

82 Sinking and floating rates of natural phytoplankton assemblages in Lake Erken

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with 5 figures and 3 tables

Abstract: Sinking rates of the <120 μm size phytoplankton fraction of water from Lake Erken were determined during the summer 1992 by following the increase of chlorophyll *a* in the 10 ml-bottom layer in replicate 100 ml settling cylinders. Changes in chlorophyll *a* concentrations as a function of incubation time allowed two fractions to be separated. Fast sinking rates varied between values of 1.9 m/day when pennate and centric diatoms and coccal cyanobacteria were dominant (in cell concentration) and values of 0.5 m/day when cryptophytes and chrysophytes dominated the <120 μm size fraction. Slow sinking rates decreased from 0.04 m/day at the beginning of July to 0.02 m/day in late July. Photosynthesis-Irradiance parameters (P_{max}^B , light saturated photosynthesis and $\#\alpha^{\#B}$, light limited photosynthesis) were lower in the fast sinking fraction ($P_{max}^B = 1.3\text{--}2.4 \mu\text{gC}/\mu\text{gChl/h}$ and $\#\alpha^{\#B} = 0.01\text{--}0.04 \mu\text{gC}/\mu\text{gChl/h}/(\mu\text{E}/\text{m}^2/\text{s})$) than in the slow or non-sinking one ($P_{max}^B = 3.9\text{--}6.4 \mu\text{gC}/\mu\text{gChl/h}$ and $\#\alpha^{\#B} = 0.03\text{--}0.08 \mu\text{gC}/\mu\text{gChl/h}/(\mu\text{E}/\text{m}^2/\text{s})$). P_{max}^B and $\#\alpha^{\#B}$ of the planktonic *Gloeotrichia echinulata*, a colonial bloom-forming cyanobacterium, were similar to those found in the fast sinking fraction. Mean floating rates of *G. echinulata* were around 43 m/d from 15 to 27 July and increased by a factor of two afterwards. *G. echinulata* colonies migrating upwards from sediments and captured in inverted traps showed a mean floating rate of 104 m/d.

Introduction

Phytoplankton settling has received considerable attention in the literature, mainly in the oceanographic field but also in freshwater ecosystems, because settling can affect both vertical distribution of phytoplankton biomass and the carbon budget in the photic zone of aquatic ecosystems (PARSON & TAKAHASHI 1973, BIENFANG 1981). Measurements of sinking rates of freshwater phytoplankton provides important information on the size, ecology, environment and physiology (i.e. age) of the phytoplankton and those conditions may be related to the turbulence of the lake in which phytoplankton resides (TITMAN 1975). Many phytoplankters have evolved mechanisms which directly, or incidentally, reduce average density in order to reduce their sinking rates (REYNOLDS 1984). These mechanisms include (i) storage of relatively light lipids, (ii) regulation of ions, (iii) secretion of mucilage and, in the cyanobacteria, (iv) provision of gas vacuoles. The influence of phytoplankton sinking on the vertical transfer of photoautotrophic biomass accounts for the appearance of a sinking rate parameter in many ecosystem models for primary production (SMAYDA 1970, BIENFANG 1980).

REYNOLDS & WALSBY (1975) classified cyanobacteria according to their life strategies and habitats. Large colonial species, such as *Gloeotrichia echinulata* are considered to dominate in unstably stratified lakes with deep and intermittent mixing, which are characteristics that also apply to Lake Erken. As a result of their large size which allows for rapid rates of vertical migration, these species have the potential to exploit the upper portions of the euphotic zone. Furthermore, hydrodynamic models of the distribution of migrating vs neutral buoyant species suggest that, even during periods of mixing, a buoyant species such as *G. echinulata* would remain higher in the water column (HUMPHRIES & LYNE 1988, KAMYKOWSKI 1990,

YAMAZAKI & KAMYKOWSKI 1991). Other types of cyanobacteria (i.e. *Oscillatoria*), instead, have finer regulation of their buoyancy and tend to form metalimnetic maxima at optima locations along the vertical gradients of light and nutrients. Laboratory and *in situ* studies demonstrate that alterations in various chemical and physical parameters including light, inorganic nitrogen and carbon dioxide may result in increased blue-green algal buoyancy thereby contributing to bloom formation (BOOKER & WALSBY 1981, KLEMER et al. 1985, PAERL & USTACH 1982, SPENCER & KING 1985).

Certain species of spore-forming cyanobacteria have been found to spend an initial period of development in or on the sediment (ROELOFS & OGLESBY 1970) indicating that a part of the life-cycle is benthic. A significant proportion of the benthic population can leave the sediment then forming a part of the planktonic population. This is the case in Lake Erken, where a *Gloeotrichia* bloom develops every summer (PETTERSSON et al. 1990, PETTERSSON et al. 1993). The migration rates of these colonies have been reported for Lake Erken (PETTERSSON et al. 1993) as well as for other lakes, i.e. Green Lake, Seattle, USA (BARBIERO 1993). However, the floating rates of planktonic colonies when they leave the sediment in the summer period and once they are in the water column has not been documented.

Due to their large size, *Gloeotrichia echinulata* colonies are readily separated from the remaining phytoplankton by passing lake water through a 120 μm net. Such separations were made in 1992 during the period of thermal stratification so that physiological characteristics of both size classes could be examined. This was done to elucidate the physiologic controls which have shaped the life strategy of large colonial cyanobacteria such as *G. echinulata*. The parameters measured included sinking rates of the <120 μm epilimnetic fraction of lake water, the floating rates of *G. echinulata* colonies ascending from the sediments and those already found in the epilimnion of the lake. Photosynthesis vs Irradiance (PI) parameters of two water fractions with different velocities of sinking were also measured.

