



LUND UNIVERSITY

Recruitment from resting stages among bloom-forming cyanobacteria

Ståhl-Delbanco, Annika

2004

[Link to publication](#)

Citation for published version (APA):

Ståhl-Delbanco, A. (2004). *Recruitment from resting stages among bloom-forming cyanobacteria*. [Doctoral Thesis (compilation), Department of Biology]. Annika Ståhl-Delbanco, Limnology and Marine Ecology, Ecology Building, Sölveg. 37, SE-223 62 Lund,.

Total number of authors:

1

General rights

Unless other specific re-use rights are stated the following general rights apply:

Copyright and moral rights for the publications made accessible in the public portal are retained by the authors and/or other copyright owners and it is a condition of accessing publications that users recognise and abide by the legal requirements associated with these rights.

- Users may download and print one copy of any publication from the public portal for the purpose of private study or research.
- You may not further distribute the material or use it for any profit-making activity or commercial gain
- You may freely distribute the URL identifying the publication in the public portal

Read more about Creative commons licenses: <https://creativecommons.org/licenses/>

Take down policy

If you believe that this document breaches copyright please contact us providing details, and we will remove access to the work immediately and investigate your claim.

LUND UNIVERSITY

PO Box 117
221 00 Lund
+46 46-222 00 00

RECRUITMENT FROM RESTING STAGES AMONG
BLOOM-FORMING CYANOBACTERIA

Recruitment from resting stages among bloom-forming cyanobacteria

Annika Ståhl-Delbanco

Academic Dissertation for the degree of Doctor of Philosophy, to be defended in English at the Department of Ecology, Limnology and Marine Ecology, on May 6th, 2004 at 9³⁰ am, by the permission of the Faculty of Natural Science of Lund University.

Locality: Blue Hall, Ecology-building, Sölveg. 37, Lund.
Faculty opponent: Professor Kirsten Christoffersen, Freshwater Biology Laboratory,
Hillerød, Denmark.

TO MY FAMILY WITH LOVE

A doctoral thesis at a university in Sweden is produced either as a monograph or as a collection of papers. In the latter case, the introductory part constitutes the formal thesis, which summarizes the accompanying papers. These have either already been published or are manuscripts at various stages (in press, submitted or in ms).

Front cover illustration: A cyanobacterial bloom formation in Lake Ringsjön (southern Sweden).
Based on a photograph by Annika Ståhl-Delbanco, July 2003.

Layout: Gunilla Andersson/ZooBoTech & GrafikGruppen
Proofreading: Annika Ståhl-Delbanco
Printed by Xanto Grafiska AB, S Sandby

ISBN 91-7105-204-6
SE-LUNBDS/NBLI-04/1054+92 pp

Contents

Page

This thesis is based on the following papers:

- 1 Ståhl-Delbanco, A., L.-A. Hansson, and M. Gyllström. 2003. Recruitment of resting stages may induce blooms of *Microcystis* at low N:P ratios. – J. Plankton Res. 25: 1099–1106. 33
- 2 Ståhl-Delbanco, A. and L.-A. Hansson. Decreasing N:P ratios stimulate recruitment of *Microcystis*. – Manuscript. 43
- 3 Ståhl-Delbanco, A. and L.-A. Hansson. 2002. Effects of bioturbation on recruitment of algal cells from the “seed bank” of lake sediments. – Limnol. Oceanogr. 47: 1836–1843. 61
- 4 Rengefors, K., S. Gustafsson, and A. Ståhl-Delbanco. Factors regulating the recruitment of cyanobacterial and eukaryotic phytoplankton from littoral and profundal sediments. – Submitted to Aquat. Microb. Ecol. 71

Paper 1 and 3 are reprinted with permission from the publishers.

Index of summary

Recruitment from resting stages among bloom-forming cyanobacteria

WATER – A COMMON POOL RESOURCE	11
Organized work to sustain water resources	11
ANTHROPOGENIC IMPACT	12
Eutrophication	12
BLOOM-FORMING CYANOBACTERIA	13
Success-hypothesis	13
Resting stages	14
Escape in time and space	14
P translocation	14
MECHANISMS BEHIND RECRUITMENT OF RESTING STAGES	15
Temperature	15
Light/ Day-length	16
O ₂	16
Nutrients	17
Zooplankton	19
Sediment mixing	19
Littoral zone	20
REDUCING EUTROPHICATION	21
New management plans needed	21
SHORT SUMMARY OF PAPERS	23
Paper 1	23
Paper 2	23
Paper 3	23
Paper 4	23
ACKNOWLEDGEMENT	25
REFERENCES	26

Recruitment from resting stages among bloom-forming cyanobacteria

WATER – A COMMON POOL RESOURCE

Natural ecological systems provide services that are fundamental to human life, but generally not traded in economic markets. Thus, they are often taken for granted and become overused. In social science the services are named “Common Pool Resources” (CPR’s), since they can be used by anyone and are owned by nobody. In the middle of the 1960’s the famous paper “The Tragedy of the Commons” (Hardin 1968) was written, which stated that all environmental resources, not protected by private or governmental interests, would get overexploited by an increasing human population (Hardin 1968). The logic for this was that people inevitably harm natural resources when they use them, and more people do more harm, especially since people tend to suspect other people to free-ride, by overusing or underinvesting in the maintenance of the resource (Pretty 2003). It has, fortunately, turned out that Hardin was not entirely right. Since then, the human population on Earth has grown almost twofold and, despite this, many CPR’s are still functioning in a sustainable way, thanks to organizations that have managed to protect common sources without governmental or private instruments (Ostrom 1992; Ostrom et al. 1999). One example of a sustainable CPR is Maine’s lobster fishery, which

has been exploited for over 100 years and still is doing fine (Jensen 2000), (for further references about sustainable CPR’s, see Ostrom 1992). The tools providing sustainable resource use are confidence between people of social bonds and norms, and sanctions that ensure that those who break the rules know that they will get punished (Pretty 2003). In other words, people may invest in collective actions if they know that others will do so too, which means that free human access to CPR’s does not have to be a tragedy for the development of natural resources. This is important to bear in mind when confronting the facts that global supply of water with good quality is diminishing, while the demand is increasing with a growing population, a yet unsolved equation and a challenge for politicians, economists, stakeholders and, indeed, for natural scientists (Cottingham 2002; Everard 1999).

Organized work to sustain water resources

In 1992 a global meeting was held in Rio de Janeiro about the depriving ecological status of the Globe. This meeting resulted in an agenda for an ecological and socio-economic stable development to maximize the chances for environmental and social conditions to support human wellbeing and health in the future. Approximately ten years later, a directive about water planning and management

(Water Framework Directive 2000/60/EC) was implemented in the EU-states, in order to assure sustained good water quality and restore bad water bodies within member states. Important features of the directive have clear connections to the agreements from the global meeting. Member states should: 1) work on catchment levels instead of community levels in a system oriented fashion; 2) involve public participation; and 3) apply the “polluters pay principle” as parts of the process. All member states are currently working on the implementation of the directive, and by the year 2009 we will begin to see the outcome.

As it is a *framework* directive, the working details are not fixed (Moss et al. 2002), which render the member states a certain freedom. The member states themselves may for example set the way public participation should be incorporated in the process, since this is not regulated by the directive. Every environmental decision requires tradeoffs between what would be best for the environment versus different human needs and demands, and therefore should best management practice be chosen. In order to decide which is the best management practice, information about the resource and for what purpose and extent the resource is used are important. To provide information about the usage, stakeholders (people with a certain interest) should be part of the discussions and plans for the management of a certain water resource. In that way, several aspects are taken into account: both environmental, social, and economic, and at the same time, stakeholders are able to build confidence among each other (e.g. Gregory and Keeney 1994; Valiela et al. 2000; Collentine et al. 2002).

ANTHROPOGENIC IMPACT

So, what kind of environmental problems are our water resources facing? An investigation of lakes in 143 catchments with human pop-

ulations in low numbers, showed that most lakes were anthropogenically affected, by one or several of the following factors: drainage of land, pollution of toxic substances, introduction of non-native species, and eutrophication (Brunberg and Blomqvist 2001). In addition, Brönmark and Hansson (2002) identified some major ways of how anthropogenic activities are likely to affect freshwater resources in the future. These authors also identified eutrophication, contamination of toxic substances, and invasive species as the major problems of today, and also added acid rain to the list. In their predictions for the future 25 years they included global warming, UV-radiation, endocrine disrupters, and, again, invasive species as major problems, whereas eutrophication, acidification, and toxic substances were regarded as declining environmental problems in developed countries. However, with respect to developing countries, these problems were considered to become even more disastrous in the future than they are today (Brönmark and Hansson 2002).

