Ann. Limnol. - Int. J. Lim. 47 (2011) 167–173
© EDP Sciences, 2011
DOI: 10.1051/limn/2011013

Available online at:
www.limnology-journal.org

Importance of large colony formation in bloom-forming cyanobacteria to dominate in eutrophic ponds

Yoshimasa Yamamoto*, Fuh-Kwo Shiah and Yi-Lung Chen

Research Center for Environmental Changes, Academia Sinica, Taipei 11529, Taiwan

Received 5 July 2010; Accepted 11 November 2010

Abstract – The distribution of bloom-forming cyanobacteria in eutrophic to hypereutrophic ponds was studied in northern Taiwan in 2009. Eighty-four ponds were sampled in mid-summer, and the relationship between colony size and relative abundance of each cyanobacterial species was analyzed. *Anabaena crassa* and *Cylindrospermopsis raciborskii* were the dominant species in terms of frequency of appearance. The colony size of *An. crassa* increased significantly with its relative abundance. The relative abundance of *C. raciborskii* was usually below 10%, and its filament length was not correlated with its relative abundance. The colonies of *Microcystis aeruginosa* normally consisted of several tens of cells. However, when *M. aeruginosa* exclusively dominated the plankton community, the average number of cells in a colony reached several hundreds. The mean filament length of *Planktothricoides raciborskii* significantly increased with its relative abundance. The correlations between colony size and relative abundance of the ten cyanobacterial species were significantly positive for three species, insignificantly positive for five species and insignificantly negative for two species. Given the various ecological advantages of large colonies, the results of this study may suggest that the formation of large colonies of some cyanobacterial species is important to their dominance and/or bloom formation.

Key words: Colony size / cyanobacterial blooms / filament length / nutrient concentration / relative abundance

Introduction

The formation of cyanobacterial blooms is frequently observed in eutrophic freshwater environments worldwide. Much effort has been made to investigate the ecophysiology of bloom-forming cyanobacteria, and some hypotheses concerning the mechanism of their dominance have been proposed (Hyenstrand *et al.*, 1998; Dokulil and Teubner, 2000). High temperature seems to be the most important prerequisite condition, since bloom-forming cyanobacteria generally become dominant in high-temperature seasons and most species exhibit maximum growth rates at high temperatures (Robarts and Zohary, 1987). If the environmental conditions are suited to the growth of cyanobacteria, then whether they become dominant in the water body depends on their ecological strategies, which are related to their competitive advantage over co-occurring photosynthetic species and defense mechanisms against predation by zooplankton. Heterocystous genera, such as *Anabaena*, *Aphanizomenon* and *Cylindrospermopsis*, can fix N_2 (Adams and Duggan, 1999), and so are assumed to have an advantage over those that cannot fix N_2. Even non-N_2-fixing genera, such as *Microcystis*, can take up dissolved inorganic nitrogen more rapidly than many other species (Takamura *et al.*, 1987). Efficient nitrogen uptake ability, together with a large capacity for phosphorus (Sbiyyaa *et al.*, 1998), may explain why cyanobacterial blooms tend to be favored in nitrogen-limited waters (Smith and Bennett, 1999). Additionally, many cyanobacterial species produce toxic compounds that can adversely affect large filter feeders (Nogueira *et al.*, 2004; Rohrlack *et al.*, 2005). As is well known, large filter feeders often disappear from the water where cyanobacteria are blooming, and this phenomenon may be at least partially accounted for by the impact of such toxins (Fulton and Paerl, 1987).

The formation of large colonies is also effective in preventing cyanobacteria from being grazed by zooplankton (Jarvis *et al.*, 1987; Yang *et al.*, 2009). Colony formation is not only involved in defense against zooplankton grazing; some ecological advantages of cyanobacteria are strongly related to their colony morphology. Diel vertical migration or buoyancy regulation enables cyanobacteria to migrate to the optimal depth for irradiance and/or nutrients

*Corresponding author: yyama@rcec.sinica.edu.tw

(Ibelings *et al.*, 1991; Brookes and Ganf, 2001), and the velocity of their migration varies positively with colony size (Kromkamp and Walsby, 1990). The effectiveness of phosphorus uptake by large colonies has been demonstrated in *Microcystis* (Shen and Song, 2007), although thick diffusion boundary layers around colonies may restrict nutrient uptake from low external concentrations (Beardall *et al.*, 2009). Moreover, large colonies are at an advantage in reducing damage from ultraviolet radiation (Sommaruga *et al.*, 2009), although they may exhibit self-shading, restricting the absorption of photosynthetically active radiation.