Material and methods

The experiments were carried out with water from Lake Erken (area = 24 km², maximum depth = 21 m, mean depth = 9 m), a moderately eutrophic lake in southern Sweden which was stratified from the beginning of June to the middle of August during the summer of 1992. Epilimnetic water samples were taken at the deepest part of the lake with a 2 m-long tube-sampler. In each 2 m stratum water was sampled proportionally to the volume it represented in the lake. Sample collection was carefully carried out to minimize light shock to the phytoplankton, using dark bottles to keep the samples until the experiments were performed. The lake water was filtered through a 120 μm plankton net and the *G. echinulata* colonies collected on the net were immediately resuspended in 0.45 μm filtered lake water. The *G. echinulata* colonies were later assayed for buoyancy and the <120 μm size fraction for sinking rates.

Inverted traps were used to collect colonies leaving the sediment. These traps were 20 cm- \emptyset funnels located approximately 50 cm above the sediment. The floating rates of the macroscopic *G. echinulata* colonies (1–2 mm in diameter) from the water column and from the inverted traps were determined by visually timing their ascent in a quiescent column of filtered lake water. The column was 10 cm in diameter and 40 cm in height and the colonies were gently injected to the bottom part by means of a 1 ml syringe through a port in the bottom of the cylinder.

Sinking rates of the smaller size fraction were estimated using replicate 100 ml settling cylinders (WALSBY & REYNOLDS 1980), which were kept in the dark at lake temperature in a water bath. The bottom and top 10 ml of individual cylinders were sampled at varying intervals (every 30 min. the first 2 hours and every 2–4 hours the rest of the incubation time) and fluorometrically analyzed for chlorophyll *a*. Sinking rates were estimated from the increase of chlorophyll *a* in the bottom. The presence of buoyant algae in the <120 μm size fraction was determined by increases in the chlorophyll concentration in the upper 10 ml fraction. This chlorophyll, when present, was subtracted from the initial chlorophyll concentration in the cylinders prior to calculating sinking rates. Chlorophyll *a* was also determined in wellmixed aliquots (average of triplicates) of the original sample to measure the homogeneous chlorophyll content in the 100 ml

cylinders at the beginning of the incubation time. Also, the homogeneous chlorophyll content was determined at the end of the incubation, as a control. Percentage of chlorophyll in the 10 ml-bottom fraction was calculated as following:

$$\%Chla = \frac{[Chl a]^1 \times 0.01}{[Chl a]^2 \times 0.1} \times 100$$

where

$[Chl a]^1$ = concentration of chlorophyll *a* (in $\mu\text{g/l}$) in the 10 ml bottom fraction.

$[Chl a]^2$ = concentration of chlorophyll *a* (in $\mu\text{g/l}$) in the wellmixed aliquot of the original sample at the beginning of the incubation time.

The $<120 \mu\text{m}$ fraction was also simultaneously incubated in the larger cylinders (3.1 liters). After 4–5 h of incubation in the same conditions as described above, the top 100 ml layer was removed and thrown out, and the next and bottom 100 ml layers were extracted and used for the determination of photosynthetic parameters (P_{max}^B , the light saturated photosynthesis and α^B , light limited photosynthesis). *G. echinulata* colonies collected from the epilimnion of the lake were also analyzed for these photosynthetic parameters. Photosynthesis-Irradiance relationships were obtained by incubating a single ^{14}C enriched water sample at a large number of light intensities using the short time (20 min.) photosynthetron (PSTRON) incubation method of LEWIS & SMITH (1983) described in detail in PIERSON (1990) and PIERSON et al. (1992). Triplicate samples for chlorophyll *a* analysis were filtered onto Whatman GF/F glass fiber filters and immediately extracted in 10 ml of 90 % acetone. After 24–36 h of extraction in the dark and at 4 °C, the chlorophyll *a* concentration was determined fluorometrically according to STRIKLAND & PARSONS (1988).

Results and discussion

Sinking rates of the $<120 \mu\text{m}$ fraction

Fig. 1 A shows the time distribution of chlorophyll *a* concentration in the epilimnion of Lake Erken and in the *G. echinulata* fraction from 29 June to 17 August 1992. The phytoplanktonic cell density and its biomass (excluding *G. echinulata* colonies) is also shown. The pigment concentration in the epilimnion increased to a maximum value of $12 \mu\text{g Chl } a/l$ on 10 August, when a decline in phytoplankton started. Chlorophyll in *G. echinulata* fraction showed the same tendency as total epilimnetic chlorophyll. On 6 July the phytoplankton (Fig. 1 B) was mainly composed by diatoms (pennate and centric) and coccal cyanobacteria (151×10^4 , and 76×10^4 ind./l, respectively). These values represent 47 % and 24 % of $<120 \mu\text{m}$ -total phytoplankton cell numbers (excluding *G. echinulata*) (Fig. 2 A). The biomass of diatoms represented 43 % of $<120 \mu\text{m}$ -total biomass (excluding *G. echinulata*) and coccal cyanobacteria accounted for 4 % of total biomass (Fig. 2 B). The dinoflagellate *Ceratium hirundella* represented 40 % of total phytoplanktonic biomass although in terms of individual numbers it was less than 1 %. On 14 July (Fig. 1 B) the diatoms continued being the most abundant algal group in cell numbers (34 %) and also in biomass (53 %). Fifteen days later (27 July), the situation changed drastically and cryptophytes were then the predominant phytoplankters (57 % of individuals and 31 % of biomass) followed by the chrysophytes (28 % in individuals although only 4 % in biomass). On 3 August cryptophytes were still the predominant group of phytoplankton with 43×10^4 ind./l in the epilimnion of the lake, whereas the other phytoplankters decreased considerably except *G. echinulata* which reached its maximum biomass.