My summary is too short to be able to discuss every single one of those threats, and I will therefore focus on one of them, eutrophication, since this threat is of importance for the development of cyanobacteria, the target organisms of my thesis.

Eutrophication

During the last century, human activities have led to increasing concentrations of nitrogen (N) and phosphorus (P) in natural aquatic systems. The amount of anthropogenically fixed nitrogen (by making fertilizers, planting of legumes, and burning of fossil fuels) has, for example, more than doubled during the last hundred years (Lubchenco 1998). More nutrients to an aquatic system mean a higher carrying capacity, that is, more organisms are able to grow and reproduce, and eutrophication is a fact.

In most freshwater systems, phosphorus limits further growth. Hence, eutrophication of freshwater systems are mainly due to elevated phosphorus loads, from anthropogenic sources such as industry, sewage and enhanced agricultural production (Reynolds and Davies 2001).

In the 1970s in Sweden, large investments were made to remove phosphorus from the sewage water. Since then, the major nutrient loads of both phosphorus and nitrogen are in the form of nonpoint source pollutions, derived from activities dispersed over wide areas of land. Above all, excessive use of fertilizers and high-density livestock operations are the ultimate causes of non-point pollution from agricultural lands. On a global scale, more nutrients are added as fertilizers than are removed as produce, the underlying cause of nonpoint pollution from agriculture (Carpenter et al. 1998).

BLOOM-FORMING CYANOBACTERIA

Increased eutrophication processes have stimulated growth of especially one group of phytoplankton, namely cyanobacteria, into extremely high abundances, blooms. Cyanobacterial blooms are natural phenomena, dating beyond human influence (Bianchi et al. 2000). However, since the middle of the last century, cyanobacterial blooms in eutrophicated water bodies have become a common problem in freshwaters as well as in estuarine areas. In Sweden, the intensity of blooms increased until the 1970s, when phosphorus concentrations in sewage waters were lowered. Since then, the intensity and frequency of blooms have remained constant. The reasons for this are that eutrophicated lakes suffer from internal phosphorus loading (phosphorus recycling from the sediment), and from continued nutrient pollution in the form of non-point source pollutions.

So, what is a bloom and what harm do they do? In short, a bloom can be described as a heavy growth of a dominating phytoplankton species into abundances that are visible to the bare eye. Sometimes the abundances are so high that the water column looks like spinach soup (e.g. see front cover). Besides, decomposing phytoplankton material can gather in the surface layers and form scums with bad odours. In addition, decomposing material consume oxygen to a high extent, which can render anoxia and fish death. Another unpleasant feature is that several cyanobacterial species are able to produce toxins that render lethal or sublethal effects within all trophic levels of water ecosystems, and may accumulate in the food web (Christoffersen 1996). The toxins are neuro- and hepatotoxic and affect both animals and human beings (Codd 2000). Overall, cyanobacterial blooms considerably reduce the quality of water resources.

Success-hypothesis

Why cyanobacterial blooms develop in eutrophicated water bodies are not fully understood, but a range of hypotheses have been put forward to explain their success (for references, see Paerl 1988; Shapiro 1990; Hyenstrand et al. 1998; Dokulil and Teubner 2000). One of these hypotheses is that they have a high temperature optimum, rendering them an advantage over other algae during warm summer days. Another, very debated, hypotheses is that they should prefer low N:P ratios, both due to their low internal optimum N:P ratios, and to their ability to fix nitrogen; a feature that several cyanobacteria have evolved.

A third hypothesis refers to their ability to control their buoyancy. Thereby, they are able to proliferate over other algae by simply migrating to nutrient rich water layers during nutrient deficiency, or to the surface where they shade their competitors from light access.

Resting stages

Related to their migratory behavior is their ability to form resting stages, which deposit at the sediment surface during sub-optimal growth conditions. These resting stages can become active and recruit to the water column, where the growth is continued, when the environment is suitable again. In some species (e.g. *Anabaena* and *Aphanizomenon*) a distinct cell-type called akinete is formed (Reynolds and Walsby 1975; Fryxell 1983) but in others (e.g. *Woronichinia*, *Microcystis*), the resting stage simply consists of a vegetative colony (e.g. Reynolds and Walsby 1975; Reynolds and Rogers 1976; Preston et al. 1980; Fallon and Brock 1981; Takamura et al. 1984; Boström et al. 1989).

The pool of resting stages can become large. Boström et al. (1989) found for example that the benthic biomass of *Microcystis* throughout the year was larger than or similar to the planktonic biomass during the peak of the bloom. Other examples are from Baker (1999), who found abundances of almost 10^5 akinetes g^{-1} wet weight fine textured clay sediments, and from Reynolds et al. (1981) who found more than 2000 colonies of *Microcystis* ml^{-1} surface sediment. These figures are comparable to findings from marine sediments of viable resting stages from diatoms and dinoflagellates (McQuoid et al. 2002), species common in bloom formations.

Resting stages can be an important feature in determining the phytoplankton composition and succession patterns as they may provide inoculum of new species (e.g. Reynolds and Rogers, 1976; Head et al. 1998; Baker 1999; Head et al. 1999a; Karlsson Elfgren 2003), and since the recruitment sometimes is heavy (Barbiero and Welch 1992) and may result in blooms (Reynolds 1972; Reynolds and Walsby, 1975; Perakis et al. 1996; **Ståhl-Delbanco et al. 2003 Paper 1**). Actually, Hansson (1996a) found that recruiting species dominated more often than by chance,

which imply that resting stages could be an important feature to tackle when addressing problems with water blooms.

Escape in time and space

Resting stages can survive for a long time. Cronberg (1986) found, for example, akinetes at a sediment depth that corresponded to the 14th century and Stockner and Lund (1970) managed to culture cells that were almost 200 years old (unclear what species though). Anyhow, Livingstone and Jaworski (1980) managed to germinate akinetes that were at least 60 years old, why the conclusion is that resting stages can remain vital for decades or more.

Another adaptive response is that they can survive extreme conditions, such as drought (Forsell, 1998) and anoxia (Brunberg and Blomqvist, 2002), as well as darkness and high water pressure (Tsujimura et al. 2000).

Important consequences of long-term survival are that species may return decades later or get transferred to new ecosystems (by migrating animals for example). Sudden outbreaks of new species to ecosystems do happen from time to time (Cronberg 1982; Hadas et al. 1999; Tsujimura et al. 2001; Rekar and Hindák 2002), which probably is a result of transport of resting stages from deeper sediment layers or from other ecosystems. *Aphanizomenon* was, for example, observed for the first time in Lake Kinneret, Israel, after the reconstruction of an old wetland upstream the same catchment (Pollinger et al. 1998). Ecosystems without a history of the new species may lack competitors or suitable herbivores, why outbursts of such “new” species may render problems with extreme bloom formations.

P translocation

Before migrating to the water phase, recruiting organisms are able to assimilate nutrients

from the interstitial water of the sediment. This can result in heavy subsidies of phosphorus from the sediment to the water phase and thereby increase the internal load (e.g. Trimbee and Harris 1984; Barbiero and Welch 1992; Pettersson et al. 1993). Boström et al. (1989) found, for example, that the biomass-bound phosphorus in benthic *Microcystis* colonies constituted approximately 10% of the phosphorus content of the lake sediments, while Brunberg (1995) found that *Microcystis* was responsible for two-thirds of the total phosphorus release from the uppermost sediment surface. Phosphorus transport from the sediment has also been recovered from *Gloeotrichia* (Istvánovics et al. 1993), *Aphanizomenon* (Osgood 1988; Barbiero and Kann 1994), and *Oscillatoria* (Head et al. 1999b).

MECHANISMS BEHIND RECRUITMENT OF RESTING STAGES

Recruitment of resting stages to the water column is an active process, initiated by some factor that is often species specific (Hansson 1993; Hansson et al. 1994), for example elevated temperatures, light and nutrient availability, oxygen concentrations, low grazing pressures, and sediment mixing (Figure 1).