Recently, Yamamoto and Shiah (2010) suggested that the growth mechanism of *Microcystis aeruginosa* serves to increase the number of large colonies as the bloom proceeds. Considering the ecological advantages of large colonies, as described above, the growth mechanism of *M. aeruginosa* seems reasonable to facilitate its dominance in the plankton community. This supposition leads to the hypothesis that, if the colony size of a certain cyanobacterial species is part of an ecological strategy to dominate in the water, then colony size will increase with its relative abundance in the community of photosynthetic plankters. The aim of this study was to test this hypothesis by elucidating the relationship between relative abundance of a cyanobacterial species and its mean colony size among ponds in northern Taiwan.

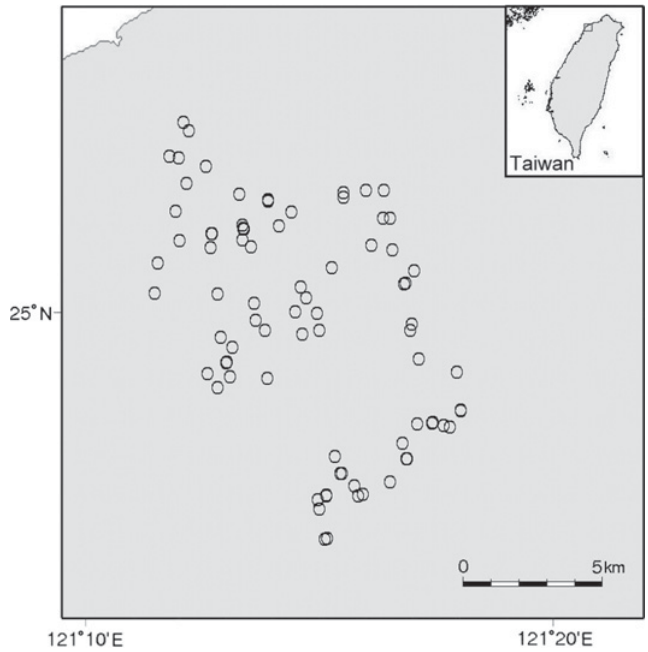

Fig. 1. Locations of sampling sites. Some points that mark locations of nearby ponds are overlapped.

Materials and methods

Sampling

The study site is located in Taoyuan, northern Taiwan (Fig. 1). The climate of this area is humid subtropical. The study site includes approximately 300 freshwater ponds, most of which are used for fisheries or irrigation. The study ponds were selected depending on accessibility and the granting of permission by the pond owners to sample the pond water. Eighty-four ponds were sampled from 18 August to 4 September 2009. Samples were taken between 11:00 a.m. and 18:00 p.m. The surface water temperature was measured using a water quality checker U-52G (Horiba, Kyoto, Japan). Thereafter, 100 mL of surface water was collected in a polycarbonate bottle, and brought in a cool box to the laboratory. Fifty milliliters of subsamples were preserved at $-20\,^{\circ}C$ until the concentrations of total nitrogen (TN) and total phosphorus (TP) were analyzed.

Measurement of nutrient concentrations

The TN concentration was determined as NO_3^--N concentration under acidic conditions using an SP-8001 spectrophotometer (Metertech Inc., Taipei, Taiwan) following hydrolysis with alkaline potassium persulfate in an autoclave at 121 °C for 30 min (Crumpton *et al.*, 1992). The TP concentration was spectrophotometrically measured as PO_4^{3-}-P concentration (Murphy and Riley, 1962) following hydrolysis with potassium persulfate in an autoclave at 121 °C for 30 min.

Counting of photosynthetic microorganisms

A 5 mL aliquot of each water sample was fixed with 50 μL Lugol's solution to count the photosynthetic plankters. The species composition was observed under an inverted microscope (Axio Observer A1, Carl Zeiss, Göttingen, Germany) at ×200 or ×400 magnification. The population densities of the photosynthetic plankters in most of the samples were very high. Therefore, to facilitate measurement, only plankters with population densities of over 20 cells.mL^{-1}, or at least one cell or colony in 50 μL of sample water, were counted. However, in the enumeration of cyanobacterial species, the lowest measurable population density was set to 1 colony.mL^{-1}. The mean numbers of cells in colonies of *Microcystis* and *Anabaena* were determined by the method of Yamamoto and Nakahara (2009). However, when all of the observed colonies contained easily enumerable cells – fewer than 30 – the cells were counted directly under an inverted microscope. Images of each species were captured using a digital CCD camera (AxioCam MRm, Carl Zeiss, Göttingen, Germany), and basic information that is required to calculate the biovolume of each species was extracted using AxioVision 4.7 software (Carl Zeiss, Göttingen, Germany). The cell or colony volumes of the enumerated species were calculated geometrically by assuming them to be cylindrical, spherical, ellipsoidal or some other appropriate regular shape for convenience,

and the number of cells or colonies of each plankter was thus converted to a biovolume.

