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Factors regulating recruitment from the sediment to the water column in the bloom-forming cyanobacterium *Gloeotrichia echinulata*

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SUMMARY

1. The influence of light, temperature, sediment mixing and sediment origin (water depth) on the recruitment of the cyanobacterium *Gloeotrichia echinulata* was examined in the laboratory.
2. Light and temperature were the most important factors initiating germination in *G. echinulata*.
3. The extent of germination (recruited biovolume) was mainly regulated by temperature and sediment mixing. Furthermore, sediment mixing significantly enhanced the frequency of observed heterocysts and colonies.
4. Despite the fact that the deep and shallow sediments contained a similar number of akinete colonies, the highest recruitment occurred from shallow sediments, indicating that akinetes from shallow sediments have a higher viability than those from deeper parts of the lake.
5. Our results support the hypothesis that shallow sediments are more important than profundal sediments for the recruitment of *G. echinulata* to the pelagic zone.

Keywords: akinete, germination, *Gloeotrichia echinulata*, migration, recruitment, resting stages

Introduction

Organisms with a life cycle, in which part of the time is spent on the sediment as resting stages and part of the time in the pelagic, have recently received increased interest (see reviews by Marcus & Boero, 1998; Schindler & Scheuerell, 2002). A benthic–pelagic life cycle has an ecological significance as an adaptive strategy for survival, as well as a biogeochemical or environmental significance (Barbiero & Welch, 1992). It may also influence the succession of different species in the plankton (McQuoid & Hobson, 1995; Rengefors & Anderson, 1998) and be part of the explanation of the dominance of some species (e.g. Hansson *et al.*, 1994; Head, Jones & Bailey-Watts, 1999). The influence of benthic resting stages on pelagic populations of cyanobacteria has been addressed in a number of studies during the last decade (Barbiero & Welch, 1992; Hansson *et al.*, 1994; Head *et al.*, 1999). These studies have shown large variations in the importance of recruitment to the pelagic population depending on the species studied and the lake in question. *Gloeotrichia echinulata* (Smith) Richter is the only filamentous cyanobacterial species in which pelagic populations have been shown to be substantially influenced by recruitment from the sediment, *c.* 40% of the weekly increase (Barbiero & Welch, 1992) compared with 8.2% of the weekly increase of *Aphanizomenon flos-aquae* Linnaeus (Barbiero & Kann, 1994).

Gloeotrichia echinulata is an akinete-producing, filamentous cyanobacterium, predominantly forming spherical colonies that can be several millimetres in

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diameter (Forsell & Pettersson, 1995). It often forms blooms in moderately eutrophic lakes during summer and in Lake Erken, Sweden, the regular occurrence of *G. echinulata* blooms has been described since the 1940s (e.g. Skuja, 1948; Nauwerck, 1963). Its life cycle comprises both pelagic and benthic stages, differentiating it from other *Gloeotrichia* species, which are mainly benthic (Komárek & Anagnostidis, 1989). Benthic–pelagic coupling may have several implications for both the autoecology of this species and for the lake ecosystem. These include survival during unfavourable conditions (e.g. Barbiero, 1993) and regulation of seasonal succession (e.g. Baker, 1999). The switch between the benthic and pelagic life stage in *G. echinulata* is preceded by germination of the akinetes, followed by a period of growth on the sediment (Roelofs & Oglesby, 1970; Barbiero, 1993) before gas vesicles are formed and the new colonies migrate up into the water. Recruitment of akinete-forming cyanobacteria from the sediment into the water column can be active or passive. In this paper, recruitment is defined as the entire process from germination to migration from the sediment, although it is actually migration that has been measured in most other studies. Active recruitment is when vegetative colonies or filaments migrate actively into the water column through the formation of gas vesicles (Trimbee & Harris, 1984; Barbiero & Welch, 1992; Hansson, 1996). Passive recruitment takes place when turbulence resuspends the resting cells to an environment conducive of vegetative growth and formation of colonies subsequently takes place in the water column (Lund, 1954; Reynolds, 1972). To date, there have been few studies aimed at determining how these different strategies can be used by the same species.