The sinking rates of the $<120 \mu\text{m}$ size fraction changed during the summer period. Changes in chlorophyll *a* concentrations in the 10 ml-bottom cylinder samples as a function of incubation time allowed two fractions to be separated (Fig. 3 A). The rate of the fast sinking populations was highest on 8 and 17 July, with corresponding sinking rates of 1.9 m/day (Fig. 3 B), whereas the slow sinking population showed rates of 0.04 and 0.03 m/day respectively. These measurements coincided with the predominance of non-motile population of phytoplankton (diatoms and coccal cyanobacteria; Fig. 2).

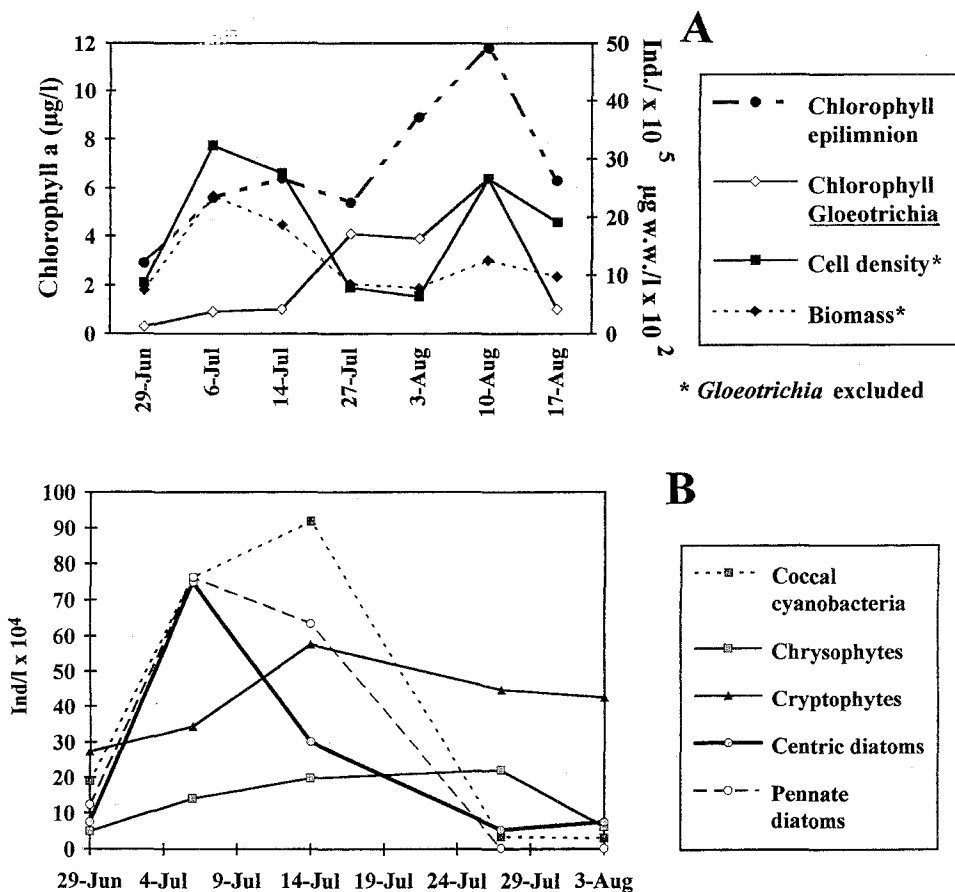


Fig. 1. A: Time variation of the chlorophyll *a* concentration in epilimnion of Lake Erken and in the *G. echinulata* fraction together with phytoplanktonic cell density and biomass (excluding *G. echinulata*) from 29 June to 17 August. B: Time variation of the number on individuals per liter of main groups of phytoplankton in Lake Erken from 29 June to 3 August.

On 24 July the sinking rate of the fast fraction decreased considerably (Fig. 3 A and B) to 0.5 m/day coinciding with the dominance of motile species of phytoplankton (cryptophytes and chrysophytes) which actively avoid fast sedimentation. Thus, motility provides an advantage to flagellated organisms by enabling the cells to remain in a certain position (REYNOLDS 1984). Of course, these sinking rates are valid for a calm situation; in a turbulent environment such as Lake Erken, cell loss through sinking would be slower. A sinking experiment was also performed on 1 August (data non shown), but, the presence of vacuolated *Anabaena circinalis* made it impossible to measure reliable sinking velocities. The *Anabaena* cells remained adhered to the walls of the cylinders after aspirating out the sample, resulting in large errors in the sinking determinations.