Data analysis

The relationships between relative abundance and mean colony size (number of cells in a colony or filament length), between relative abundance and nutrient (TN or TP) concentration, and between colony size and nutrient concentration were analyzed for each species. The presence of a significant correlation was identified using Pearson's correlation.

Results

The surface water temperatures in the ponds ranged from 26.72 to 34.32 °C (data not shown). The concentrations of TN and TP were 25.5–563 μM and 0.596–34.3 μM, respectively (data not shown). A significant positive correlation existed between TN and TP concentrations ($r = 0.783$, $n = 84$, $P < 0.001$).

Table 1 shows the detected cyanobacterial species and the number of ponds in which each species was detected. Fifty-nine of the studied ponds contained at least one detectable bloom-forming cyanobacterial species. The most widely found species were *Anabaena crassa* and *Cylindrospermopsis raciborskii*, followed by *M. aeruginosa* and *Anabaena reniformis*. The frequencies of appearance of *Anabaena planctonica*, *Aphanizomenon flos-aquae*, *Arthrospira maxima* and *Raphidiopsis mediterranea* were very low.

The relationships between colony size or filament length and relative abundance of each species are shown in Figure 2 and Table 2. The relative abundance of cyanobacteria varied largely among species and ponds. The relative abundance of *An. crassa* ranged from < 0.1 to 54.6% and was not significantly correlated with colony size ($r = 0.242$, $n = 42$, $P > 0.05$). However, a significant positive correlation between relative abundance and colony size ($r = 0.351$, $n = 41$, $P < 0.05$) was detected when an outlier (relative abundance = 54.6%, cell number in a colony = 8.4) was excluded from the analysis. *An. planctonica* and *Ap. flos-aquae* with large filaments dominated in different ponds; their mean filament lengths were smaller in other ponds in which their relative abundances were lower. The relative abundance of *Ar. maxima* was less than 2.5%. Its filament length increased insignificantly with relative abundance. Despite the wide distribution of *C. raciborskii*, its relative abundance was mostly below 10%. The mean filament length of *C. raciborskii* ranged from 22.6 to 174 μm when its relative abundance was below 10%; however, when its relative abundance exceeded 10%, the mean filament length was substantially constant – between 88.5 and 103 μm. The number of cells per colony of *M. aeruginosa* was typically under 50 when its relative abundance was between < 0.1 and 85.2%; however, this value reached several hundreds when its relative abundance exceeded 98%. The relative abundance of *Planktothricoides raciborskii* ranged from <0.1 to 29.4%. The mean filament length of *P. raciborskii* increased significantly with its relative abundance. The relative abundance of *Planktothrix agardhii* was below 5% except in two ponds (13.2 and 19.2%). No significant correlation existed between relative abundance and filament length for this species. The correlations between relative abundance and colony size were insignificantly negative in *An. reniformis* and *Microcystis wesenbergii*.

The relative abundances of detected cyanobacterial species, except for *Ap. flos-aquae*, tended to decrease as TN concentration increased; a significant correlation between relative abundance and TN concentration was detected only for *An. crassa* (Table 3). The relative abundance of *An. crassa* was also negatively correlated with TP concentration (Table 3). The relationships between relative abundance and TP concentration were insignificantly negative for other species except for *Ar. maxima* and *M. aeruginosa*, which exhibited insignificant positive correlations. A significant negative correlation between mean colony size and TN concentration was observed in *An. crassa* (Table 4). In contrast, the mean colony size of *M. wesenbergii* was significantly positively correlated with TN concentration. No species showed a significant correlation between mean colony size and TP concentration (Table 4).

Table 1. Detected cyanobacterial species and number of ponds in which each species was detected.

Species	No.
Anabaena crassa	42
Anabaena planctonica	3
Anabaena reniformis	17
Aphanizomenon flos-aquae	3
Arthrospira maxima	3
Cylindrospermopsis raciborskii	35
Microcystis aeruginosa	19
Microcystis wesenbergii	7
Planktothricoides raciborskii	6
Planktothrix agardhii	14
Raphidiopsis mediterranea	1

Table 2. Correlation coefficients between size of colony or filament length and relative abundance.