Recruitment in cyanobacteria has been related to a number of factors including light (Kezhi, Guoliang & Cheng, 1985; Van Dok & Hart, 1997), temperature (Konopka & Brock, 1978; Robarts & Zohary, 1987), oxygen (Trimbee & Harris, 1984; Barbiero, 1993) and water mixing (Robarts & Zohary, 1987). However, all previous studies of factors that regulate the germination and migration of *G. echinulata*, are based on field observations and correlations. Here, we present results from a laboratory experiment, designed to identify the key factors initiating or promoting recruitment. Our hypothesis is that shallow sediments are more important than profundal sediments in the recruitment of *G. echinulata*. This includes the expectation that light and temperature are most important in the recruitment of this species.

Methods

Study site

Lake Erken, Sweden (59°25′N, 18°15′E), is naturally moderately eutrophic (yearly mean total nitrogen 657 ± 127 μg L^{-1}, yearly mean total phosphorus 27 ± 9.6 μg L^{-1}), with an area of 24 km^2, a mean depth of 9 m and a maximum depth of 21 m (Håkanson, 1978). The lake is covered by ice from December to April on average and the water is thermally stratified during the summer months (Weyhenmeyer, 1999).

Sampling

Triplicate sediment samples were collected from three sites in Lake Erken (depths 1.5, 4.5 and 14 m) on 7 May 2001 using a core sampler with a diameter of 7 cm. Temperature loggers at the sampling sites recorded a temperature of *c.* 7 °C (6.6, 6.8 and 7.2 °C) at all three depths. Cores were then sliced into 2 cm sections, of which the top 2 cm were retained in plastic containers and stored in the laboratory at 4 °C in darkness. Prior to initiating the experiment, aliquots were taken out from each sediment sample for akinete colony enumeration. In Lake Erken, akinetes are to a large extent retained in the aggregate of partly degraded filaments and mucus, which are deposited on the sediment each autumn. These aggregates are here referred to as akinete colonies.

Experimental design

A four-way factorial design with three replicates for each treatment was used in this experiment. The treatments were sediment origin (from 1.5, 4.5 and 14 m water depth), temperature (7 or 17 °C), light (light or dark) and sediment mixing (mixing or no mixing). The sediments had a water content of 95, 85 and 80% at 1.5, 4.5 and 14 m, respectively. The triplicate sediment samples (from each water depth) were combined for the germination experiment and 3-mL sediment was added to a test tube. Twenty-five millilitres of filtered (Whatman GF/C, 1.2 μm;

Whatman, Maidstone, U.K.) lake water was then added to each tube and the tubes that represented the dark treatments were covered with aluminium foil. The tubes were kept at constant temperature (7 or 17 °C) and 16 : 8 light : dark cycle (at a light intensity of 8 μmol photons m^{-2} s^{-1}). The 7 °C treatment lasted for 20 days but the 17 °C treatment was stopped after 16 days due to a breakdown of the climate chamber. In the field, the amount and type of sediment mixing due to bioturbation would depend on the benthic fauna present at the different depths. To reduce the variation and still induce sediment mixing, manual resuspension was performed immediately following sampling with a pipette. Every second day, 20 mL of water was withdrawn from each test tube and new water added (filtered lake water), either carefully to avoid disturbing the sediments, or rapidly to stir the sediment. Samples were fixed with Lugol's solution and stored for counting. All sampling was performed in red light (*c.* 650 nm, 0.05 μmol photons m^{-2} s^{-1}). All samples were subsequently counted in settling chambers using an inverted microscope. The number and length of single filaments were noted, filament bundles were measured for average filament length and the number of filaments in the bundles estimated in the entire 20 mL sample. Colonies were measured for average radius (filament length) and the number of filaments was estimated. The biovolume was then calculated using these data (Hillebrand *et al*., 1999).