Temperature

In laboratory experiments both Huber (1985), Karlsson Elfgrén (2003) and Tsujimura and Okubo (2003) found that elevated temperatures were needed to germinate akinetes of *Nodularia*, *Gloeotrichia*, and *Anabaena*. Besides, elevated temperatures are often found to be correlating with the onset of cyanobacterial recruitment in the field (e.g. Reynolds 1972; McQueen and Lean 1987; Barbiero 1993). In a combined laboratory and field study (Paper 4), I found that elevat-

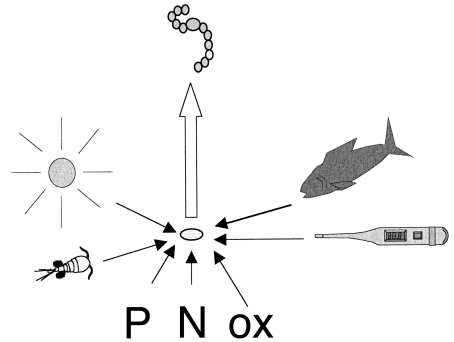


Fig. 1. Illustration of different factors (solar radiation, temperature, nutrients, oxygen concentrations, grazer abundance, sediment mixing) that can be involved in the recruitment from resting stages into planktonic stages.

ed temperatures could be important for recruitment of cyanobacteria. The main aim with this study was to investigate the importance of the littoral zone as the inoculum site compared with the profundal zone. Included in the laboratory experiment was a test of how elevated temperatures, light availability and sediment mixing (factors that differ between the littoral and profundal zone) affected recruitment rate of natural resting stages. The study showed that the littoral zone was the major site for recruitment (Figure 2). Light, sediment mixing and temperature were all found to both trigger and enhance recruitment rate.

In one of my other studies I also found that high recruitment rates of *Microcystis* were correlated with elevated temperatures (Paper 2). This was a long-term investigation of recruitment rate of *Microcystis* in two lakes of different nutrient status (hypertrophic Lake Finjasjön and mesotrophic Lake Krankesjön in southern Sweden), in combination with a laboratory experiment. From the long-term survey, I wanted to distil the major triggering factors for recruitment of *Microcystis*, so along with the recruitment data I collected 14 different physical and biological variables, and

analyzed the material with different statistical methods (regression analysis and Principle Component Analysis). I hereby found that elevated temperatures and low N:P ratios played a significant role in determining recruitment rate and abundance of *Microcystis* (Paper 2).

Light/Day-length

Light is a prerequisite for autotrophic growth, why it seems natural to include this abiotic factor to the list. Besides, in several laboratory studies, light has been found to be essential, at least in small amounts, to germinate akinetes of *Nodularia*, *Anabaena* respectively *Gloeotrichia*, (Huber 1985; van Dok and Hart 1997; Karlsson Elfgren 2003; Tsujimura and Okubo 2003). Recruitment correlating with improving light conditions has also been found in several field studies (e.g. Reynolds 1972; Barbiero 1993; Barbiero and Kann 1994). However, in a field study by Sonnichsen et al. (1997), it was found that cyanobacteria recruited to traps despite that those were covered from light intrusion. It does not say anything about how long they were covered though, which implies that the

germination process could have started before the coverage was applied.

In one of my own laboratory studies, I found that light was important for recruitment of *Anabaena* (Paper 4). In another study in the field, I found that recruitment of *Microcystis* was correlated with prolonged day-length, an indirect measure of light availability (Paper 2). The length of the photoperiod has also been found to be important for the recruitment of some species of diatoms (Eilertsen et al. 1995).

Barbiero and Kann (1994) suggested that the temperature needed to be above a certain threshold to initiate recruitment, and maybe this holds true for light intensity/ photoperiod as well.

O₂

Anoxic conditions or conditions with very low oxygen concentrations (<2 mg l⁻¹) are often mentioned to be triggering recruitment of cyanobacteria (Reynolds et al. 1981; Cáceres and Reynolds 1984; Trimbee and Harris 1984; Trimbee and Prepas 1988). However, Reynolds (1972), Osgood (1988) and Barbiero (1993) found that *Anabaena*,

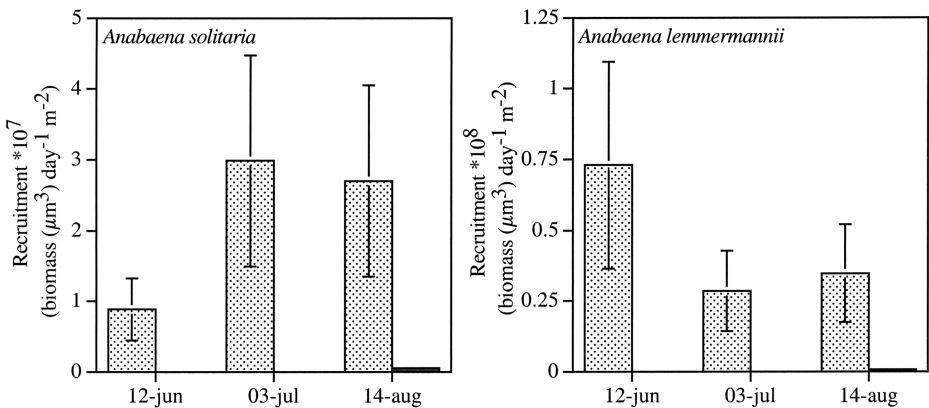


Fig. 2. Recruitment of *Anabaena solitaria* and *Anabaena lemmermannii* at a littoral (light patterned bars) and profundal (dark grey bars) site in eutrophic Lake Erken. Y-bars denote ± 1 S. E. Modified from Paper 4.

Aphanizomenon, respectively *Gloeotrichia* germinated on oxygenated sediments. Furthermore, in one of my own field studies I found that recruitment of *Microcystis* seemed to be stimulated by either very low oxygen concentrations (<3 mg l⁻¹) or by oxygen concentrations between 7–12 mg l⁻¹ (Paper 2), which might indicate that oxygen concentrations are without importance (Figure 3). This interpretation corresponds to the results of Head et al. (1999a). They did not find any correlation between recruitment of cyanobacteria and any of the environmental variables: oxygen concentration, light intensity and temperature regime.

Nutrients

Resting stages are formed at nutrient deficiency (e.g. van Dok and Hart 1996; Meeks and Campbell 2002), why it seems natural to believe that nutrients are required for germination. In fact, in laboratory studies, Reddy

(1984) found that supply of both nitrogen and phosphorus were needed to germinate akinetes of *Anabaena*, and Huber (1985) and van Dok and Hart (1997) found that a phosphorus source was needed to germinate akinetes of *Nodularia* respectively *Anabaena*.

In my studies, I have tested whether nutrient concentrations or ratios between phosphorus and nitrogen were of importance for recruitment of *Microcystis*. My findings suggest that ratios are important at a given nutrient concentration (Ståhl-Delbanco et al. 2003 Paper 1; Paper 2). My first study was conducted as an enclosure experiment in Lake Krankesjön in southern Sweden. Here, I tested the importance of nutrient additions and reduced grazing pressure from large herbivores on recruitment rate of natural occurring *Microcystis* colonies. The experiment ran for six weeks, and once a week nutrients were added (at four levels of increasing concentrations of nitrate-nitrogen and phosphate-phosphorus), and samples for recruitment of

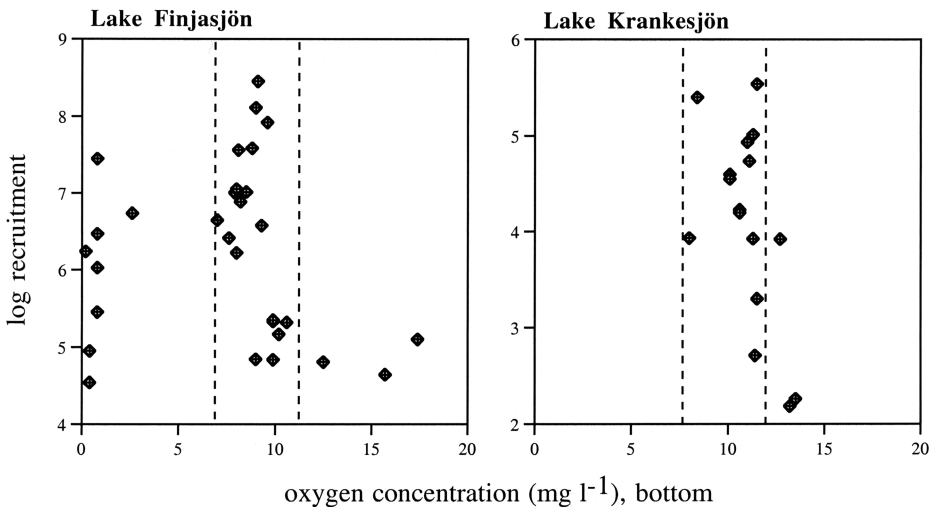


Fig. 3. Recruitment (# m⁻² day⁻¹; log-transformed) of *Microcystis* as a function of oxygen concentrations (mg l⁻¹) at the sediment surface in hypertrophic Lake Finjasjön (left-handed graph) and mesotrophic Lake Krankesjön (right-handed graph). Dashed lines enclose cases where oxygen concentrations were associated with optimal recruitment. Redrawn from Paper 2.

cyanobacteria from the sediment surface were taken by a trap. Grazing pressure was regulated by additions of fish, which efficiently consumed the large herbivores.