Sinking rates of natural phytoplankton populations from freshwater and marine or coastal ecosystems together with some cultures of phytoplankton species are summarized in Table 1. In most lakes phytoplankton sinking velocities are in the range of 0.1–2 m/day (HUMPHRIES &

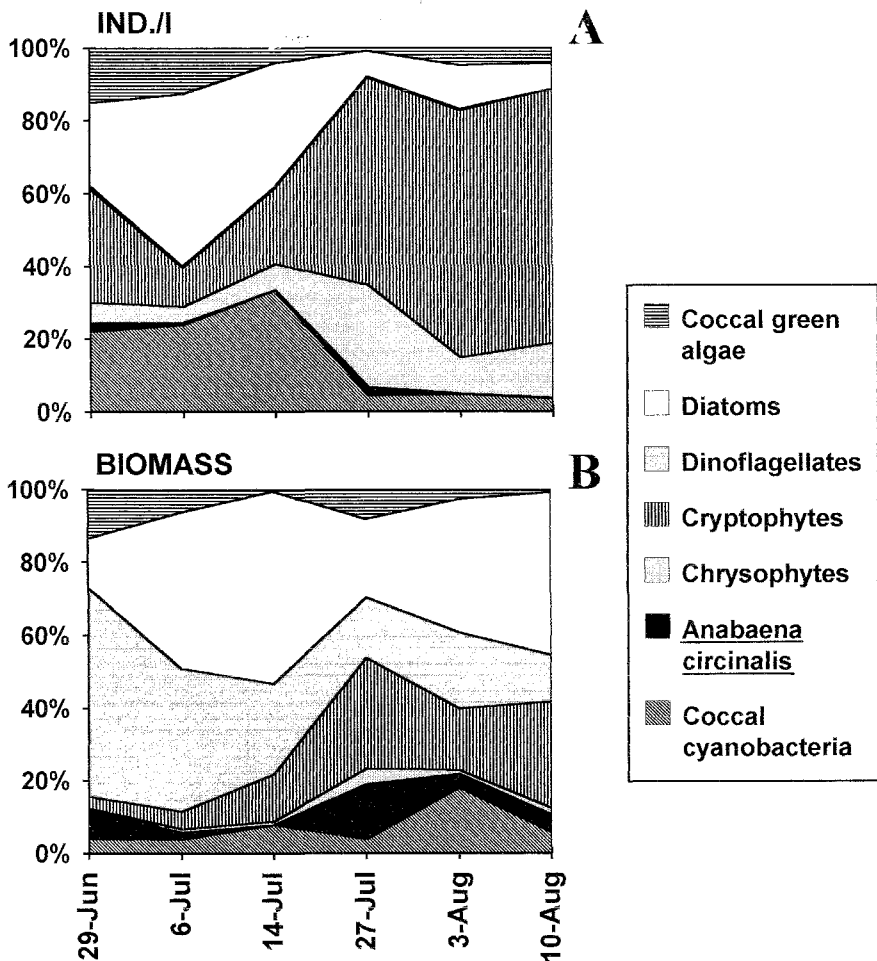


Fig. 2. Time variation of the percentage of phytoplankton cell density (A) and biomass (B). *G. echinulata* excluded in all cases due to size considerations and its floating capacity.

LYNE 1988). SMAYDA (1970) stated that rates of sedimentation of the phytoplankton are commonly about 0.5 m/day, although BODUNGEN and coworkers (1981) reported an extreme value of 30–50 m per day for the dominant species *Skeletonema costatum* in Bornholm Sea (Baltic Sea). However, the sinking rates depend very much on the phytoplankton assemblages found in the lake. Here we present a good example of how phytoplanktonic succession causes different sinking velocities.

Phytoplankton sinking rates are dependent upon physical (e.g. size and shape) factors (SMAYDA 1970, BIENFANG 1980). Concerning size, TAKAHASHI & BIENFANG (1983) were not able to measure sinking rates in the ultraplankton fraction (<3 μm , see Table 1). However, laboratory studies of sinking have shown that rates are determined not only by physical factors associated with size and shape, but also by physiological properties of the cells (DINSDALE & WALSBY 1972, REYNOLDS 1973, TITMAN & KILHAM 1976, SOMMER 1984). SMAYDA (1970) and also TITMAN & KILHAM (1976) reported that sinking rates of stationary phase populations

Table 1. Sinking rates of some natural phytoplankton populations from freshwater and marine ecosystems together with specific settling rates under different conditions.

Sinking rate m/day	Phytoplankton characterization	References
Freshwater		
0.16–1.2	Species complex mainly composed by <i>Chlorella</i> and <i>Cyclotella</i>	OLIVIER et al. 1981
0.2	Diatom bloom: growing populations	GIBSON 1984
0.4	after silica depletion	
0.72–7.5	Diatoms in 0–20 m and 20–120 m depth	SOMMER 1984
0.22–3.2	Desmidiaceae in 0–20 m and 20–120 m depth	
0.10–0.70	Chlorococci in 0–20 m and 20–120 m depth	
0.03–0.04	Cyanobacteria in 0–20 m and 20–120 m depth	
0.1–2		HUMPHRIES & LYNE 1988
Marine		
0.5		SMAYDA 1970
0.63	3–20 μm fraction	BIENFANG 1980
1.37	20–120 μm fraction	
0.32–1.69	non size-fractionated	BIENFANG 1981
*	<3 μm fraction	TAKAHASHI & BIENFANG 1983
0.09	3–20 μm fraction	
0.29	>20 μm fraction	
0.23		BIENFANG 1984
0.07		BIENFANG & HARRISON 1984
0.96	Assemblage composed by large centric diatoms	BIENFANG & HARRISON 1984
0.22	Subtropical assemblage composed by coccolithophorids and dinoflagellates	
0.22		JOHNSON 1986
0.14	Flagellate-dominated community	CULVER & SMITH 1989
0–0.91		PITCHER et al. 1989
Cultures		
0.31	Diatoms: exponential growth	TITMAN & KILHAM 1976
1.12	Diatoms: stationary phase	

