

Review

Recruitment of bloom-forming cyanobacteria and its driving factors

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Based on most of the literature, this paper reviewed the progress made in following aspects: cognition to cyanobacteria recruitment, various traps for studying cyanobacteria recruitment in lakes, recruitment patterns of some species of cyanobacteria, and the driving factors for recruitment. Additionally, perspective studies of cyanobacteria recruitment in lakes were pointed out. In light of the existing knowledge, cyanobacteria recruitment could be regarded as a process that benthic overwintering cyanobacteria migrated to the pelagic phase after germination and growth renewal under suitable conditions. This process was divided into three consecutive phases: germination, a potential growth phase, and migration to the pelagic phase. Previous studies mostly focused on the migration from sediments to water. To date, several kinds of traps had been designed to investigate cyanobacteria recruitment. Some studies showed that amounts of cyanobacteria recruitment were higher in shallow regions than deep regions of lakes, and the recruitment rates mostly peaked in a given time of year before blooms onset. Temperature, resuspension and bioturbation had been recognized to be the most important factors for driving cyanobacteria recruitment. Other factors (such as light, nutrients, anoxia, etc.) also played a role.

Key words: Cyanobacteria, recruitment, driving factors, blooms.

INTRODUCTION

Many eutrophicated lakes worldwide have been dominated by cyanobacteria (also known as blue-green algae) for the last decades (Dokulil and Teubner, 2000; Hyenstrand et al., 1998; Oliver and Ganf, 2000). The prevailing species of cyanobacteria (such as *Anabaena*, *Aphanizomenon*, *Microcystis*, and so on) were capable of nuisance growth and forming cyanobacteria blooms, which posed serious threats to water resources for drinking, recreational, and industrial use (Paerl, 1988; Pizzolon et al., 1999; Robarts, 1985). Considerable studies had explored the forming mechanisms of cyanobacteria blooms. According to these studies, Kong and Gao (2005) proposed a hypothesis that a series of processes which were inter-linked in relation to blooms

formation: autumnal sedimentation of declining blooms biomass (Fallon and Brock, 1980; Reynolds and Wiseman, 1982; Takamura and Yasuno, 1988; Visser et al., 1995), subsequent overwintering on lake surface sediments (Brunberg and Blomqvist, 2002; Fallon and Brock, 1981; Preston et al., 1980; Takamura et al., 1984; Tsujimura et al., 2000), recruitment in spring (Barbiero and Kann, 1994; Brunberg and Blomqvist, 2003; Hansson et al., 1994; Karlsson-Elfgren and Brunberg, 2004; Ståhl-Delbanco and Hansson, 2002; Verspagen et al., 2005), biomass increase (Cao et al., 2005; Head et al., 1999; Huovinen et al., 1999) and blooms formation (Jacoby et al., 2000).

As the abundance of overwintering cyanobacteria on sediments was significantly larger than pelagic proportions (Brunberg and Blomqvist, 2003; Karlsson-Elfgren and Brunberg, 2004; Tsujimura et al., 2000), thus recruitment of benthic cyanobacteria could serve as a 'seek bank' for the pelagic phase. Moreover, mathematic

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model calculations showed that the absence of benthic recruitment would reduce the summer blooms by 50% (Verapagen et al., 2005). Therefore, recruitment of cyanobacteria became a 'hot spot' bearing much importance in the life cycle of bloom-forming cyanobacteria, and progressed quickly in studies on cyanobacteria blooms. In this paper, historical advances in cyanobacteria recruitment were reviewed based on most of the literature.

CYANOBACTERIA RECRUITMENT

In autumn, a large proportion of cyanobacteria is decomposed and deformed during sedimentation (Fallon and Brock, 1980). Some species developed 'dormant stages', such as akinetes of *Aanabaena* (Paerl, 1988). As to *Microcystis*, the autumnal sedimentation occurred as a consequence of carbohydrate increase and buoyancy decrease at reduced temperature (Visser et al., 1995). These overwintering cyanobacteria on sediments were supposed to renew growth and return to the pelagic phase under suitable conditions.

In light of the existing knowledge, cyanobacteria recruitment could be regarded as a process that benthic overwintering cyanobacteria migrated to the pelagic phase after germination and growth renewal under suitable conditions. It is a pathway via which bloom-forming cyanobacteria returned to water and continued its life cycle. From this, two criteria were derived: suitable conditions for growth renewal (quality) and the amount of recruitment (quantity). Moreover, the process of recruitment could be divided into three consecutive phases: germination, growth, and migration to the pelagic phase.