My major findings were that high nutrient additions (total phosphorus $> 100 \mu\text{g l}^{-1}$) played a significant role in triggering recruitment rate when the ratio between dissolved nitrogen and total phosphorus was low (5, by weight). However, at higher nutrient additions (total phosphorus = $225 \mu\text{g l}^{-1}$), the N:P ratios in the water were also higher (15, by weight), and the recruitment rate was significantly lower. Recruitment rate was also lower at lower nutrient levels (total phosphorus $< 60 \mu\text{g l}^{-1}$), where the N:P ratios were low (< 5 , by weight) (Figure 4). From this, I concluded that recruitment was stimulated by low N:P ratios, provided that the nutrient concentrations were high (Ståhl-Delbanco et al. 2003 Paper 1).

On the other hand, I found another pattern in a second study, consisting of both long-term field surveys of two different lakes (hypertrophic Lake Finjasjön and mesotrophic Lake Krankesjön in southern Sweden), and in a laboratory experiment (Paper 2).

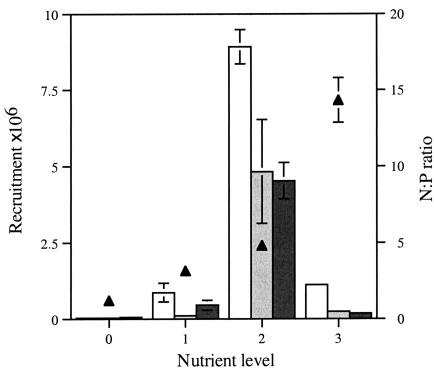


Fig. 4. Recruitment of *Microcystis* (# of colonies enclosure⁻¹ day⁻¹) at increasing nutrient (0, 1, 2, 3) and fish (zero, white bar; medium, grey bar; high, black bar) levels. Y-bars denote ± 1 S. E. Details in the text. Modified from Paper 1.

In this study, I found that recruitment of *Microcystis* in the field was initiated when N:P ratios were low or declining, while the laboratory experiment revealed that recruitment of *Microcystis* was stimulated by high or declining N:P ratios. Declining N:P ratios, indicating that optimal growth conditions (for *Microcystis*) are to come, could be responsible for the elevated recruitment rate. This would explain the discrepancy between the results, but this needs to be followed up in a new experiment.

In both the long-term study and in the laboratory experiment I also found that nutrient concentrations seemed to be important for the level of recruitment; recruitment of *Microcystis* was higher at higher nutrient concentrations (Paper 2).

To my knowledge, the importance of N:P ratios in initiating recruitment of cyanobacteria have not been investigated before. The reason why I wanted to investigate this is coupled to findings by Redfield (1958). He found that all living matter in marine systems had approximately the same atomic ratio between carbon (C), nitrogen and phosphorus (C:N:P = 106:16:1 by atoms; 40:7:1 by mass), which can be applied to freshwater systems as well, although variations between different phytoplankton groups occur (Rhee and Gotham 1980). Many cyanobacterial species have, for example, a lower optimum ratio than given by Redfield. Based on their lower optimum ratios, Smith (1983) generated a theory about cyanobacterial dominance at low N:P ratios, a pattern often found in nature (e.g. McQueen and Lean 1987; Stockner and Shortreed 1988; Hendzel et al. 1994; Jacoby et al. 2000). This theory has been much debated, and still is (e.g. Bulgakov and Levich 1999; Reynolds 1999; Smith and Bennet 1999; Downing et al. 2001). For example, Reynolds (1999) calls attention to the fact that the cell functions can not react to ratios between two concentrations, but to actual concentrations.

However, another way of reasoning is given by Sommer (1999), who advocates that nutrient ratios are important, since they may set the ground for competition between species. The closer the initial ratio is to the optimal ratio of the starting group of phytoplankton, the less nutrients will be left over for other groups with other optimal ratios (Sommer 1999). At the same time Reynolds (1999) stated that the phosphorus demand to satisfy growth rate of phytoplankton is only $3 \mu\text{g P l}^{-1}$ (dissolved phosphorus). However, despite that phosphorus demand is very low, local depletion may occur, why nutrient ratios may be of importance for continued growth, which is supported by my findings (cf. Ståhl-Delbanco et al. 2003 Paper 1; Paper 2).

Zooplankton

Herbivore abundance is found to be important for recruitment of flagellated algal species (Hansson 1996b; Rengefors et al. 1998; Hansson 2000). Both Hansson (1996b; 2000) and Rengefors et al. (1998) found that recruiting flagellates are able to adjust their behavior by avoiding recruitment at times of high grazing pressures. However, in my enclosure study I did not find any direct effects of grazing pressure on the recruitment rate of cyanobacteria. On the contrary, recruitment rate was large, both when large grazers were present and absent (Ståhl-Delbanco et al. 2003 Paper 1), a result that confirms previous findings by Hansson (2000). The reason for this could be that since cyanobacteria are difficult to graze due to their large size, poor nutritional value, and, possibly their toxicity, they do not have to avoid recruitment at times of high zooplankton abundances.

However, presence of large grazers, such as *Daphnia*, could be important for the recruitment rate of cyanobacteria in another way. *Daphnia* is an organism with a low body ratio between nitrogen and phosphorus, leading to that they generate sub-optimal

nutrient ratios for cyanobacteria by their nutrient recycling (Andersen and Hessen 1991; Attayde and Hansson 1999; Elser 1999). Pateron et al. (2002) discovered for example, that in the presence of *Daphnia*, N:P ratios in the water column increased due to increased phosphorus sedimentation and increased concentrations of dissolved nitrogen. A similar pattern was found in the above-mentioned study (Ståhl-Delbanco et al. 2003 Paper 1), which partly could explain the higher N:P ratios found in the highest nutrient treatment (Figure 4).

Sediment mixing

Bioturbation can have both positive and negative impacts on recruitment rate. Stockner and Lund (1970) found for example, that the maximum depths to which viable resting cells were found, were partly correlated with the density of burrowing, benthic invertebrates. However, Marcus and Schmidt-Gengenbach (1986) found that feeding activities by polychaeta promoted the recruitment of buried copepod eggs, since the eggs were unaffected by the feeding and simply translocated into a better position. Besides, Huber (1984) found viable akinetes at a sediment depth corresponding to an age of 1000 years, but believed that it is unrealistic that the akinetes could have survived for so long. Instead, she advocated that movements from bioturbating activities of polychaeta worms could explain their position, and provided a picture of a germinating akinete from a fecal pellet to force her argument further (Huber, 1984). Furthermore, Kremp et al. (2003) demonstrated that deposit-feeder gut passage might even enhance germination of dinoflagellate resting cysts.

In two of my own studies (Ståhl-Delbanco and Hansson 2002 Paper 3; Paper 4), I have found positive impact of sediment mixing activities upon recruitment rate. My third study was a pure laboratory one, aiming to

see the effects of different bioturbating animals on recruitment rate from resting stages. The experimental set-up consisted of different aquaria, with a layer of sieved sediment on the bottom and filtered lake water above. Two treatments and a control were used, and the treatments consisted of either *Asellus aquaticus* or *Chironomus plumosus*, in abundances representative for natural environments. In this study I found that recruitment was promoted in the *Asellus*-treatment (Figure 5), where also a high mechanical disruption of the sediment surface was created. High mechanical disruption is also created with benthic feeding fish. For example, Breukelaar et al. (1994) found that sediment resuspension increased linearly with biomass of benthivorous fish. They also found that chlorophyll *a* levels and total concentrations of nitrogen and phosphorus increased (Breukelaar et al. 1994). Their results make me wonder whether the

increase in chlorophyll *a* levels was due to stimulated pelagic growth of phytoplankton caused by the elevated nutrient concentrations, or if it originated from recruitment of resting stages, or possibly, a combination of both. However, this was not discussed by the authors.