Species	*r*
Anabaena crassa	**0.351**
Anabaena planctonica	0.991
Anabaena reniformis	− 0.099
Aphanizomenon flos-aquae	0.793
Arthrospira maxima	0.967
Cylindrospermopsis raciborskii	0.052
Microcystis aeruginosa	**0.724**
Microcystis wesenbergii	− 0.150
Planktothricoides raciborskii	**0.879**
Planktothrix agardhii	0.121

Bold values are significant at the 5% level. One outlier in the data for *An. crassa* was excluded from the analysis.

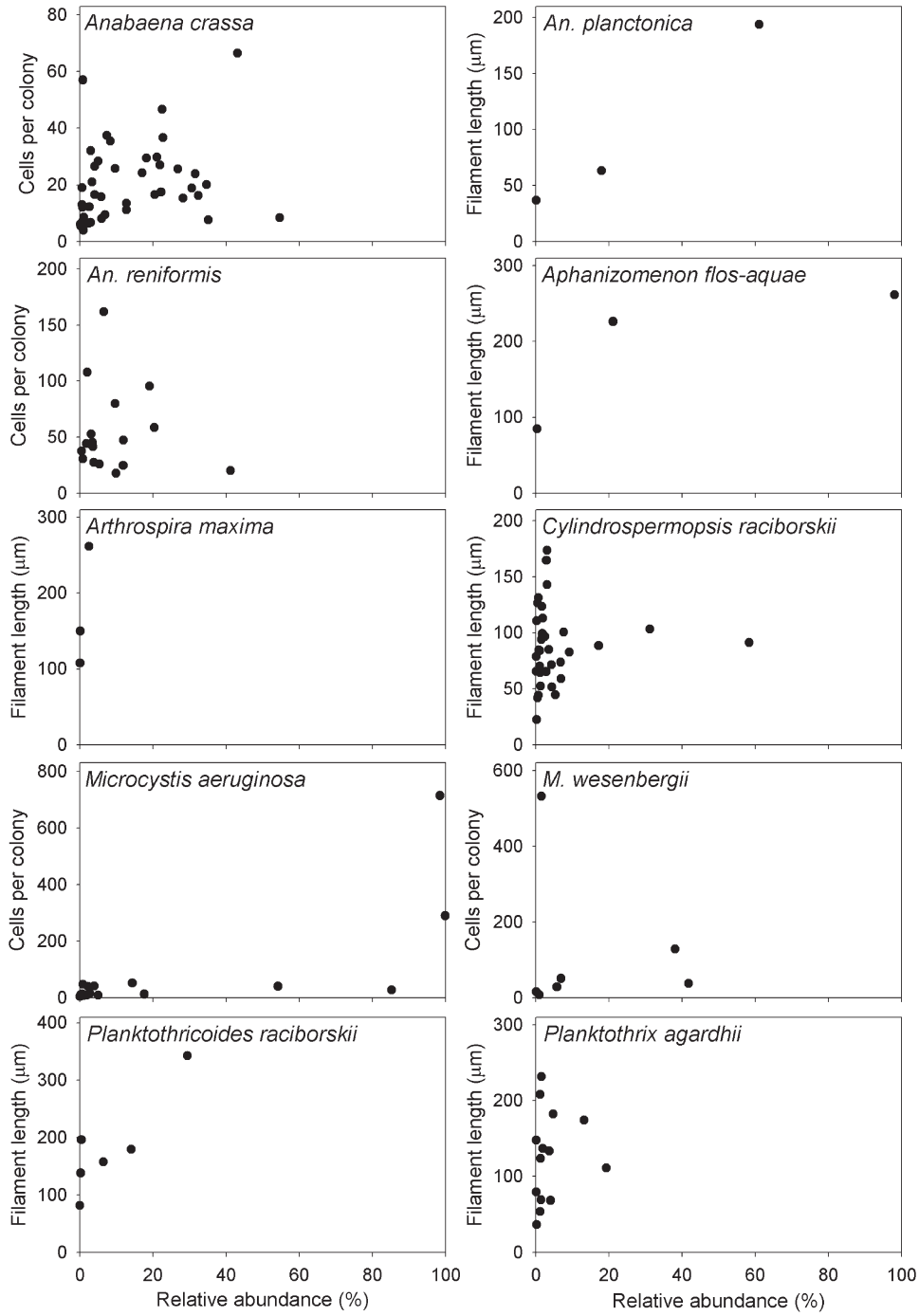

Fig. 2. Relationship between colony size or filament length and relative abundance of each cyanobacterial species.