Statistical analyses

To evaluate the results, graphs and repeated ANOVA were examined visually for the analysis of time series and treatments. The data have to be interpreted with caution because of non-homogenous variances, as many samples had zero recruitment. A non-parametric test (logistic regression) was also performed, evaluating the effect of the different treatments on presence or absence of *G. echinulata* in the samples. The statistical analyses were performed with the statistical analysis program JMP version 4.

Results

The initial concentrations of akinete colonies in the different lake sediments (48 ± 5 mL^{-1} at 1.5 m, 42 ± 6 mL^{-1} at 4.5 m and 50 ± 4 mL^{-1} at 14 m) did not differ significantly. The presence of *G. echinulata* filaments was recorded in all factor combinations except for 7 °C, both dark and light, 1.5 m, without sediment mixing and 7 °C/14 m/dark/with sediment mixing, although in some treatments (without sediment mixing and especially at 7 °C), the number of filaments was very low. A MANOVA between subjects *F*-test for the whole experiment showed a significant effect (<0.05) of a number of single factors and combinations of factors on germination (Table 1).

Table 1 MANOVA between subjects *F*-test for the whole experiment, showing which factors had a significant effect on the observed biovolume in the different treatments

Factor	Value	Exact *F*	Number (d.f.)	Density (d.f.)	*P* > *F*
T	0.1860	116	1	624	<0.0001
SM	0.0750	46.92	1	624	<0.0001
T*SM	0.0520	39.91	1	624	<0.0001
L*SM	0.0016	6.21	1	624	0.0130
L	0.0580	36	1	624	<0.0001
SO	0.0470	14.7	2	624	<0.0001
T*SO*L	0.0120	3.81	1	624	<0.0226

T, temperature; L, light; SM, sediment mixing; SO, sediment origin.

Light and dark treatments

Light significantly increased the response in recruited filaments of *G. echinulata*, while dark treatments showed very low numbers of filaments, if any, except for the dark treatment with sediment mixing at 17 °C. The first filament in the treatments with light was observed on day 2 (Table 2). The first filament bundle and colony was found on day 6 and the highest biovolume occurred on day 12 (Fig. 1a). Heterocysts were observed from day 4. All recorded first observations occurred at 17 °C with sediment mixing (Fig. 1a). Filaments and bundles were observed in two of the dark treatments with the highest biovolume occurring at 17 °C with sediment mixing on day 10 (Fig. 1e). In the treatments exposed to light, temperature and sediment mixing were the most important factors giving a significantly higher result until day 12 when sediment origin also became a positive significant factor (Table 3). The presence or absence of light significantly affected the presence of germinated *G. echinulata* in the treatments (logistic regression, Pearson $R^2 = 0.232$). Further analysis showed that light had a positive effect and that dark

Table 2 First recorded occurrence (sampling day) of filaments, bundles, heterocysts and colonies for the different treatments

	7 °C	17 °C	Light	Dark	With mixing	Without mixing
First recorded filament	8	2	2	*	2	6
First recorded bundle	12	6	6	*	6	8
Highest biovolume	18	12	12	8*	12	16
First recorded colony	None	6	6	*	6	10
First recorded heterocyst	None	4	4	*	4	8

*Very low biovolume of *G. echinulata* was observed in the dark treatments, except for 17 °C with sediment mixing between day 6 and 10.

had no significant positive effect ($P < 0.05$) except at 17 °C with sediment mixing.

Temperature

High temperature significantly shortened the time period preceding germination, as well as the development of bundles, colonies and heterocysts. At 7 °C, the first filament was observed on day 8 and the first bundle was observed on day 12, in treatments with light and sediment mixing. The highest biovolume was found on day 18 in the presence of light and sediment mixing (Fig. 1c). In that treatment, the biovolume consisted, to a large extent, of bundles by day 18, while in light without sediment mixing the filament volume dominated over the bundle volume (Fig. 1d). After day 20, the opposite relationship was observed. No colonies or heterocysts were observed at 7 °C. At 7 °C, no significant factor could be found until day 12, when depth and light could explain *c.* 60% of the variation (Table 3). Very few filaments were found in the dark treatment with sediment