My last study included a laboratory test of how sediment mixing affected recruitment rate of natural resting stages (Paper 4). It revealed that sediment mixing both triggered and enhanced recruitment rate of *Anabaena* spp. Karlsson Elfgrén (2003) also found similar results for *Gloeotrichia*.

Littoral zone

Placing and availability of the seed pool might also be important for the recruitment process. In one of the laboratory experiments, I tested whether sediment origin was impor-

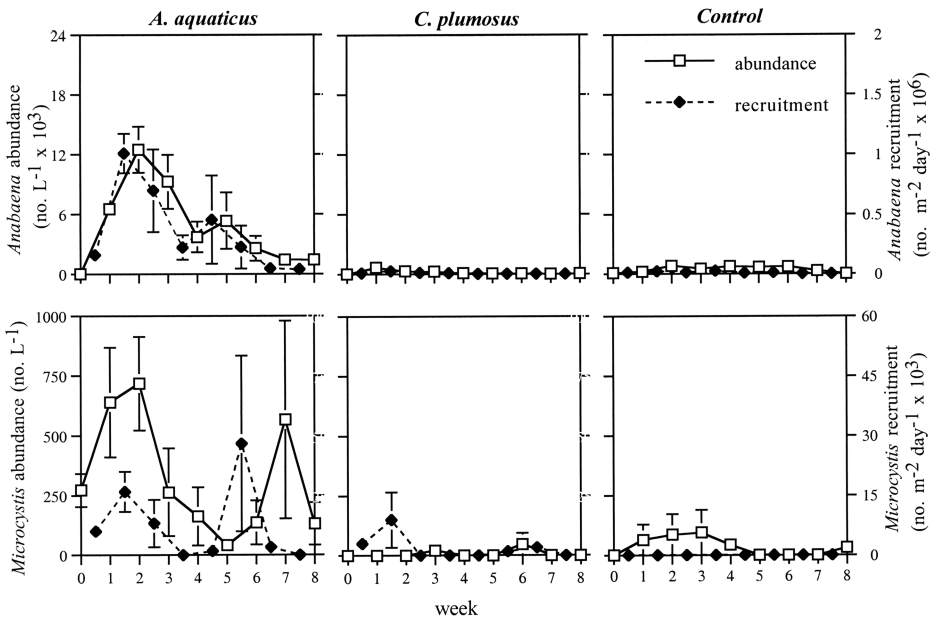


Fig. 5. Differences in recruitment rates (filled diamonds) and abundances (open squares) of *Anabaena* and *Microcystis* at different bioturbation pressures; high, *Asellus aquaticus*; medium, *Chironomus plumosus*; and low, Control. Y-bars denote ± 1 S. E. Modified from Paper 3.

tant for the recruitment rate, provided that the same triggers were applied, but I did not find any such relationship (Paper 4). Based on this, I conclude that the seed pool can be evenly spread over the sediment area, but that littoral inocula are more likely to recruit, since they have a more easy access to triggering factors (light, elevated temperature and sediment mixing) than profundal ones. This was also confirmed in the field (Figure 2) (Paper 4). The importance of the littoral zone as the major recruitment site has been addressed by others as well (Hansson 1996a; Forsell 1998; Karlsson Elfgrén 2003). Forsell (1998) found, for example, that the main part of the *Gloeotrichia* recruitment came from the littoral zone, where the major pool of akinetes was found.

REDUCING EUTROPHICATION

Cyanobacterial blooms are stimulated by anthropogenic impacts, such as a high nutrient load. Furthermore, recruitment from resting stages initiates or strengthens the blooms. In order to diminish the problem with algal blooms, stimuli factors for recruitment from resting stages could be dealt with, thereby reducing the recruitment capacity. In my studies, I have for example found that the ratio between nitrogen and phosphorus may be an important triggering factor and that the amount of nutrients sets the recruitment and growing capacities (Ståhl-Delbanco et al. 2003 Paper 1; Paper 2). Thus, nutrient reductions of both nitrogen and phosphorus are necessary. That nutrient loads must decrease is not a new statement, and it is already in progress in national nutrient reduction programs. The focus for these programs is nowadays primarily on the problem with marine eutrophication, mostly caused by high nitrogen loads (Granéli et al. 1990), why nitrogen reduction is the main target. However,

as phosphorus still is the main actor in the eutrophication process of freshwaters, phosphorus load needs to be reduced too, thereby avoiding situations where the N:P ratios stimulate cyanobacterial recruitment and growth.

If nutrient loading and resulting nutrient concentrations are low, then an upper limit on algal biomass is set, which precludes algal blooms (Elser 1999). So, to what nutrient loads should we strive? OECD has set a threshold level of lake eutrophy to $35 \mu\text{g P l}^{-1}$ (Reynolds and Davies 2001). Besides, according to Downing et al. (2001) the risk of major cyanobacterial dominance is very small (10%) at total phosphorus (TP) concentrations less than $30 \mu\text{g l}^{-1}$, while the risk is major (80%) at TP concentrations of $100 \mu\text{g l}^{-1}$.

Since a major part of the phosphorus load comes from agricultural land, actions need to be taken to reduce their pollution effects. In a recent investigation of the run-off from areas with intense agricultural impact (56% agricultural cover) it was found that the N:P ratios always were low and that phosphorus load was 300 times higher than from areas with low agricultural impact (4% agricultural cover) (Rybak 2002). Thus, the way we manage our land resources is of crucial importance for the effect on lake-ecosystems.

New management plans needed

Prevention of further pollution is among the most cost-effective means of increasing water supplies on a global scale (Carpenter et al. 1998). But, in order to deal with the environmental problems we need more tools than are provided by natural science. Actions need to be taken both in the field and in the people's minds. We need to focus on the management of human usage of the environmental resources, as well as on management of the specific resources. The Water Framework Directive is a step in the right direction. Pollution is prevented, management is done on a catch-

ment level, and stakeholder participation is included.

With catchment-based management plans we can catch the opportunity to take advantage of the water resources in the best way. To restore water systems to conditions where only minimal management is needed, would be most cost-effective (Moss 1999). New ways of regarding water as a resource instead of a problem are developing (Carpenter and Cottingham 1997; Brönmark and Hansson 2002). Furthermore, Postel (2000) advocates for that we should work for doubling the water productivity, that is, to get twice as much service, satisfaction, and benefit out of each unit of water. Her suggestions are similar to the ideas from Brönmark and Hansson (2002). They suggest that we should change our way of regarding water systems as problem areas that need restoration, into viewing them as productive resources, as we do with

arable land and forests. As such, diversified use would be the model, where pristine water bodies for supply of drinking water or for protection of rare species could be situated upstream areas confronting major anthropogenic impact (Brönmark and Hansson 2002). Furthermore, lakes for fish production could be located in areas known to render impact from eutrophication. This would require centralized planning of the water resources in each catchment, a situation likely to come with the implementation of the Water Framework Directive.

Eutrophication is the major target problem the Water Framework Directive is facing. Since cyanobacterial blooms are direct symptoms of eutrophication, reductions of stimuli factors generating these mass-formations will improve the water quality multifold. Hopefully, this thesis will contribute to this work and serve as one of many management tools.

SHORT SUMMARY OF PAPERS

Bellow follows comprehensive summaries of my different papers.

Paper 1

My first study was conducted as an enclosure experiment in the mesotrophic Lake Krankesjön in southern Sweden. I hereby tested the importance of nutrient additions and reduced grazing pressure from large herbivores on recruitment rate of natural occurring *Microcystis* colonies. The experiment ran for six weeks, and once a week, nutrients were added (in four levels with increasing nitrogen and phosphorus concentrations) and samples for measuring recruitment rates were taken by a trap. Grazing pressure was regulated by additions of fish (in three levels), which consumed the large herbivores efficiently.

My major findings were that high nutrient additions ($TP > 100 \mu\text{g l}^{-1}$) played a significant role in triggering recruitment rate when the ratio between dissolved nitrogen and total phosphorus was low (5, by weight). However, at higher N:P ratios (15, by weight), in even higher nutrient additions ($TP = 225 \mu\text{g l}^{-1}$), and in the lower nutrient levels ($TP < 60 \mu\text{g l}^{-1}$), recruitment rate was significantly lower (Figure 4).

Furthermore, I did not find any direct effects of grazing pressure on the recruitment rate.

Paper 2

My second study was a long-term investigation of recruitment rates of *Microcystis* in two lakes of different trophical status (hypertrophic Lake Finjasjön and mesotrophic Lake Krankesjön in southern Sweden), in combination with a laboratory experiment. From the long-term study, I wanted to distil the major triggering factors for cyanobacterial recruitment, so along with the recruitment data

I collected 14 different physical and biological variables, and analyzed the material with different statistical methods (regression analysis and Principle Component Analysis).