TRAPS FOR STUDYING CYANOBACTERIA

Most cyanobacteria recruitment studies in lakes were performed by using traps of various designs. The first recruitment trap was designed by Reynolds (1975) and used by Trimbee and Harris (1984) in Guelph Lake (Canada), which consisted of a black polyvinyl chloride cylinder (16.5 cm high and 8.0 cm wide) fitted with an inverted funnel. This trap could collect cyanobacteria migration from sediments under static conditions, but did nothing to exclude zooplankton predation and cyanobacteria lateral migration. Another version of trap was engineered by Hansson et al. (1994). It was a glass jar filled with filtered lake water, with a funnel through the lid. A 300 µm mesh net covered the funnel entrance to exclude predation by zooplankton. Still, however, it failed to eliminate lateral immigration of cyanobacteria cells and colonies. Brunberg and Blomqvist (2003) constructed a recruitment trap (a 20-L flask) made of transparent plastic, which was open at the bottom and had two openings on the side. These openings were covered with a 40 µm mesh net. Such a trap design, to an extent, excluded

lateral migration and potential zooplankton grazing. Cao et al. (2005) designed a new version of recruitment trap, which was also made of transparent plastic. It was a 30-L flask with 1 cm-wide holes on the sidewall, where a thin nylon filter (3 µm mesh) was covered in order to prevent cyanobacteria cells through. The water within the trap was removed by using a bilge pump powered with a 12-volt accumulator. This kind of trap was able to eliminate lateral 'contamination' of phytoplankton into the trap while maintaining a homogeneous internal and external environment. Verspagen et al. (2005) used another kind of recruitment trap. It consisted of an anchored cylinder, in which there was a down-ward bottle with a funnel. This trap, like that used by Trimbee and Harris (1984), was also unable to prevent lateral migration and zooplankton grazing.

CYANOBACTERIA RECRUITMENT FROM LAKE SEDIMENTS AND INOCULA TO THE PELAGIC PHASE

Cyanobacteria recruitment from sediments to water had been studied in some lakes. Such a migration could play two roles in the cyanobacteria life cycle and blooms formation: either as benthic inocula for initiating pelagic growth or as biomass supplement to the pelagic proportions already present in water. Some studies reported that cyanobacteria had a relatively large amount of recruitment from sediments (Barbiero and Kann, 1994; Trimbee and Harris, 1984; Zhang et al., 2005), which confirmed the hypothesis that pelagic cyanobacteria in lakes were mainly derived from benthic stocks via recruitment. Additionally, other studies showed that benthic contribution to pelagic growth via recruitment was rather small compared to the maximum standing crop in water (Barbiero and Welch, 1992; Head et al., 1999). But if the given species from benthic stock was the 'seed' for pelagic initial growth, however the recruitment size was small, benthic recruitment would be significant to the pelagic phase. Here below are recruitment estimates for some species of cyanobacteria in different lakes.

Anabaena

In Green Lake, Barbiero and Welch (1992) found the average *Aanabaena* recruitment amounts accounted for 0.62% of the pelagic abundance in summer. A higher recruitment of 8% was reported in Agency Lake (U.S.A.), which was a shallow hypereutrophic lake (Barbiero and Kann, 1994).

In Esthwaite Water (U.K.), *Anabaena flos-aquae* was one of the dominant species, its recruitment peaked in late May and early June at the shallow sites, which also coincided with the pelagic development of *A. flos-aquae*. In this lake, *Aanabaena solitaria* had smaller amounts of recruitment during the same period, but its pelagic development in June initiated after recruitment. This re-

sult implied that in Esthwaite Water benthic recruitment of *A. solitaria* would be the seed source for pelagic growth (Head et al., 1999).

Aphanizomenon

In Guelph Lake, the cumulative recruitment of *Aphanizomenon flos-aquae* accounted for 62% of its maximum pelagic abundance. What is more? All of the *Aphanizomenon* filaments collected in recruitment traps were positively buoyant (Trimbee and Harris, 1984).

In Esthwaite Water, recruitment of *A. flos-aquae* peaked in late May and early June at the shallow sites, which also coincided with its development in pelagic phase (Head et al., 1999).