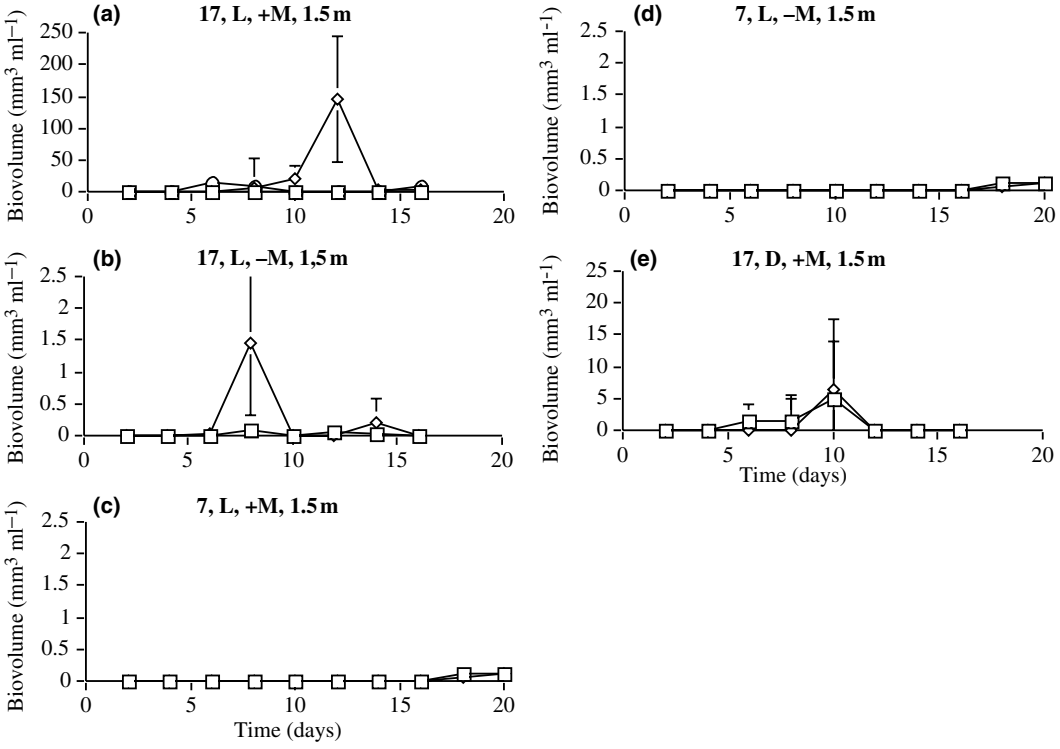

Fig. 1 Average recruited biovolume ($mm^3\ mL^{-1}$) per sampling day of *G. echinulata* from 1.5 m sediment, illustrating the effect of five different treatments. The 1.5 m samples are shown because the highest recruitment occurred from this sediment. Biovolume is divided into filaments (—□—), bundles (- - -◇- - -) and colonies (- -○- -). Note that the scales are of different magnitude. Error bars show standard deviation. Treatments (a–d) with light and (e) without light, which made a significant contribution to the recruited biovolume. Abbreviations used in the figure are: 7 (7 °C), 17 (17 ° C), L (light), D (dark) and +/− M (with or without mixing).

Table 3 Standard least squares for log total average biovolume, percentage of variation explained for the different treatments and significant factors ($F < 0.05$) for each sampling day