* Reliable measurements could not be made.

of phytoplankton are higher than those of rapidly growing cultures. Similarly, WAITE & THOMPSON (1992) found that the size vs sinking relationship depends on the physiological state of the cell: small cells of the marine diatom *Ditylum brightwellii* sank more rapidly than large cells under saturating light, but under severe energy limitation sinking rates were directly proportional to cell volume. In non-motile green algae, the cellular shape and the possession of mucilage tend to reduce sedimentation loss. Active motility also reduces considerably the rate of sinking. SOMMER (1984) found zero settling velocities for *Rhodomonas* sp. and *Cryptomonas* sp. which is in agreement with the observations of LIVINGSTONE & REYNOLDS (1981) and REYNOLDS & WISEMAN (1982). These data are also in agreement with the observation here that sinking rates in the <120 μm phytoplankton community decreased when cryptophytes and chrysophytes were dominant. PITCHER et al. (1989) found that sinking rates of phytoplankton populations were significantly correlated not to any of the environmental parameters measured but to taxonomic properties of the assemblages.

SMAYDA & BIENFANG (1983) determined the sinking rate characteristics of a natural community of phytoplankton in the size range from 5 to 102 μm and observed the sinking rates of

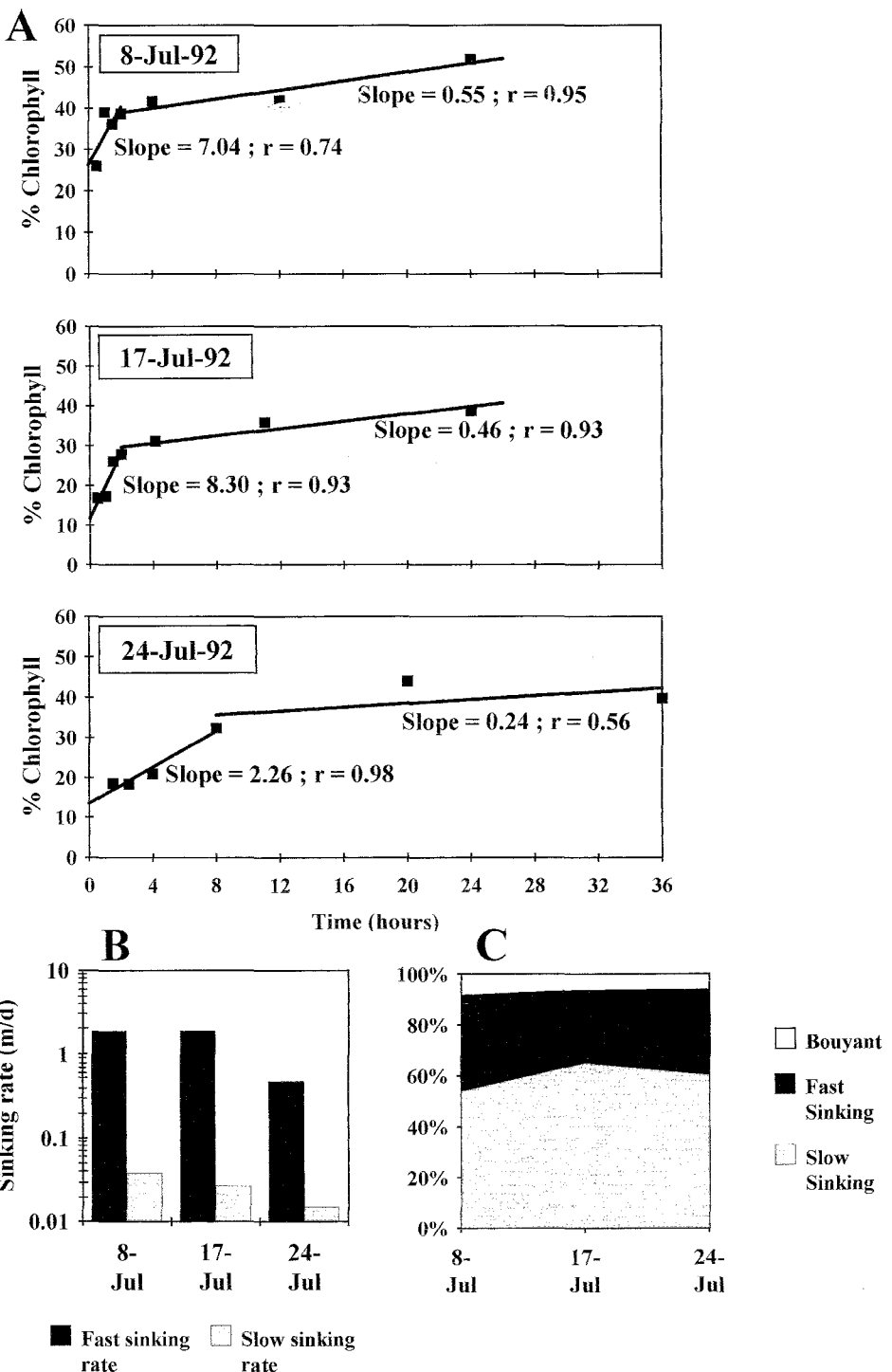


Fig. 3 A: Sedimentation of chlorophyll *a* in the bottom 10 ml of the cylinders as a percentage of the total chlorophyll in the 100 ml-cylinder, during the incubation. B: Sinking rates of the <120 μm -size fraction calculated from sedimented chlorophyll *a*. C: Percentage of total chlorophyll accounted for by the two sinking fractions and one floating fraction in the <120 μm -size water.