Gloeotrichia

Recruitment of *Gloeotrichia echinulata* kept rising from June to September in Lake Erken, the most recruitment occurred between middle June and late July. Taking no loss into account, recruitment would represent approximately 2.6% of the maximum pelagic abundance (Karlsson-Elfgren and Brunberg, 2004).

Gomphosphaeria

In Guelph Lake, *Gomphosphaeria lacustris* colonies recovered in late July and August, the cumulative recruitment of *Gomphosphaeria* from sediments accounted for 10.5% of the maximum standing crop in water (Trimbee and Harris, 1984).

In Esthwaite Water, *G. naegeliana* recruitment was of fewer amounts and the pelagic development initiated after its recruitment in late May. Much larger recruitment of *G. naegeliana* occurred in August and September (Head et al., 1999).

Microcystis

Recruitment of *Microcystis* colonies peaked in late July and August in Lake Guelph, its cumulative recruitment could constitute 4.2% of the maximum standing crop during the sampling period (Trimbee and Harris, 1984).

In Lake Mendota (U.S.A.), *Microcystis* recruitment began two weeks before the maximum abundance appeared in water. The major part of the recruitment occurred at shallower stations, whereas small amounts of *Microcystis* originated from the intermediate and deeper stations (Hansson et al., 1994).

In Lake Limmaren (Sweden), recruitment of *Microcystis* peaked in August and mainly occurred in shallow regions. Three species of *Microcystis* (*Microcystis aeruginosa*, *Microcystis viridis*, and *Microcystis wesenbergii*) were all present in the recruitment traps, with *Microcystis aerugi-*

nosa being the dominant species (Brunberg and Blomqvist 2003).

Recruitment of *Microcystis* started in March and kept increasing until June in Lake Taihu (China). The recruitment amounts accounted for 9.33% of the maximum pelagic abundance (Zhang et al., 2005).

Oscillatoria

In Esthwaite Water, *Oscillatoria agardhii* had a rather small size of recruitment, only accounting for some one-fold of the prevailing *Aphanizomenon flos-aquae*. However, the pelagic development of *O. agardhii* in June initiated after its recruitment in late May (Head et al., 1999).

These studies above showed that different species of cyanobacteria shared some common traits in recruitment. They all acted in a similar manner of migrating from sediments, contributing to pelagic development and forming blooms ultimately. Another similarity was that they mainly peaked in a given time of year before blooms onset. In addition, shallow regions had higher recruitment than deep regions in lakes.

DRIVING FACTORS FOR CYANOBACTERIA RECRUITMENT

A number of environmental factors affected the rate of cyanobacteria recruitment, such as temperature (Fay, 1988; Latour et al., 2004; Li et al., 2004; Tao et al., 2005), light (Barbiero, 1993; Forsell and Petterson, 1995; Reynolds et al., 1981), resuspension (Karlsson-Elfgren et al., 2003; Rengefors et al., 2004; Verspagen et al., 2004) and bioturbation (Ståhl-Delbanco and Hansson, 2002), nutrients (Ståhl-Delbanco et al., 2003), anoxia (Lund and Reynolds, 1982; Trimbee and Harris, 1984; Trimbee and Prepas, 1988), and so on. Earlier studies on factors driving cyanobacteria recruitment were mainly based on field observation. Recently, simulation studies had been conducted to provide new insight into how cyanobacteria recruitment was affected by environmental factors.

Temperature and light

Generally, the optimum temperature for cyanobacteria recruitment was in agreement with the optimum temperature for its growth. As to *Anabaena circinalis*, the optimum temperature for growth, as well as recruitment, was found to be 22-24°C, germination occurred at diminishing rates down to 15°C and up to 30°C (Fay, 1988). In Lake Limmaren, the maximum recruitment rates coincided with the maximum water temperature of approximately 18-21°C during July and early August. What is more? From a physiological viewpoint, viability of *Microcystis aeruginosa* on surface sediments of the Grangent Reservoir

(France), which was indicated by esterase activity, increased gradually as temperature increased (Latour et al., 2004).

Sediments collected from lakes were used for recruitment simulation in laboratory. Tao et al. (2005) performed a simulation experiment with sediment samples from Lake Taihu. Results showed that no cyanobacteria recruitment was found below 14 and the largest amount of recruitment occurred at 18-20°C. Moreover, Li et al. (2004) found that *Microcystis* recruitment initiated at 15°C and the optimum temperature was 20°C. They also discovered that *Microcystis* pretreated under low temperature (4°C) showed fluorescence intensity increased together with temperature rose, which implied that the photosystem II (PS II) of *Microcystis* at low temperature was intact and can be reactivated when environment conditions turned suitable.