Treatments/ day	2	4	6	8	10	12	14	16
Light	ns	33% T, SM, T*SM	87% T, SM, T*SM	68% T, SM, T*SM	77% T, SM, T*SM	57% SO, T, T*SO, SM	55% T, SO, T*SM	26% SO, T*SO
+ Mixing	ns	32% T	88% T	83% T	78% T	71% T, L, SO*L	65% T, L, SO	44% L, SO
− Mixing	ns	ns	70% T, SO, T*SO, L	ns	39% T	19% T	25% L	ns
7 °C	ns	ns	ns	ns	ns	60% SO, SO*L, L	56% SO, SO*L, L	64% SO, SO*L, L, SO*SM
17 °C	ns	26% SM, L	70% SM, SO, SO*SM, L	48% SM	24% SM	18% SM	35% L, SM	6% L
Entire study	ns	34% T, SM, T*SM	86% T, SM, T*SM, SO, L	69% T, SM, T*SM	68% T, SM, T*SM	52% T, SO*L, SO, T*SO, SM	52% L, T, SO	31% L, SO

ns, Not significant; T, temperature; L, light; SM, sediment mixing; SO, sediment origin.

Table 4 The presence (1) or absence (0) of colonies and heterocysts in 17 °C and light, which was the only combination of factors in which they occurred

	With sediment mixing		Without sediment mixing	
Day	Heterocyst	Colony	Heterocyst	Colony
2	0	0	0	0
4	0	0	0	0
6	1	1	1	0
8	1	1	1	0
10	1	0	0	0
12	1	0	0	0
14	1	0	1	0
16	1	1	1	1

mixing at 7 °C, otherwise no filaments were found in the dark at low temperature. In contrast to the low temperature treatment, at 17°C the first filaments were observed already on day 2 and the first heterocyst was recorded on day 4 (light and sediment mixing treatment). The highest biovolume was found as bundles (10-fold higher than the maximum biovolume at 7 °C) on day 12 and the first recorded colony was found on day 6 (Fig. 1a, Table 4). In the 17 °C treatment, sediment mixing was most important until day 14, when light became the most important factor (Table 3). Temperature significantly affected the presence of germinated *G. echinulata* in the treatments (logistic regression, Pearson $R^2 = 0.159$, Fig. 1a–d).

Sediment mixing

Sediment mixing affected both timing of the first occurrence of the different recruited stages and the biovolume recorded. The first filaments were recorded on day 2, the first heterocyst on day 4 and the first bundle and colony on day 6, all in treatments with sediment mixing, light and 17 °C. The highest biovolume was recorded as bundles on day 12 (Fig. 1a). In the treatments without sediment mixing, the first recorded filaments did not occur until day 6; furthermore, the first bundle and heterocyst and the first colony appeared 4 days later than at 17 °C (Table 2). The highest biovolume was recorded on day 8 as bundles in the 17 °C treatment (Fig. 1b). In the treatments without sediment mixing, temperature and light could explain between 19 and 50% of the variation on the days when significant differences could be found. In the treatments with sediment mixing, light was the most important factor from day 4 onwards (Table 3).

Sediment origin

Comparison of the sediments from three different water depths, showed that the highest biovolume (in all treatments) was recruited from the shallow (1.5 m) sediment, but the variation was large. The maximum biovolume from the 1.5 m sediment was almost seven times higher than from the deep (14 m) sediment.

