. Standard correlations between pelagic photosynthesis and light. *Mem. Ist. Ital. Idrobiol* 18(suppl):365–81.

Rother, J. A. & Fay, P. 1977. Sporulation and development of planktonik blue-green algae in two *Salopian meres*. *Proc. R. Soc. Lond. B* 196:317–32.

Trimbee, A. & Harris, G. P. 1984. Phytoplankton population dynamics of a small reservoir: use of sedimentation traps to quantify the loss of diatoms and recruitment of summer bloom-forming blue-green algae. *J. Plankton Res.* 6:897–918.

Trimbee, A. & Prepas, E. E. 1988. The effect of oxygen depletion on the timing and magnitude of blue-green algal blooms. *Verh. Int. Verein. Limnol.* 23:220–6.

Van Dok, W. & Hart, B. T. 1997. Akinete germination in *Anabaena circinalis* (Cyanophyta). *J. Phycol.* 33:12–7.

Whitton, B. A. 1987. Survival and dormancy of blue-green algae. *In* Hennis, Y. [Ed.] *Survival and Dormancy of Microorganisms*. John Wiley & Sons, New York, pp. 109–67.

Whitton, B. A. & Brook, A. J. [Eds.] 2002. *The Freshwater Algal Flora of the British Isles*. Cambridge, The Natural History Museum, 702 pp.

Wildman, R. B., Loescher, J. H. & Winger, C. L. 1975. Development and germination of akinetes of *Aphanizomenon flos-aquae*. *J. Phycol.* 11:96–104.

Willén, T. 1962. Studies on the phytoplankton of some lakes connected with or recently isolated from the Baltic. *Oikos* 13: 169–99.