From this long-term study I found that nutrients (low nitrogen to phosphorus ratio) and elevated temperatures were often related with high recruitment rates and abundances of *Microcystis*. The accompanying laboratory experiment (with sediment from eutrophic Lake Ringsjön in southern Sweden) revealed that high or declining N:P ratios stimulated recruitment rate of *Microcystis*. From this I concluded that declining N:P ratios could be triggering the recruitment rate, but further research is needed to evaluate this better.

Furthermore, recruitment rate also seemed to be associated by either very low oxygen concentrations ($< 3 \text{ mg l}^{-1}$) or by oxygen concentrations between 7–12 mg l^{-1} (Figure 3).

Paper 3

My third study was a pure laboratory one, aiming to see the effects of different bioturbating animals on recruitment rate from resting stages. The experimental set-up consisted of different aquarium, with a layer of sieved sediment (from the eutrophic Lake Dagstorpsjön in southern Sweden) on the bottom and filtered lake-water above. Two treatments and a control were used, and the treatments consisted of either *Asellus aquaticus* or *Chironomus plumosus*, in abundances representative for natural environments.

I found that recruitment was promoted in the *Asellus*-treatment (Figure 5), where also a high mechanical disruption of the sediment surface was created.

Paper 4

The last study was a combined laboratory and field study to investigate the importance of the littoral zone as the primer inocula site

compared to the profundal zone. Eutrophic Lake Erken in south-eastern Sweden was chosen for the experiment.

Included in the laboratory experiment was a test of how elevated temperatures, light availability and sediment mixing (factors that differ between the littoral and profundal

zone) affected recruitment rate of natural resting stages.

From both the laboratory and field study the littoral zone was found to be the major site for recruitment (Figure 2). Light, sediment mixing and temperature were all found to both trigger and enhance recruitment rate.

ACKNOWLEDGEMENT

Lars-Anders Hansson, Lars Leonardsson and Wilhelm Granéli gave constructive input to a former version of this summary. Inger Ståhl improved the English language of the text.

During my PhD-studies, MISTRA has supplied me with financial support via VASTRA. In addition, the EU-project SWALE (contract no ENV4-CT97-0420), supported me with funding for research material.

There are so many people to thank for helping me getting this far and I will mention a few by names. First of all, I would like to thank my supervisor professor Lars-Anders Hansson, Lasse. Without him, my contribution to this research field would have been none. Thank you for introducing me to these questions and multi-people projects, and for sharing your enthusiasm and ideas!

Lars Leonardsson, Leo, my vice supervisor, is the reason why I wanted to become a limnologist in the first run. Thank you for inviting me to this interesting field of ecology!

Mikael Gyllström, my dear office-mate, and first colleague – thank you for everything! We have shared rooms, computers, research material, samples, field and lab work, statistical problems, and a couple of parties during this time and it has always been a lot of fun (even the statistics!).

Marie Svensson, has been an angel (dressed in black, though ☺), always willing to help with various matters, and to discuss important parts of life such as movies, books, and music.

Anders Kullberg, without your help sorting out various problems with my computer, I would have gone crazy (i.e. more than I am now).

Gertrud Cronberg has been a wonderful taxonomic help with my, sometimes seemingly, endless pyhotplankton samples.

Now, the list has come to the part were I start to lump people together. Discussions within the Benthic-Pelagic Research group have been valuable for planning of experiments and writing of papers.

My theoretical knowledge of ecology and limnology improved considerably with literature studies within the CEMA-group.

Multidisciplinary work within CATCH has been very interesting and it has been fun to get familiar with parts of the social and economic science as well.

Former and present colleagues have all contributed to make Limnology in Lund be one of the best places of work. I have really enjoyed being part of it!

My family has been supportive and understanding. Especially my mother has been extremely helpful, both as a baby-sitter for my daughter and as a proofreader of my texts.

Last, but not least, I would like to mention my dear husband Jonas. Thank you for all support during this time! You have never had doubts in me as a researcher, but instead given me strength to continue at times of distrust. Thanks as well for all amazing dinner creations; there has been more than one greedy glimpse on my lunch packets in the dining room at the Limnology!

REFERENCES

- Andersen, T. and D. O. Hessen. 1991. Carbon, nitrogen, and phosphorus content of freshwater zooplankton. *Limnol. Oceanogr.* 36: 807–814.
- Attayde, J. L. and L.-A. Hansson. 1999. Effects of nutrient recycling by zooplankton and fish on phytoplankton communities. *Oecologia*. 121: 47–54.
- Baker, P. D. 1999. Role of akinetes in the development of cyanobacterial populations in the lower Murray River, Australia. *Mar. Fresh. Res.* 50: 265–279.
- Barbiero, R. P. 1993. A contribution to the life history of the planktonic cyanophyte, *Gloeotrichia echinulata*. *Arch Hydrobiol.* 127: 87–100.
- Barbiero, R. P. and E. B. Welch. 1992. Contribution of benthic blue-green algal recruitment to lake populations and phosphorus translocation. *Freshwater Biology* 27: 249–260.
- Barbiero, R. P. and J. Kann. 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.
- Bianchi, T.S., E. Engelhaupt, P. Westman, T. Andrén, C. Rolff, and R. Elmgren. 2000. Cyanobacterial blooms in the Baltic Sea: Natural or human-induced? *Limnol. Oceanogr.* 45: 716–726.
- Boström, B., A.-K. Pettersson, and I. Ahlgren. 1989. Seasonal dynamics of a cyanobacteria-dominated microbial community in surface sediments of a shallow eutrophic lake. *Aquatic Sciences* 51: 153–178.
- Breukelaar, A. W, E. H. R. R. Lammens, J. G. P. K. Breteler, and I. Tátrai. 1994. Effects of benthivorous bream (*Abramis brama*) and carp (*Cyprinus carpio*) on sediment resuspension and concentrations of nutrients and chlorophyll a. *Freshwater Biology.* 32: 113–121.
- Brunberg, A.-K. 1995. Microbial activity and phosphorus dynamics in eutrophic lake sediments enriched with *Microcystis* colonies. *Freshwater Biology* 33.
- Brunberg, A.-K. and P. Blomqvist. 2001. Quantification of anthropogenic threats to lakes in a lowland county of central Sweden. *Ambio* 30: 127–134.
- Brunberg, A.-K. and P. Blomqvist. 2002. Benthic overwintering of *Microcystis* colonies under different environmental conditions. *J. Plankton Res.* 24: 1247–1252.
- Brönmark, C. and L.-A. Hansson. 2002. Environmental issues in lakes and ponds: current state and perspectives. *Environmental Conservation* 29: 290–306.
- Bulgakov, N. G. and A. P. Levich. 1999. The nitrogen:phosphorus ratio as a factor regulating phytoplankton community structure. *Arch. Hydrobiol.* 146: 3–22.
- Cáceres, O. and Reynolds, C. S. 1984. Some effects of artificially-enhanced anoxia on the growth of *Microcystis aeruginosa* Kütz. Emend. Elenkin, with special reference to the initiation of its annual growth cycle in lakes. *Arch. Hydrobiol.* 99: 379–397.
- Carpenter, S. R. and K. L. Cottingham. 1997. Resilience and restorations of lakes. *Conservation Ecology*. Online: <http://www.consecol.org/vol1/iss1/art2>.
- Carpenter, S. R., N. F. Caraco, D. L. Correll, R. W. Howarth, A. N. Sharpley, and V. H. Smith. 1998. Nonpoint pollution of surface waters with phosphorus and nitrogen. *Ecological Applications* 8: 559–568.
- Christoffersen, K. 1996. Ecological implications of Cyanobacterial toxins in aquatic food webs. *Phycologia* 35: 42–50.
- Codd, G. A. 2000. Cyanobacterial toxins, the perception of water quality, and the prioritisation of eutrophication control. *Ecol. Eng.* 16: 51–60.
- Collentine, D., Å. Forsman, V. Galaz, S. Kallner Bastviken, and A. Ståhl-Delbanco. 2002. CATCH: decision support for stakeholders in catchment areas. *Water Policy* 4: 447–463.
- Cottingham, K. L. 2002. Tackling biocomplexity: the role of people, tools and scale. *BioScience.* 52: 793–799.
- Cronberg, G. 1982. Phytoplankton changes in Lake Trummen induced by restoration. Long term whole-lake studies and food-web experiments. Doctoral Thesis Lund, Lund University.
- Cronberg, G. 1986. Blue-green algae, green algae and Crysophyceae in sediments. In: *Handbook of holocene palaeoecology and palaeohydrology*, by B. E. Berglund (Ed.). John Wiley and Sons Ltd.