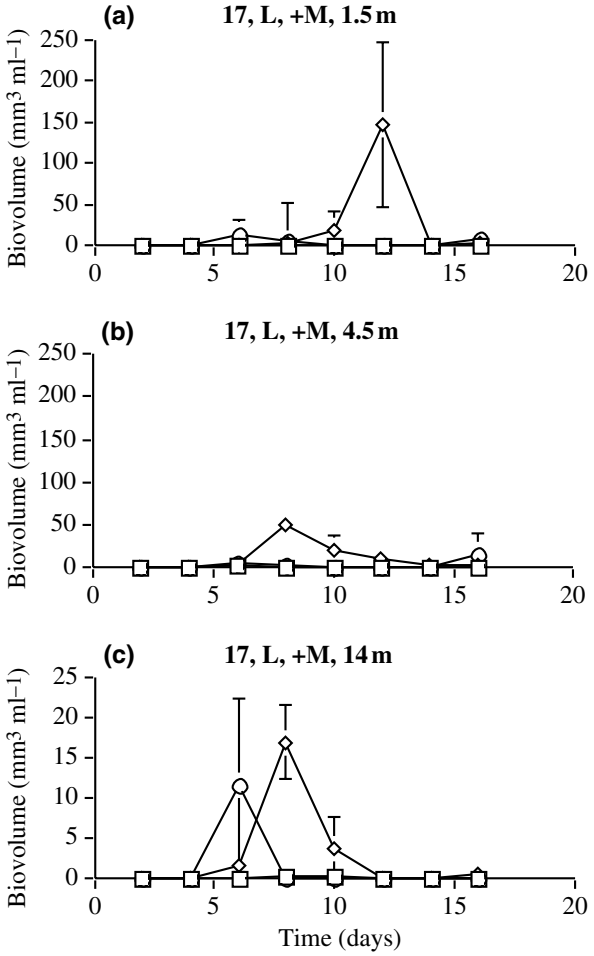

Fig. 2 Treatments at 17 °C, with light and sediment mixing are presented according to sediment depth to show the difference in recruitment among the sediments from different water depths. Note that the scales are of different magnitude. The average recruited biovolume (mm^3 mL^{-1}) of *G. echinulata*, is divided into filaments (—□—), bundles (- - -◇- - -) and colonies (- -○- -). Abbreviations used in the figure are: 7 (7 °C), 17 (17 °C), L (light), D (dark) and +/− M (with or without mixing).

Maximum biovolume occurred at different days in the different sediment types, starting with day 8 in the mid and deep sediments and occurring after 12 days in the shallow sediments (Fig. 2a–c). At 7 °C the highest recruitment occurred after day 18 (Fig. 1c,d).

Discussion

Our results show that light and temperature were the most important factors initiating germination in the cyanobacterium *G. echinulata*. However, temperature and sediment mixing were the main factors regulating the extent of the germination. 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.

As expected, light had a strong positive influence on the recruitment of *G. echinulata* (Table 4). Earlier studies on germination of cyanobacteria showed that the light requirements differ between species, in quantity as well as quality of light (Nichols & Adams, 1982). Braune (1979) found that the amount of light needed for germination of *Anabaena* akinetes (0.5–1.5 μmol m^{-2} s^{-1}) was often insufficient for vegetative growth (required at least 25 μmol m^{-2} s^{-1}) and that wavelengths between 620 and 630 nm produced the highest growth rates. Furthermore, field studies (Roelofs & Oglesby, 1970) involving *G. echinulata* showed that only an increase in solar radiation could be correlated with the recruitment of new colonies. However, Barbiero (1993) found a 3-week delay in the response to light and suggested that temperature, above a certain threshold, might have more influence on recruitment than light. In contrast to these field results (Roelofs & Oglesby, 1970; Barbiero, 1993), we did not observe a long lag phase in response to light prior to recruitment. In the light treatments at 17 °C and without sediment mixing, filaments were found in the water after only 2 days incubation. Recruitment started later at 7 °C and peaked at day 18 (instead of day 12), while the biovolume was significantly lower than at 17 °C. These data are consistent with Barbiero's (1993) hypothesis that higher temperature may increase the response-velocity to light. The presence of filaments in some of the dark treatments was unexpected and may be due to experimental flaws. Light present during sampling in the lake or at the start of the experiment may have been sufficient to initiate the germination process, as shown for dinoflagellates (Binder & Anderson, 1986). It is also possible that the darkroom lamp used during sampling in the laboratory was sufficient to start the germination process. Wyman & Fay (1986) showed that a strain of *G. echinulata* had the highest growth rate in red light, although the lowest photon flux density they used (0.4 μmol photons m^{-2} s^{-1}) was higher than the 0.05 μmol photons m^{-2} s^{-1} in the dark room in our experiment. Another unexpected finding was that no heterocysts were found on filaments recruited at 7 °C. The lower rate of metabolism at low temperatures

may inhibit heterocyst formation. This temperature dependency also suggests that the early summer is very important for the inoculum, as a warm spring and early summer would induce earlier migration and a higher percent of germination. This may be one explanation for the large differences in the size and timing of pelagic population maxima that occur in Lake Erken during different years (Forsell & Pettersson, 1995). Heterocysts are formed soon after germination at the centre of the germling, dividing it into two filaments, after which the typical radial arrangement of the filaments occurs (Wesenberg-Lund, 1904). Furthermore, the formation of colonies occurred only in the treatments with 17 °C and light (Table 4). This can also be taken as a strong indication that shallow sediments are important for recruitment of *G. echinulata*.