Discussion

All study ponds can be classified as eutrophic or hypereutrophic based on TP concentration (Lampert and Sommer, 1997). Extremely high TP concentrations are probably associated with the continuous feeding of farmed fish. As expected, bloom-forming cyanobacterial species were frequently detected in many of these ponds. Since high-temperature seasons favor cyanobacterial dominance (Paerl and Huisman, 2008; Yamamoto and Nakahara, 2009), the sampling period is assumed to be the period of greatest dominance of cyanobacteria. Downing *et al.* (2001) reported that the relative abundance of cyanobacteria tends to increase with nutrient concentrations. However, this relationship does not always hold, especially in hypereutrophic waters (Jensen *et al.*, 1994; Chen *et al.*, 2003). As also observed in this study, the relative abundances of cyanobacteria in waters with very high nutrient concentrations were generally small; in such cases, diatoms and/or green algae commonly dominated.

Table 3. Correlation coefficients between relative abundance and nutrient concentration.

Species	TN	TP
Anabaena crassa	**−0.365**	**−0.348**
Anabaena planctonica	−0.663	−0.279
Anabaena reniformis	−0.226	−0.342
Aphanizomenon flos-aquae	0.268	−0.501
Arthrospira maxima	−0.697	0.514
Cylindrospermopsis raciborskii	−0.236	−0.253
Microcystis aeruginosa	−0.079	0.126
Microcystis wesenbergii	−0.050	−0.287
Planktothricoides raciborskii	−0.505	−0.376
Planktothrix agardhii	−0.294	−0.186

Bold values are significant at the 5% level.

Table 4. Correlation coefficients between colony size or filament length and nutrient concentration.

Species	TN	TP
Anabaena crassa	**−0.385**	−0.264
Anabaena planctonica	−0.755	−0.402
Anabaena reniformis	−0.301	−0.213
Aphanizomenon flos-aquae	−0.374	−0.925
Arthrospira maxima	−0.856	0.280
Cylindrospermopsis raciborskii	−0.166	−0.122
Microcystis aeruginosa	0.190	0.276
Microcystis wesenbergii	**0.832**	0.448
Planktothricoides raciborskii	−0.801	−0.674
Planktothrix agardhii	−0.238	0.030

Bold values are significant at the 5% level.

Yamamoto and Shiah (2010) suggested that the active growth of *M. aeruginosa* occurs mainly inside colonies, and when the growth of these cells begins to be suppressed as a result of self-shading, peripheral cells separate as smaller colonies. Since the growth rate of small colonies exceeds that of peripheral cells, this growth mechanism enables a population of *M. aeruginosa* to maintain high growth activity (Yamamoto and Shiah, 2010). The present study revealed that large colonies of *M. aeruginosa* formed only when this species exclusively dominated the community of photosynthetic plankters; the colonies were not significantly large even when the cyanobacterium accounted for 54.1 or 85.2% of the total biovolume of the photosynthetic plankters. This finding implies that the formation of large colonies of *M. aeruginosa* contributes to the maintenance of its heavy bloom after it dominates in the water. The number of cells per colony of *M. aeruginosa* was in the range of several hundreds, suggesting that colony size never increases indefinitely. Although having ecological advantages, large colonies exhibit a variety of disadvantages (Beardall *et al.*, 2009), which may determine the upper limit of effective colony size. The hypothesis about the relationship between large colony and dominance, however, seems not to hold for *M. wesenbergii*, because extremely large colonies of this species appeared even when its relative abundance was 1.5%. Although the DNA sequence similarity among apparent *Microcystis* species, including *M. aeruginosa* and *M. wesenbergii*, has been shown to be sufficiently high to classify these species as a single species (Otsuka *et al.*, 2001), their ecophysiological features may vary owing to morphological variation.

Our previous study showed that the pattern of seasonal change in the abundance of *P. raciborskii* (called *Planktothrix raciborskii* in our earlier paper) in Hirosawa-no-ike Pond was similar to that of the mean filament length, and that filament length was positively correlated with water temperature (Yamamoto and Nakahara, 2009). In the present study, the filament length of *P. raciborskii* significantly increased with its relative abundance. These results suggest that the formation of long filaments is closely related to the dominance of *P. raciborskii*.