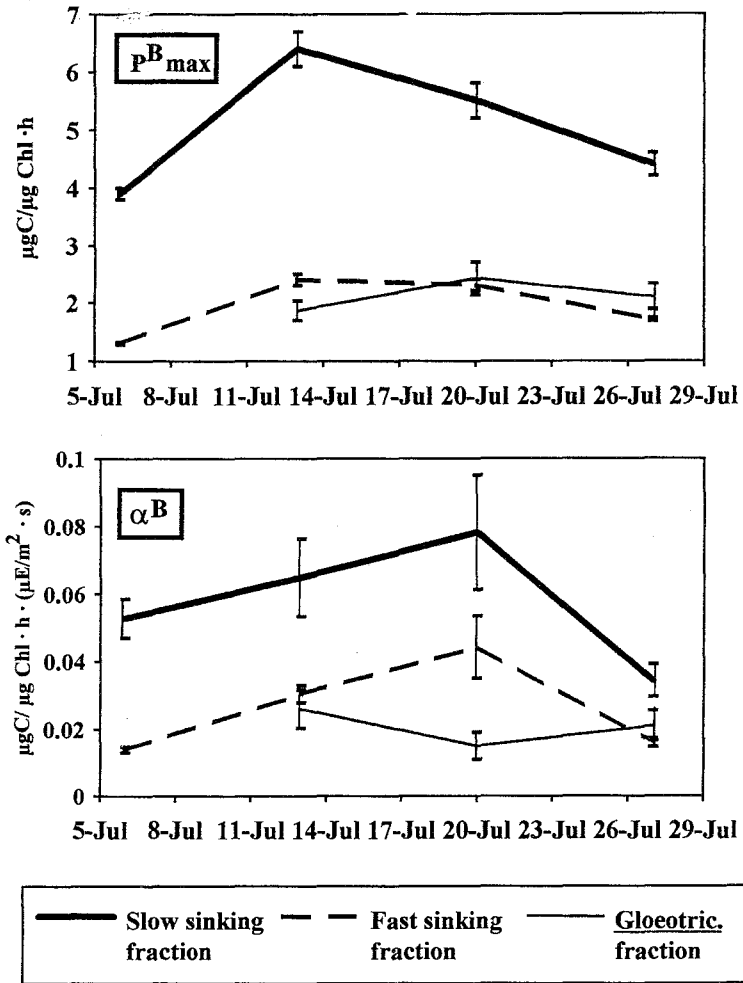


Fig. 4. Temporal variations in the PI parameters (A: P_{max}^B and B: α^B) measured in the $<120\ \mu\text{m}$ fast and slow sinking fractions and *G. echinulata* colonies. Vertical bars indicate standard errors.

coccolithophorids > dinoflagellates > diatoms. However the swimming rate of dinoflagellates appeared to be considerably greater than their sinking rates. Also, the formation of spores in some phytoplankton species may increase the sinking rates (BIENFANG 1981).

Photosynthesis vs Irradiance parameters in the fast and slow sinking fractions and *Gloeotrichia* colonies

There are large differences between the PI parameters (P_{max}^B and α^B) in the slow and fast sinking fractions (Fig. 4). Whereas in the slow fraction P_{max}^B (light saturated photosynthesis) varied between 3.9 and 6.4 $\mu\text{gC}/\mu\text{gChl}/\text{h}$ the fast sinking fraction showed lower values ranging between 1.3 and 2.4 $\mu\text{gC}/\mu\text{gChl}/\text{h}$. The maximum values of P_{max}^B were obtained on 13 July in both fast and slow sinking fractions. Regarding α^B (light limited photosynthesis) values of

0.03–0.08 $\mu\text{gC}/\mu\text{Chl}/\text{h}/(\mu\text{E}/\text{m}^2/\text{s})$ were found in the slow fraction and only 0.01–0.04 $\mu\text{gC}/\mu\text{gChl}/\text{h}/(\mu\text{E}/\text{m}^2/\text{s})$ in the fast sinking fraction. Both sinking fractions showed the maximum α^B value on 20 July. Fig. 4 also shows the PI parameters of the *G. echinulata* fraction. It can be observed that P_{max}^B values were similar to those found in the fast sinking <120 μm fraction and also α^B values were closer to fast sinking fraction.

Both parameters were reduced in the fast sinking fraction. In the case of α^B its reduction may be explained by pigment packaging effects (KIRK 1975, 1976, MOREL & BRICAUD 1981) in large cells in comparison to smaller ones, assuming that a higher proportion of larger cells were in the bottom layers. Also, the increased packaging effects can be due to light adaptation which lead to decreased α^B . It seems to be the case of the fast sinking fraction because the values of α (the initial slope of the non chlorophyll normalised PI curve) are higher in the fast sinking fraction which must be low light adapted (otherwise, the lower α^B values would be the result of a high percentage of inactive cells).

Reduction of the light saturated photosynthesis (P_{max}^B) can probably be explained by surface area/volume considerations, which would limit the diffusion of nutrients and CO_2 into large cells (TAGUCHI 1976, PAERL 1983), assuming that in the fast sinking fraction there is a higher proportion of larger cells. The reduction of P_{max}^B and α^B in the *G. echinulata* fraction can be due to large algal size as well as exposures to high irradiance (photoinhibition), as it has been demonstrated previously also in Lake Erken (PIERSON et al. 1994).