- Dokulil, M. T. and K. Teubner. 2000. Cyanobacterial Dominance in Lakes. *Hydrobiologia* 438: 1–12.
- Downing, J. A., S. B. Watson, and E. McCauley. 2001. Predicting Cyanobacteria dominance in lakes. *Can. J. Fish. Aquat. Sci.* 58: 1905–1908.
- Eilertsen, H. C., S. Sandberg, and H. Tøllefsen. 1995. Photoperiodic control of diatom spore growth: a theory to explain the onset of phytoplankton blooms. *Mar. Ecol. Prog. Ser.* 116: 303–307.
- Elser, J. J. 1999. The pathway to noxious Cyanobacteria blooms in lakes: the food web as the final turn. *Freshwater Biology* 42: 537–543.
- Everard, M. 1999. Towards sustainable development of still water resources. *Hydrobiologia* 395/396: 29–38.
- Fallon, R. D. and T. D. Brock. 1981. Overwintering of *Microcystis* in Lake Mendota. *Freshwater Biology* 11: 217–226.
- Flett, R. J., D. W. Schindler, R. D. Hamilton, and N. E. R. Campbell. 1980. Nitrogen fixation in Canadian Precambrian shield lakes. *Can. J. Fish. Aquat. Sci.* 37: 494–505.
- Forsell, L. 1998. Migration from the littoral zone as an inoculum for phytoplankton. *Arch. Hydrobiol. Spec. Issues Advanc. Limnol.* 51: 21–27.
- Fryxell, G. A. (Ed.) 1983. *Survival strategies of the algae*. Cambridge, Cambridge University Press.
- Granéli, E., K. Wallström, U. Larsson, W. Granéli, and R. Elmgren. 1990. Nutrient limitation of primary production in the Baltic Sea area. *Ambio* 19: 142–151.
- Gregory, R. and R. L. Keeney. 1994. Creating policy alternatives using stakeholder values. *Management Science* 40: 1035–1048.
- Hadas, O., R. Pinkas, E. Delphine, A. Varid, A. Kaplan, and A. Sukenik. 1999. Limnological and ecophysiological aspects of *Aphanizomenon ovalisporum* bloom in Lake Kinneret, Israel. *J. Plankton Res.* 21: 1439–1453.
- Hansson, L.-A. 1993. Factors initiating algal life-form shift from sediment to water. *Oecologia* 94: 286–294.
- Hansson, L.-A. 1996a. Algal recruitment from lake sediments in relation to grazing, sinking, and dominance patterns in the phytoplankton community. *Limnol. Oceanogr.* 41: 1312–1323.
- Hansson, L.-A. 1996b. Behavioural response in plants: Adjustment in algal recruitment induced by herbivores. *Proc. R. Soc. Lond.* 263: 1241–1244.
- Hansson, L.-A. 2000. Synergistic effects of food chain dynamics and induced behavioral responses in aquatic ecosystems. *Ecology* 81: 842–851.
- Hansson, L.-A., L. G. Rudstam, T. B. Johnson, P. Soranno, and Y. Allen. 1994. Patterns in algal recruitment from sediment to water in a dimictic, eutrophic lake. *Can. J. Fish. Aquat. Sci.* 51: 2825–2833.
- Hardin, G. 1968. The tragedy of the commons. *Science* 162: 1243–1248.
- Head, R. M., R. I. Jones, and A. E. Bailey-Watts. 1998. Akinete germination and recruitment of planktonic cyanobacteria from lake sediments. *Verh. Internat. Verein. Limnol.* 26: 1711–1715.
- Head, R. M., R. I. Jones, and A. E. Bailey-Watts. 1999a. An assessment of the influence of recruitment from the sediment on the development of planktonic populations of cyanobacteria in a temperate mesotrophic lake. *Freshwater Biology* 41: 759–769.
- Head, R. M., R. I. Jones, and A. E. Bailey-Watts. 1999b. Vertical movements by planktonic cyanobacteria and the translocation of phosphorus: implications for lake restoration. *Aquatic Conserv: Mar. Freshw. Ecosyst.* 9: 111–120.
- Henzel, L. L., R. E. Hecky, and D. L. Findlay. 1994. Recent changes of N₂-fixation in Lake 227 in response to reduction of the N:P loading ratio. *Can. J. Fish. Aquat. Sci.* 51: 2247–2253.
- Huber, A. L. 1984. *Nodularia* (Cyanobacteriaceae) akinetes in the sediments of the Peel-Harvey Estuary, Western Australia: Potential inoculum source for *Nodularia* blooms. *Applied and Environmental Microbiology* 47: 234–238.
- Huber, A. L. 1985. Factors affecting the germination of akinetes of *Nodularia spumigena* (Cyanobacteriaceae). *Applied and Environmental Microbiology* 49: 73–78.
- Hyenstrand, P., P. Blomqvist, and A. Pettersson. 1998. Factors determining Cyanobacterial success in aquatic systems – a literature review. *Adv. Limnol.* 51: 41–62.

- Istvánovics, V., K. Pettersson, M. A. Rodrigo, D. Pierson, J. Padišák, and W. Colom. 1993. *Gleotrichia echinulata*, a colonial Cyanobacterium with a unique phosphorus uptake and life strategy. *J. Plankton Res.* 15: 531–552.
- Jacoby, J. M., D. C. Collier, E. B. Welch, F. J. Hardy, and M. Crayton. 2000. Environmental factors associated with a toxic bloom of *Microcystis aeruginosa*. *Can. J. Fish. Aquat. Sci.* 57: 231–240.
- Jensen, M. N. 2000. Common sense and common-pool resources. Researchers decipher how communities avert the tragedy of the commons. *BioScience*. 50: 638–644.
- Karlsson Elfgrén, I. 2003. Studies on the life cycles of akinete forming cyanobacteria. Doctoral Thesis. Uppsala, Uppsala University.
- Kremp, A., D. H. Shull, and D. M. Anderson. 2003. Effects of deposit-feeder gut passage and fecal pellet encapsulation on germination of dinoflagellate resting cysts. *Mar. Ecol. Prog. Ser.* 263: 65–73.
- Livingstone, D. and G. H. M. Jaworski. 1980. The viability of akinetes of blue-green algae recovered from the sediments of Rostherne Mere. *Br. Phycol. J.* 15: 357–364.
- Lubchenco, J. 1998. Entering the century of the environment: A new social contract for science. *Science* 279: 491–497.
- Marcus, N. H. and J. Schmidt-Gengenbach. 1986. Recruitment of individuals into the plankton: The importance of bioturbation. *Limnol. Oceanogr.* 31: 206–210.
- McQueen, D. J. and D. R. S. Lean. 1987. Influence of water temperature and nitrogen to phosphorus ratios on the dominance of blue-green algae in Lake St. George, Ontario. *Can. J. Fish. Aquat. Sci.* 44: 598–604.
- McQuoid, M. R., A. Godhe, and K. Nordberg. 2002. Viability of phytoplankton resting stages in the sediments of a coastal Swedish fjord. *Eur. J. Phycol.* 37: 191–201.
- Meeks, J. C. and E. L. Campbell. 2002. Cellular differentiation in the cyanobacterium *Nostoc punctiforme*. *Arch. Microbiol.* 178: 395–403.
- Moss, B. 1999. Ecological challenges for lake management. *Hydrobiologia*. 395/396: 3–11.
- Moss, B., D. Stephen, C. Alvarez, E. Becares, W. van de Bund, S. E. Collings, E. van Donk, E. de Eyto, T. Feldmann, C. Fernández-Aláez, M. Fernández-Aláez, R. J. M. Franken, F. García-Criado, E. M. Gross, M. Gyllström, L.-A. Hansson, K. Irvine, A. Järvalt, J.-P. Jensen, E. Jeppesen, T. Kairesalo, R. Kornijów, T. Krause, H. Künnap, A. Laas, E. Lill, B. Lorens, H. Luup, R. Miracle, P. Nöges, T. Nöges, M. Nykänen, I. Ott, W. Peczuła, E. T. H. M. Peeters, G. Phillips, S. Romo, V. Russell, J. Salujõe, M. Scheffer, K. Siewerten, H. Smal, C. Tesch, H. Timm, L. Tuvikene, I. Tonno, T. Virro, E. Vicente, and D. Wilson. 2003. The determination of ecological status in shallow lakes – a tested system (ECOFRAME) for implementation of the European Water Framework Directive. *Aquatic Conserv: Mar. Freshw. Ecosyst.* 13: 507–549.
- Osgood, R. A. 1988. A hypothesis on the role of *Aphanizomenon* in translocating phosphorus. *Hydrobiologia* 169: 69–76.
- Ostrom, E. 1990. Governing the commons. The evolution of institutions for collective action. Cambridge: Cambridge University Press 280 pp.
- Ostrom, E., J. Burger, C. B. Field, R. B. Norgaard, and D. Policansky. 1999. Revisiting the commons: Local lessons, global challenges. *Science* 284: 278–282.
- Paerl, H. W. 1988. Nuisance phytoplankton blooms in coastal, estuarine, and inland waters. *Limnol. Oceanogr.* 33: 823–847.
- Paerl, H. W. 1997. Coastal eutrophication and harmful algal blooms: Importance of atmospheric deposition and groundwater as “new” nitrogen and other nutrient sources. *Limnol. Oceanogr.* 42: 1154–1165.
- Paterson, M. J., D. L. Findlay, A. G. Salki, L. L. Hendzel, and R. H. Hesslein. 2002. The effects of *Daphnia* on nutrient stoichiometry and filamentous cyanobacteria: a mesocosm experiment in a eutrophic lake. *Freshwater Biology* 47: 1217–1233.
- Perakis, S. S., E. B. Welch, and J. M. Jacoby. 1996. Sediment-to-water blue-green algal recruitment in response to alum and environmental factors. *Hydrobiologia*. 318: 165–177.
- Pettersson, K., E. Herlitz, and V. Istvánovics. 1993. The role of *Gleotrichia echinulata* in the transfer of phosphorus from sediments to water in Lake Erken. *Hydrobiologia* 253: 123–129.
- Pollinger, U., O. Hadas, Y. Z. Yacobi, T. Zohary, and T. Berman. 1998. *Apabnizomenon ovalis-*