Reynolds et al. (1981) found that the formation of new recruiting colonies was stimulated when light penetrated to the lake bottom. In addition, it was reported that recruitment of *Gloeotrichia echinulata* also favored sunlight (Barbiero, 1993; Forsell and Petterson, 1995). But these phenomena were not found in Esthwaite Water (Head et al., 1999). Thus, light was not an absolute prerequisite in direct connection with recruitment (Karlsson-Elfgren and Brunberg, 2004)

Resuspension and bioturbation

Verspagen et al. (2005) observed that resuspension of sediment particles attached to benthic *Microcystis* acted an important part in recruitment, thus recruitment would be also a passive process facilitated by resuspension. In laboratory studies, Rengefors et al. (2004) found that sediment mixing was the most important factor in initiating and enhancing the recruitment of cyanobacteria. Moreover, when Ståhl-Delbanco and Hansson (2002) used *Asellus aquaticus* and *Chironomus plumosus* for simulating bioturbation, results demonstrated that bioturbation increased recruitment rates of *Microcystis* and *Anabaena*.

Nutrients

With an enclosure experiment in Lake Krankesjön (Sweden), Ståhl-Delbanco et al. (2003) found that recruitment and growth of *Microcystis* were most pronounced at concentrations of 0.498 mg/L dissolved nitrogen and 0.134 mg/L total phosphorus. The nutrient salts concentrations in regulating *Microcystis* recruitment rate corresponded to the requirement for cyanobacteria growth, namely high nutrients addition and low N:P ratio.

Anoxia

Lund and Reynolds (1982) suggested that *Microcystis* re-

ruitment was also a secondary response to environment changes in some regions where anoxic layers were formed. Additionally, the increase of the anoxic zone during stratification had been supposed to promote cyanobacteria recruitment (Trimbee and Prepas, 1988). Moreover, recruitment of cyanobacteria in Guelph Lake coincided with warmer temperature and the development of anoxia condition, which would be expected to stimulate the formation of new cyanobacteria colonies or filaments (Trimbee and Harris, 1984). However, Hansson et al. (1994) suggested that anoxic condition per se was the driving factor for cyanobacteria recruitment from sediments to water was not corroborated.

Other factors

Besides, some researchers assumed that potential factors, which affected cyanobacteria recruitment, also included zooplankton grazing (Ståhl-Delbanco et al. 2003), water stratification in deep lakes (Trimbee and Harris, 1984), dissolved oxygen in water (Lynch, 1980; Lynch and Shapiro, 1981), and so on.

Based on the studies above, it seemed that no single over-riding environmental factor triggered the recruitment of cyanobacteria. In the main, temperature, resuspension and bioturbation were recognized to be the most important factors for cyanobacteria recruitment according to field studies and simulation experiments. Other factors (such as light, nutrients, anoxia, etc.) also played a role.

CONCLUSIONS AND PERSPECTIVES

Cyanobacteria recruitment could be regarded as a process that benthic overwintering cyanobacteria migrated to the pelagic phase after germination and growth renewal under suitable conditions. It is a pathway via which bloom-forming cyanobacteria returned to water and continued its life cycle. The process of recruitment could be divided into three consecutive phases: germination, a potential growth phase, and migration to the pelagic phase. To date, several kinds of traps had been designed to study recruitment of benthic over-wintering cyanobacteria. Many cases showed that cyanobacteria recruitment in lakes were higher in shallow regions than deep regions. No single over-riding environmental factor triggered the recruitment of cyanobacteria. However, temperature, resuspension and bioturbation are recognized to be the most important environmental factors for driving cyanobacteria recruitment according to field studies and simulation experiments. Other factors (such as light, nutrients, anoxia, etc.) also played important roles.

Some species of cyanobacteria recruitment had been investigated. These studies mostly focused on the migration from sediments to water. Therefore, germination and

growth renewal mechanisms of the overwintering cyanobacteria on sediments merit further exploration.