Poulíčková *et al.* (2004) demonstrated that although large filaments of *P. agardhii* dominated during the active growth phase, its dominance in terms of biovolume during summer was composed of smaller filaments. This finding may imply that the formation of large filaments does not significantly contribute to the dominance of *P. agardhii*, as was also weakly indicated by the present study.

The filament length of *Ap. flos-aquae* tended to increase with its relative abundance, despite its very low frequency of appearance. The filament length of *Ap. flos-aquae* tends to increase during the period of its high abundance (Yamamoto, 2009), suggesting a close relationship between the formation of large filaments and its dominance.

A noteworthy finding of this study is that *C. raciborskii* – a tropical/subtropical species whose geographically expanding coverage in temperate regions has attracted special attention (Padisák, 1997; Wood and Stirling, 2003; Hamilton *et al.*, 2005) – is extensively distributed in northern Taiwan. *C. raciborskii* typically exhibits high abundance during summer months (Briand *et al.*, 2002; Hamilton *et al.*, 2005; Mohamed, 2007). Nevertheless, its relative abundance was generally low in this study, possibly owing to its low competitiveness despite the good adaptability (Briand *et al.*, 2002). The mean filament lengths of *C. raciborskii* were not very large even when, exceptionally unusually, the species represented a large fraction of the phytoplankton community, suggesting that the formation of large filaments does not contribute to its dominance.

Previous field surveys have shown that the colony size of *Anabaena* species tends to decline with time, seemingly independently of abundance (Smith and Gilbert, 1995; Yamamoto and Nakahara, 2009). The colony size of *An. crassa* increased with its relative abundance, whereas that of *An. reniformis* exhibited an opposite trend, suggesting that the ecological roles of large colonies of these species may differ. Adjacent coils in an *An. reniformis* colony tightly contract around each other to form a pipe-like structure. The availability of light inside such a "pipe" declines significantly as the colony size increases, which may partially explain the disadvantage of large colony formation of *An. reniformis*. Large filaments of *An. planctonica* tended to dominate in the water,

but the actual ecological importance of large filament formation in this species remains unclear, owing to its very low frequency of appearance.

Several abiotic factors, such as nutrient concentration (Hašler *et al.*, 2003; Kruskopf and Du Plessis, 2006), water temperature (Seki *et al.*, 1981) and irradiance (Hašler *et al.*, 2003), are known to influence the colony size of cyanobacteria. Furthermore, seasonal change in the colony size or filament length of a certain species may be attributable to the succession of different genotypes, given the presence of several genotypes in a population (Kardinaal *et al.*, 2007) and the genotype-dependent range of colony size (Wilson *et al.*, 2006). Grazing by zooplankton may further alter the distribution of sizes of cyanobacterial colonies; some species reduce cyanobacterial colony size (Burns and Xu, 1990), whereas others may lead to the dominance of large colonies by reducing the number of smaller colonies (Holm *et al.*, 1983). These findings imply that the distribution of sizes of cyanobacterial colonies is determined by a complex interaction of abiotic and biotic factors. Nevertheless, this study demonstrated that many cyanobacterial species exhibit a positive correlation between colony/filament size and their relative abundance. Despite possible disadvantages in relation to light or nutrient acquisition, large colony/filament formation accompanies various ecological advantages (Beardall *et al.*, 2009), which may significantly facilitate the dominance of some cyanobacterial species.

Acknowledgements. We would like to thank K.-Y. Li for his editorial assistance, as well as T. Knoy for correcting the English in the manuscript.

References

Adams D.G. and Duggan P.S., 1999. Heterocyst and akinete differentiation in cyanobacteria. *New Phytol.*, *144*, 3–33.

Beardall J., Allen D., Bragg J., Finkel Z.V., Flynn K.J., Quigg A., Rees T.A.V., Richardson A. and Raven J.A., 2009. Allometry and stoichiometry of unicellular, colonial and multicellular phytoplankton. *New Phytol.*, *181*, 295–309.

Briand J.F., Robillot C., Quiblier-Llobéras C., Humbert J.F., Couté A. and Bernard C., 2002. Environmental context of *Cylindrospermopsis raciborskii* (Cyanobacteria) blooms in a shallow pond in France. *Water Res.*, *36*, 3183–3192.

Brookes J.D. and Ganf G.G., 2001. Variations in the buoyancy response of *Microcystis aeruginosa* to nitrogen, phosphorus and light. *J. Plankton Res.*, *23*, 1399–1411.

Burns C.W. and Xu Z., 1990. Calanoid copepods feeding on algae and filamentous cyanobacteria: rates of ingestion, defaecation and effects on trichome length. *J. Plankton Res.*, *12*, 201–213.