G. echinulata floating rates

The floating rates of *G. echinulata* colonies from lake water (Fig. 5) showed an increasing tendency as summer advanced (significant regression coefficient). Before 27 July, the mean floating rate was 34 ± 12 m/day, and this increased to 67 ± 16 m/day by 10 August. Although the standard deviations of the mean were large, the ANOVA analyses showed that the mean floating rates were significantly different between samplings (Table 2). FORSELL & PETERSSON (1995) found that the epilimnetic *Gloeotrichia* population maximum was reached on 27 of July 1992. After this, the population remained high for two weeks before quickly decreasing.

Rising velocities of *Microcystis* colonies of 0.5–3 mm in diameter from Burrinjuck Reservoir ranged between 10–250 m/day (see Table 3; HUMPHRIES 1982). GANF (1974) reported a floating rate of intact colonies of >100 μm \varnothing of *Microcystis aeruginosa* as 91.9 m/day. However, REYNOLDS (1971) recorded maximum rates of flotation determined *in vitro* for *Gloeotrichia echinulata* of 19.6 m/day, a lower value than that obtained in Lake Erken. REYNOLDS (1971) demonstrated a relationship between the size of the cells/colonies and the floating capacity: those with the largest colonies rise fastest in their natural gas-vacuolate state but also sink most rapidly when their vacuoles are collapsed by pressure.

Akinetes and colonies of *G. echinulata* have been found in large quantities in the sediments of Lake Erken (PETERSSON et al. 1993) and in some other wind-exposed lakes (ROELOFS & OGLESBY 1970, BARBIERO & WELCH 1992). These colonies migrate from the sediment to form part of the phytoplanktonic population in amounts that lead to an important in-

Table 2. ANOVA results of floating rates of *G. echinulata* on sampling date and colony origin.

Factor	d.f.	F
Sampling date		
colonies from water column	246	18.14**
colonies from sediment traps	268	5.20*
Colony origin	515	153.84**

*: $p < 0.01$; **: $p < 0.001$

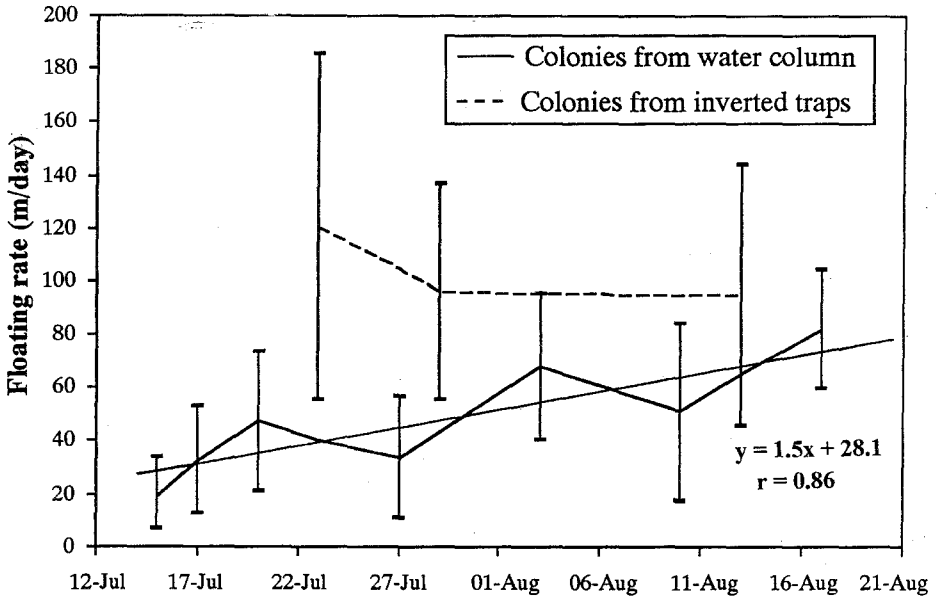


Fig. 5. Mean floating rates of *G. echinulata* colonies from the epilimnetic water column (solid line) of Lake Erken and from the sediment collected with inverted traps (dashed lines). Vertical bars indicate standard deviation.

Table 3. Floating rates of several planktonic phytoplankton species including *G. echinulata* from Lake Erken.

Species	Floating rate m/da	References
<i>Oscillatoria agardhii</i>	0.04	WALSBY & KLEMER 1974
<i>Aphanizomenon flos-aquae</i>	1-4	REYNOLDS 1971
	9.6-66	PAERL & USTACH 1982
<i>Anabaena spiroides</i>	2.6	REYNOLDS 1971
<i>Anabaena circinalis</i>	5.1	REYNOLDS 1972
<i>Coelosphaerium naegelianum</i>	3.6	REYNOLDS & WALSBY 1975
<i>Microcystis aeruginosa</i>	9.2	REYNOLDS & WALSBY 1975
	91.9	GANF 1974
	10-250	HUMPHRIES 1982
<i>Gloeotrichia echinulata</i>	19.6	REYNOLDS 1971
	51 (water column)	This paper
	104 (from sediment)	

ternal loading of phosphorus (PETTERSSON et al. 1993). Colonies from the sediment collected with inverted traps in Lake Erken showed a higher mean floating rate (104 ± 15 m/d) than the colonies collected directly from the epilimnion of the lake (see Fig. 5 and Table 2). The former colonies also showed higher standard deviations than the latter ones. Nevertheless, the ANOVA analyses showed that the mean floating rate was different at each date (Table 2).

Rising colonies could easily travel through the thermocline and remain positively buoyant (HUMPHRIES & LYNE 1988). Scaling arguments show that even with a large temperature

change (5 °C), water within a colony equilibrates in temperature rapidly relative to the time taken to rise any distance, so the rising velocity is almost independent of the external temperature gradient. Empirical test also showed that colonies remained positively buoyant upon transfer from 20° to 38° (HUMPHRIES 1982).