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REFERENCES

- Barbiero RP, 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: 1581-1588.
- Barbiero RP, Welch EB (1992). Contribution of benthic blue-green algal recruitment to lake populations and phosphorus translocation. *Freshwater Biol.* 27: 249-260.
- Barbiero RP (1993). A contribution to the life history of the planktonic cyanophyte, *Gloeotrichia echinulata*. *Arch. Hydrobiol.* 127:87-100.
- Brunberg AK, Blomqvist P (2002). Benthic overwintering of *Microcystis* colonies under different environmental conditions. *J. Plankton Res.* 24: 1247-1252.
- Brunberg AK, Blomqvist P (2003). Recruitment of *Microcystis* from lake sediments: the importance of littoral inocula. *J. Phycol.* 39: 58-63.
- Cao HS, Kong FX, Tan JK, Zhang XF, Tao Y, Yang Z (2005). Recruitment of total phytoplankton, chlorophytes and cyanobacteria from lake sediments recorded by photosynthetic pigments in a large, shallow lake (Lake Taihu, China). *Int. Rev. Hydrobiol.* 90: 345-355.
- Dokulil M, Teubner K (2000). Cyanobacterial dominance in lakes. *Hydrobiologia.* 438: 1-12.
- Fallon RD, Brock TD (1980). Planktonic blue-green algae: production, sedimentation, and decomposition in Lake Mendota, Wisconsin. *Limnol. Oceanogr.* 25:72-88.
- Fallon RD, Brock TD (1981). Overwintering of *Microcystis* in Lake Mendota. *Freshwater Biol.* 11: 217-226.
- Fay P (1988). Viability of akinetes of the planktonic cyanobacterium *Anabaena circinalis*. *Proc. R. Soc. Lond. Ser. B.* 234 :283-301.
- 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: 287-293.
- Hansson LA, Rudstam LG, Johnson TB, Soranno P, Allen Y (1994). Patterns in algal recruitment from sediment to water in a dimictic, eutrophic lake. *Can. J. Fish Aquat. Sci.* 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 Biol.* 41: 759-769.
- Huovinen PS, Brett MT, Goldman CR (1999). Temporal and vertical dynamics of phytoplankton net growth in Castle Lake, California. *J. Plankton Res.* 21: 373-385.
- Hyenstrand P, Blomqvist P, Pettersson A (1998). Factors determining cyanobacterial success in aquatic systems – a literature review. *Arch. Hydrobiol. Spec. Issues Advanc. Limnol.* 51: 41-62.
- Jacoby JM, Collier DC, Welch EB, Hardy FJ, Crayton M (2000). Environmental factors associated with a toxic bloom of *Microcystis aeruginosa*. *Can. J. Fish Aquat. Sci.* 57: 231-240.
- Karlsson-Elfgren I, Brunberg AK (2004). The importance of shallow sediments in the recruitment of *Anabaena* and *Aphanizomenon* (cyanophyceae). *J. Phycol.* 40: 831-836.
- Karlsson-Elfgren I, Rydin E, Hyenstrand P, Pettersson K (2003). Recruitment and pelagic growth of *Gloeotrichia echinulata* (cyanophyceae) in Lake Erken. *J. Phycol.* 39: 1050-1056.
- Kong FX, Gao G (2005). Hypothesis on cyanobacteria bloom-forming mechanism in large shallow lakes, allelopathy. *Acta Ecol. Sin.* 25: 589-595.
- Latour D, Sabido O, Salencon MJ, Girauset H (2004). Dynamics and metabolic activity of the benthic cyanobacterium *Microcystis aeruginosa* in the Grangent reservoir (France). *J. Plankton Res.* 26: 719-726.
- Li KY, Song LR, Wan N (2004). Studies on recruitment and growth characteristic of *Microcystis* in sediment. *Acta Hydrobiologica Sin.* 28: 113-118.
- Lund JWG, Reynolds CS (1982). The development and operation of large limnetic enclosures in Blelham Tarn, English Lake District, and their contribution to phytoplankton ecology. *Prog. Phycol. Res.* 1: 1-65.
- Lynch M (1980). Aphanizomenon Blooms: Alternate Control and Cultivation by *Daphnia pulex*. In: Kerfoot WC (eds) *Evolution and Ecology of Zooplankton Communities*, University Press of New England, Hanover, pp. 299-304.