Chen Y., Qin B., Teubner K. and Dokulil M.T., 2003. Long-term dynamics of phytoplankton assemblages: *Microcystis*-domination in Lake Taihu, a large shallow lake in Chuna. *J. Plankton Res.*, *25*, 445–453.

Crumpton W.G., Isenhart T.M. and Mitchell P.D., 1992. Nitrate and organic N analyses with second-derivative spectroscopy. *Limnol. Oceanogr.*, *37*, 907–913.

Dokulil M.T. and Teubner K., 2000. Cyanobacterial dominance in lakes. *Hydrobiologia*, *438*, 1–12.

Downing J.A., Watson S.B. and McCauley E., 2001. Predicting cyanobacteria dominance in lakes. *Can. J. Fish. Aquat. Sci.*, *58*, 1905–1908.

Fulton R.S. III and Paerl H.W., 1987. Toxic and inhibitory effects of the blue-green alga *Microcystis aeruginosa* on herbivorous zooplankton. *J. Plankton Res.*, *9*, 837–855.

Hamilton P.B., Ley L.M., Dean S. and Pick F.R., 2005. The occurrence of the cyanobacterium *Cylindrospermopsis raciborskii* in Constance Lake: an exotic cyanoprokaryote new to Canada. *Phyclogia*, *44*, 17–25.

Hašler P., Poulíčková A. and Vařeková Š., 2003. Comparative studies on two strains of the genus *Planktothrix* (Cyanophyta, Cyanoprokaryota). *Algol. Stud.*, *108*, 31–43.

Holm N.P., Ganf G.G. and Shapiro J., 1983. Feeding and assimilation rates of *Daphnia pulex* fed *Aphanizomenon flos-aquae*. *Limnol. Oceanogr.*, *28*, 677–687.

Hyenstrand P., Blomqvist P. and Pettersson A., 1998. Factors determining cyanobacterial success in aquatic systems – a literature review. *Arch. Hydrobiol.*, *51*, 41–62.

Ibelings B.W., Mur L.R. and Walsby A.E., 1991. Diurnal changes in buoyancy and vertical distribution in populations of *Microcystis* in two shallow lakes. *J. Plankton Res.*, *13*, 419–436.

Jarvis A.C., Hart R.C. and Combrink S., 1987. Zooplankton feeding on size fractionated *Microcystis* colonies and *Chlorella* in a hypertrophic lake (Hartbeespoort Dam, South Africa): implications to resource utilization and zooplankton succession. *J. Plankton Res.*, *9*, 1231–1249.

Jensen J.P., Jeppesen E., Olrik K. and Kristensen P., 1994. Impact of nutrients and physical factors on the shift from cyanobacterial to chlorophyte dominance in shallow Danish lakes. *Can. J. Fish. Aquat. Sci.*, *51*, 1692–1699.

Kardinaal W.E.A., Janse I., Kamst-van Agterveld M., Meima M., Snoek J., Mur L.R., Huisman J., Zwart G. and Visser P.M., 2007. *Microcystis* genotype succession in relation to microcystin concentrations in freshwater lakes. *Aquat. Microb. Ecol.*, *48*, 1–12.

Kromkamp J. and Walsby A.E., 1990. A computer model of buoyancy and vertical migration in cyanobacteria. *J. Plankton Res.*, *12*, 161–183.

Kruskopf M. and Du Plessis S., 2006. Growth and filament length of the bloom forming *Oscillatoria simplicissima* (Oscillatoriales, Cyanophyta) in varying N and P concentrations. *Hydrobiologia*, *556*, 357–362.

Lampert W. and Sommer U., 1997. Limnoecology: the ecology of lakes and streams, Oxford University Press, New York, 382 p.

Mohamed Z.A., 2007. First report of toxic *Cylindrospermopsis raciborskii* and *Raphidiopsis mediterranea* (Cyanoprokaryota) in Egyptian fresh waters. *FEMS Microbiol. Ecol.*, *59*, 749–761.

Murphy J.B. and Riley J.P., 1962. A modified single solution method for the determination of phosphate in natural waters. *Anal. Chim. Acta*, *27*, 31–36.

Nogueira I.C.G., Saker M.L., Pflugmacher S., Wiegand C. and Vasconcelos V.M., 2004. Toxicity of the cyanobacterium *Cylindrospermopsis raciborskii* to *Daphnia magna*. *Environ. Toxicol.*, *19*, 453–459.