- porum* (Forti) in Lake Kinneret, Israel. J. Plankton Res. 20: 1321–1339.
- Postel, S. 2000. Entering an era of water scarcity: the challenges ahead. Ecological Applications 10: 941–948.
- Preston, T., W. D. P. Stewart, and C. S. Reynolds. 1980. Bloom-forming cyanobacterium *Microcystis aeruginosa* overwinters on sediment surface. Nature 288: 365–367.
- Pretty, J. 2003. Social capital and the collective management of resources. Science 302: 1912–1914.
- Reddy, P. M. 1984. Effect of distilled water pretreatment, nitrate and phosphate on germination of spores of two blue-green algae. Arch. Hydrobiol. 100: 261–265.
- Redfield, A. C. 1958. The biological control of chemical factors in the environment. Am. Sci. 46: 205–221.
- Rekar, S. and F. Hindák. 2002. *Aphanizomenon slovenicum* sp. nov.: morphological and ecological characters of a new cyanophyte/ cyanobacterial species from Lake Bled, Slovenia. Ann. Limnol. 38: 271–285.
- Rengefors, K., I. Karlsson, and L.-A. Hansson. 1998. Algal cyst dormancy – a temporal escape from herbivory. Proc. R. Soc. Lond. 265: 1353–1358.
- Reynolds, C. S. 1972. Growth, gas vacuolation and buoyancy in a natural population of a planktonic blue-green algae. Freshwater Biology 2: 87–106.
- Reynolds, C. S. 1999. Non-determinism to probability, or N:P in the community ecology of phytoplankton. Arch. Hydrobiol. 146: 23–35.
- Reynolds, C. S. and A. E. Walsby. 1975. Waterblooms. Biol. Rev. 50: 437–481.
- Reynolds, C. S. and D. A. Rogers. 1976. Seasonal variations in the vertical distribution and buoyancy of *Microcystis aeruginosa* Kütz. emend. Elenkin. in Rostherne Mere, England. Hydrobiologia 48: 17–23.
- Reynolds, C. S., G. H. M. Jaworski, H. A. Cmiech, and G. F. Leedale. 1981. On the annual cycle of the blue-green alga *Microcystis aeruginosa* Kütz. Emend. Elenkin. Philos. Trans. R. Soc. Lond. B. Biol. Sci. 293: 419–477.
- Reynolds, C. S. and P. S. Davies. 2001. Sources of bioavailability of phosphorus fractions in freshwaters: a British perspective. Biol. Rev. 76: 27–64.
- Rhee, G.-Y. and I. J. Gotham. 1980. Optimum N:P ratios and coexistence of planktonic algae. J. Phycol. 16: 486–489.
- Rybak J. 2002. N:P ratio in water input to lakes: long-term variation and effects of land use. Verh. Internat. Verein. Limnol. 28: 1661–1664.
- Shapiro, J. 1990. Current beliefs regarding dominance by blue-greens: The case for the importance of CO₂ and pH. Verh. Internat. Verein. Limnol. 24: 38–54.
- Smith, V. H. 1983. Low nitrogen to phosphorus ratios favor dominance by blue-green algae in lake phytoplankton. Science 221: 669–671.
- Smith, V. H. and S. J. Bennet. 1999. Nitrogen: phosphorus supply ratios and phytoplankton community structure in lakes. Arch. Hydrobiol. 146: 37–53.
- Sommer, U. 1999. A comment on the proper use of nutrient ratios in microalgal ecology. Arch. Hydrobiol. 146: 55–64.
- Sonnichsen, J. D., J. Jacoby, and E. B. Welch. 1997. Response of Cyanobacterial migration to alum treatment in Green Lake. Arch. Hydrobiol. 140: 373–392.
- Stockner, J. G. and J. W. G. Lund. 1970. Live algae in postglacial lake deposits. Limnol. Oceanogr. 15: 41–58.
- Stockner, J. G. and K. S. Shortreed. 1988. Response of *Anabaena* and *Synechococcus* to manipulation of nitrogen: phosphorus ratios in a lake fertilization experiment. Limnol. Oceanogr. 33: 1348–1361.
- Ståhl-Delbanco, A. and L.-A. Hansson. 2002. Effects of bioturbation on recruitment of algal cells from the "seed bank" of lake sediments. Limnol. Oceanogr. 47: 1836–1843.
- Ståhl-Delbanco, A., L.-A. Hansson, and M. Gyllström. 2003. Recruitment of resting stages may induce blooms of *Microcystis* at low N:P ratios. J. Plankton Res. 25: 1099–1106.
- Takamura, N., M. Yasuno, and K. Sugahara. 1984. Overwintering of *Microcystis aeruginosa* Kütz. in a shallow lake. J. Plankton Res. 6: 1019–1029.
- Trimbee, A. M. and G. P. Harris. 1984. Phytoplankton population dynamics of a small reservoir: use of sediment traps to quantify the loss of Diatoms and recruitment of summer bloom-forming blue-green algae. J. Plankton Res. 6: 897–918.

- Trimbee, A. M. and E. E. Prepas. 1988. The effect of oxygen depletion on the timing and magnitude of blue-green algal blooms. *Verh. Internat. Verein. Limnol.* 23: 220–226.
- Tsujimura, S., H. Tsukada, H. Nakahara, T. Nakajima, and M. Nishino. 2000. Seasonal variations of *Microcystis* populations in sediments of Lake Biwa, Japan. *Hydrobiologia.* 434: 183–192.
- Tsujimura, S., K. Ishikawa, and H. Tsukada. 2001. Effect of temperature on growth of the cyanobacterium *Aphanizomenon flos-aquae* in lake Biwa and Lake Yogo. *Phycol. Res.* 49: 275–280.
- Tsujimura, S. and T. Okubo. 2003. Development of *Anabaena* blooms in a small reservoir with dense sediment akinete population, with special reference to temperature and irradiance. *J. Plankton Res.* 25: 1059–1067.
- Valiela, I., G. Tomasky, J. Hauxwell, M. L. Cole, J. Cebrián, and K. D. Kroeger. 2000. Operationalizing sustainability: Management and risk assessment of land-derived nitrogen loads to estuaries. *Ecological Applications.* 10: 1006–1023.
- van Dok, W. and B. T. Hart. 1996. Akinete differentiation in *Anabaena circinalis* (Cyanophyta). *J. Phycol.* 32: 557–565.
- van Dok, W. and B. T. Hart. 1997. Akinete germination in *Anabaena circinalis* (Cyanophyta). *J. Phycol.* 33: 12–17.