- Lynch M, Shapiro J (1981). Predation, enrichment and phytoplankton community structure. *Limnol. Oceanogr.* 26: 86-102.
- Oliver RL, Ganf GG (2000). Freshwater blooms. In: Whitton BA, Potts M (eds) *The ecology of cyanobacteria- their diversity in time and space*, Kluwer Academic Publishers, Netherlands, pp 149-194.
- Paerl HW (1988). Nuisance phytoplankton blooms in coastal, estuaries, and inland waters. *Limnol. Oceanogr.* 33: 823-847.
- Pizzolon L, Tracanna B, Prósperi C, Guerrero JM (1999). Cyanobacterial blooms in Argentinean inland waters. *Lakes Reserv. Res. Manage.* 4: 101-105.
- Preston T, Stewart WDP, Reynolds CS (1980). Bloom-forming cyanobacterium *Microcystis aeruginosa* overwinters on sediment surface. *Nature.* 288: 365-367.
- Rengefors K, Gustafsson S, Ståhl-Delbanco A (2004). Factors regulating the recruitment of cyanobacterial and eukaryotic phytoplankton from littoral and profundal sediments. *Aquat. Microb. Ecol.* 36: 213-226.
- Reynolds CS (1975). Interrelation of photosynthetic behavior and buoyancy regulation in a natural population of a blue-green alga. *Freshwater Biol.* 5: 323-338.
- Reynolds CS, Jaworski GHM, Cmiech HA, Leedale GF (1981). On the annual cycle of the blue-green alga *M. aeruginosa* Kütz Emend. Elenkin. *Phil. Trans. R. Soc. Lond. B.* 293: 419-477
- Reynolds CS, Wiseman SW (1982). Sinking loss of phytoplankton in closed limnetic systems. *J. Plankton Res.* 4: 489-522.
- Roberts RS (1985). Hypertrophy, a consequence of development. *Int. J. Environ. Stud.* 12: 72-89.
- Ståhl-Delbanco A, Hansson LA (2002). Effects of bioturbation on recruitment of algal cells from the 'seed bank' of lake sediments. *Limnol. Oceanogr.* 47: 1836-1843.
- Ståhl-Delbanco A, Hansson LA, Gyliström M (2003). Recruitment of resting stages may induce blooms of *Microcystis* at low N: P ratios. *J. Plankton Res.* 25: 1099-1106.
- Takamura N, Yasuno M, Sugahara K (1984). Overwintering of *Microcystis aeruginosa* Kütz. in a shallow lake. *J. Plankton Res.* 6: 1019-1029.
- Takamura N, Yasuno M (1988). Sedimentation of phytoplankton populations dominated by *Microcystis* in a shallow lake. *J. Plankton Res.* 10: 283-299.
- Tao Y, Kong FX, Cao HS, Zhang XF (2005). Laboratory investigations on recruitment of *Microcystis* in sediment of Taihu Lake. *J. Lake Sci.* 17: 231-236.
- Trimbee A, Prepas EE (1988). The effect of oxygen depletion on the timing and magnitude of blue-green algal blooms. *Verh. Internat. Verein. Limnol.* 23: 220-226.
- Trimbee AM, Harris GP (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.
- Tsujimura S, Tsukada H, Nakahara H, Nakajima T, Nishino M (2000). Seasonal variations of *Microcystis* populations in sediments of Lake Biwa, Japan. *Hydrobiologia.* 434: 183-192.
- Verspagen JMH, Snelder EOFM, Visser PM, Huisman J, Mur LR, Ibelings BW (2004). Recruitment of benthic *Microcystis* (Cyanophyceae) to the water column: internal buoyancy changes or resuspension? *J. Phycol.* 40: 260-270.
- Verspagen JMH, Snelder EOFM, Visser PM, Jöhnk KD, Ibelings BW,

Mur LR, Huisman J (2005). Benthic–pelagic coupling in the population dynamics of the harmful cyanobacterium *Microcystis*. *Freshwater Biol.* 50: 854-867.

Visser PM, Ibelings BW, Mur LR (1995). Autumnal sedimentation of *Microcystis* spp. as a result of an increase in carbonate ballast at reduced temperature. *J. Plankton Res.* 17: 919-933.

Zhang XF, Kong FX, Cao HS, Tan JK, Tao Y, Wang ML (2005). Research on recruitment dynamics of bloom-forming cyanobacteria in Meiliang Bay, Taihu Lake. *Chin. J. Appl. Ecol.* 16: 1346-1350.