Several studies on field populations have shown cyanobacteria colonies to remain positively buoyant during the active growth period when controlled downward displacement can not occur. This is the case of *Microcystis aeruginosa* in Crose Mere (REYNOLDS 1973), or a species of this genus in Burrinjuck Reservoir (HUMPHRIES 1982), or a *Microcystis* species in Hartbeespoort Dam (ROBART 1984). In these cases the authors conjectured that positive buoyancy *per se* provides sufficient advantage to cyanobacteria to become dominant over negatively or neutrally buoyant phytoplankton. BARBIERO (1993) pointed out that the buoyancy changes in species as *Gloeotrichia*, at least in its seasonal development, are not governed by mechanisms of turgor collapse or ballast regulation (DINSDALE & WALSBY 1972, KONOPKA et al. 1978, THOMAS & WALSBY 1985). According to this author, a more direct genetic control of gas vacuole production, tied to colonial development rather than solely to external environmental conditions, is easily reconciled in a species which exhibits striking cellular differentiation with increasing age (MILLER & LANG 1971, CMIECH et al. 1984). However we think that physiological controls which regulate the buoyancy in *G. echinulata* are the same as those found in filamentous species, which is turgor pressure collapse. For some reason such as resuspension (as supposed by PIERSON et al. 1992), light (as suggested by ROELOFS & OGLEBY 1970) or a combination of these or other factors, the *Gloeotrichia* colonies come up to the surface from the sediments. They do so with large stores of internal phosphorus (PETTERSSON et al. 1993) and are buoyant. The *Gloeotrichia* colonies in the epilimnion remain high in the water column so that rates of photosynthesis and N fixation can sustain growth (N is supplied by N-fixation, SZASZ & PETTERSSON, in press). Under these conditions, photosynthate goes towards protein synthesis (REYNOLDS 1984), turgor pressure does not increase and *Gloeotrichia* colonies remain buoyant. Toward the end of the bloom the rate of protein synthesis must decrease, photosynthate accumulates in the cytoplasm and increases in turgor pressure would cause the gas vacuoles to collapse (REYNOLDS 1984). Because of their large size, the *Gloeotrichia* colonies would sink very rapidly once their increases in density occur (REYNOLDS 1971). The above can therefore explain the rapid decline of the *Gloeotrichia* blooms in Lake Erken that has been monitored (FORSELL & PETTERSSON 1995). The reason that causes protein synthesis to decrease could be the eventual decline in phosphorus stores (because there is no uptake of P from the water column by *G. echinulata* as suggested by ISTVÁNOVICS et al. in 1993), which could either directly reduce the rate of protein synthesis, or may do so indirectly by reducing the rate of N fixation.

FORSELL (1993) first observed akinetes in *G. echinulata* in Lake Erken on the 20 of July when the epilimnion was depressed below 8 m and the P content of the colonies was low. During the weeks after, this author observed akinetes in most colonies. As akinetes lack gas vacuoles but contain large cyanophycin bodies, they sediment rapidly, and this fact can collaborate to the rapid disappearance of the bloom.

Epilimnetic growth of *G. echinulata* is limited solely by the intracellular P reserve accumulated during the benthic stage as concluded by ISTVÁNOVICS and coworkers (1993) and PETTERSSON and collaborators (1993). The C/P ratio of the *Gloeotrichia* fraction in 1991 increased gradually, since the P content diminished as summer advanced (PETTERSSON et al. 1993). Also ULÉN (1971) demonstrated a much higher phosphorus content in harvested colonies from Lake Erken in early July than later on during the season. BARBIERO & WELCH (1992) came to the same conclusion concerning *Gloeotrichia* in Green Lake. When they leave the sediment, they are rich in phosphorus but not in carbohydrates. Once in the water column and with enough light for photosynthesis, they start to accumulate carbohydrates. Some reports have stated the

buoyancy-regulating role of carbohydrates in some species of cyanobacteria (VAN RIJN & SHILO 1985). Such accumulation (which will not be enough to exceed the "critical pressure" that would collapse irreversibly the gas vesicles) could reduce the floating rates of the colonies once in the water column, but later they start to consume the carbohydrates, increasing the floating rates near the end of the season. REYNOLDS & WALSBY (1975) stated that cessation of blue-green algal growth is often accompanied by increases in gas vacuole content, due to different kinetics of cell growth and gas-vacuole formation. These authors related large increases in buoyancy in various blue-green algal populations to deficiencies in the concentration of phosphorus and nitrogen within the cells. In the same way, PAERL (1981) found that cells having relative low rates of photosynthesis tend to increase buoyancy because gas vacuole formation can proceed in a relatively unhindered fashion and cell ballast accumulation would be minimal. These reasons could explain the different floating rates of *Gloeotrichia* colonies in the water column and those collected immediately ascending from the sediment, as well as the increasing tendency of epilimnetic colonies as summer advanced.

In conclusion, when modeling primary production in aquatic ecosystems, the settling rates of phytoplankton must be determined in different moments because the time evolution of phytoplankton can considerably affect sinking rates. The high floating rates of *Gloeotrichia echinulata*, together with its special life strategy and unique phosphorus uptake (ISTVÁNOVICS et al. 1993), lead to a competitive advantage in Lake Erken, by allowing them to photosynthesize and grow at greater rates due to high rates of light absorption.

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