Otsuka S., Suda S., Shibata S., Oyaizu H., Matsumoto S. and Watanabe M.M., 2001. A proposal for the unification of five species of the cyanobacterial genus *Microcystis* Kützing ex Lemmermann 1907 under the Rules of the Bacteriological Code. *Int. J. Syst. Evol. Microbiol.*, *51*, 873–879.

Padisák J., 1997. *Cylindrospermopsis raciborskii* (Woloszynska) Seenayya et Subba Raju, an expanding, highly adaptive cyanobacterium: worldwide distribution and review of its ecology. *Arch. Hydrobiol., Suppl.*, *107*, 563–593.

Paerl H.W. and Huisman J., 2008. Blooms like it hot. *Science*, *320*, 57–58.

Poulíčková A., Hašler P. and Kitner M., 2004. Annual cycle of *Planktothrix agardhii* (Gom.) Anagn. & Kom. nature population. *Int. Rev. Hydrobiol.*, *89*, 278–288.

Robarts R.D. and Zohary T., 1987. Temperature effects on photosynthetic capacity, respiration, and growth rates of bloom-forming cyanobacteria. *N. Z. J. Mar. Freshwater Res.*, *21*, 391–399.

Rohrlack T., Christoffersen K., Dittmann E., Nogueira I., Vasconcelos V. and Börner T., 2005. Ingestion of microcystins by *Daphnia*: Intestinal uptake and toxic effects. *Limnol. Oceanogr.*, *50*, 440–448.

Sbiyyaa B., Loudiki M. and Oudra B., 1998. Nitrogen and phosphorus intracellular capacity in storage by *Microcystis aeruginosa* Kütz and *Synechocystis* sp.: toxic cyanobacteria occasionally forming blooms in Marrakesch area (Morocco). *Ann. Limnol. - Int. J. Lim.*, *34*, 247–257.

Seki H., Ozawa H. and Ichimura S., 1981. Temperature dependence of filament length of *Anabaena spiroides* Klebahn var. *crassa* Lemm. *Hydrobiologia*, *83*, 419–423.

Shen H. and Song L., 2007. Comparative studies on physiological responses to phosphorus in two phenotypes of bloom-forming *Microcystis*. *Hydrobiologia*, *592*, 475–486.

Smith A.D. and Gilbert J.J., 1995. Spatial and temporal variability in filament length of a toxic cyanobacterium (*Anabaena affinis*). *Freshwater Biol.*, *33*, 1–11.

Smith V.H. and Bennett S.J., 1999. Nitrogen:Phosphorus supply ratios and phytoplankton community structure in lakes. *Arch. Hydrobiol.*, *146*, 37–53.

Sommaruga R., Chen Y. and Liu Z., 2009. Multiple strategies of bloom-forming *Microcystis* to minimize damage by solar ultrabiolet radiation in surface waters. *Microb. Ecol.*, *57*, 667–674.

Takamura N., Iwakuma T. and Yasuno M., 1987. Uptake of ^{13}C and ^{15}N (ammonium, nitrate and urea) by *Microcystis* in Lake Kasumigaura. *J. Plankton Res.*, *9*, 151–165.

Wilson A.E., Wilson W.A. and Hay M.E., 2006. Intraspecific variation in growth and morphology of the bloom-forming cyanobacteria *Microcystis aeruginosa*. *Appl. Environ. Microbiol.*, *72*, 7386–7389.

Wood S.A. and Stirling D.J., 2003. First identification of the cylindrospermopsin-producing cyanobacterium *Cylindrospermopsis raciborskii* in New Zealand. *N. Z. J. Mar. Freshwater Res.*, *37*, 821–828.

Yamamoto Y., 2009. Environmental factors that determine the occurrence and seasonal dynamics of *Aphanizomenon flos-aquae*. *J. Limnol.*, *68*, 122–132.

Yamamoto Y. and Nakahara H., 2009. Seasonal variations in the morphology of bloom-forming cyanobacteria in a eutrophic pond. *Limnology*, *10*, 185–193.

Yamamoto Y. and Shiah F.K., 2010. Variation in the growth of *Microcystis aeruginosa* depending on colony size and position in colonies. *Ann. Limnol. - Int. J. Lim.*, *46*, 47–52.

Yang Z., Kong F., Yang Z., Zhang M., Yu Y. and Qian S., 2009. Benefits and costs of the grazer-induced colony formation in *Microcystis aeruginosa*. *Ann. Limnol. - Int. J. Lim.*, *45*, 203–208.