The depth distribution of resting cells in the sediment may depend on depth of deposition of akinetes, benthic animal activity and time of deposition. Hence, the highest concentration will not necessarily be found in the top layer of the sediment (Anderson *et al*., 1982). The distribution of *G. echinulata* in the sediment in Lake Erken extends down to at least 4 cm (Pettersson, Herlitz & Istvánovics, 1993). The akinete colonies probably remain viable for several years before they are degraded, as indicated by the range in colour from dark green to light beige discerned in Lake Erken. In a preliminary germination study, the dark green akinete colonies showed a larger proportion of germination than other colours (Karlsson-Elfgren, unpublished data). Sediment resuspension would increase the chance that green akinete colonies, which are the most abundant at 0.5–2 cm depth in the sediment (Karlsson-Elfgren, unpublished data), would reach the surface and potentially increase the germination frequency.

The depth of the mixed layer is important for the number of resting cells that may be brought to the surface. In our experiment, sediment mixing was the most important factor after temperature regulating the size of the migrating inoculum of *G. echinulata*. Sediment mixing increased the maximum recruited biovolume by as much as 10 times. In our experiment we stirred the sediment quite vigorously to increase the chances that akinete colonies would end up in the top mm of the sediment (as they often have a density similar to that of water (Rai, Rao & Singh, 1985).

The physical resuspension in lakes probably shows a high variation both within and between lakes. However, Kumagai (1988) found from a predictive model that only the very top layer of the sediment, <0.2 cm, was affected by resuspension while bioturbation may influence mixing several cm down into the sediment, depending on the species. Kearns, Hairston & Kesler (1996) found that tubificid oligochaetes and chironomid larvae jointly produced a bidirectional transport of plastic beads in the top 2 cm of sediment. As chironomids and oligochaetes are present at many depths in Lake Erken (Sandberg, 1969) this implies that the top 2 cm would regularly be turned over, so that akinete colonies would reach the surface at irregular intervals. The presence of crayfish (*Pacifastacus leniusculus*) in the shallower sediments (Söderbäck, 1992) might mean both a higher risk for burial, but also a greater chance of returning to the sediment surface. The sediment layer in the test tubes was 1.3 cm deep, which would be within the range of the sediment turned over by the dominant benthic fauna in Lake Erken. The type and amount of bioturbation varies with sediment origin (depth), as different benthic animals dominate at different depths. Ståhl-Delbanco & Hansson (2002) found that *Asellus* had the strongest positive effect on algal recruitment, while chironomids had little or no effect on recruitment. As *Asellus* is common in the shallow soft sediments in the bays of Lake Erken, this is another indication that the stores of akinetes in shallow sediments contribute most to the recruitment of *G. echinulata.*

In our experiment, both frequency of germination and biovolume were positively influenced by light, higher temperature and sediment mixing. All these factors point towards the littoral sediments being more important than the profundal sediments as germination sites. This is particularly likely in summer, when the thermocline is newly established and a large part of the pelagic is significantly colder than the shallow sediments. The importance of shallow sediments for phytoplankton recruitment has been suggested by several authors (e.g. Hansson, 1996; Forsell, 1998; Head, Jones & Bailey-Watts, 1998), although only Brunberg & Blomqvist (2003) have provided conclusive evidence. Brunberg & Blomqvist (2003) showed that three species of *Microcystis* had significantly higher recruitment in shallow compared with deep areas of a lake. However, due to a deepening thermocline, sediments at greater depth may be resuspended and hence become important regions of recruitment when the store of akinetes in shallow sediments has been exhausted.

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