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Recruitment from resting stages among bloom-forming cyanobacteria

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Annika Ståhl-Delbanco

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.

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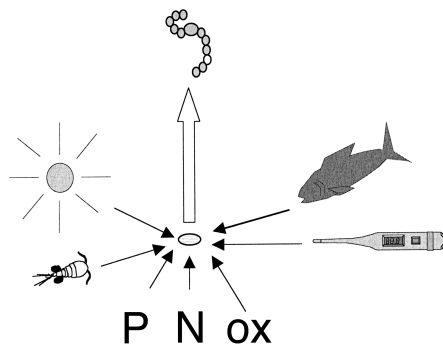
Fig. 1. Illustration of different factors (solar radiation, temperature, nutrients, oxygen concentrations, grazer abundance, sediment mixing) that can be involved in the recruitment from resting stages into planktonic stages.

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.

O$_2$

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,*
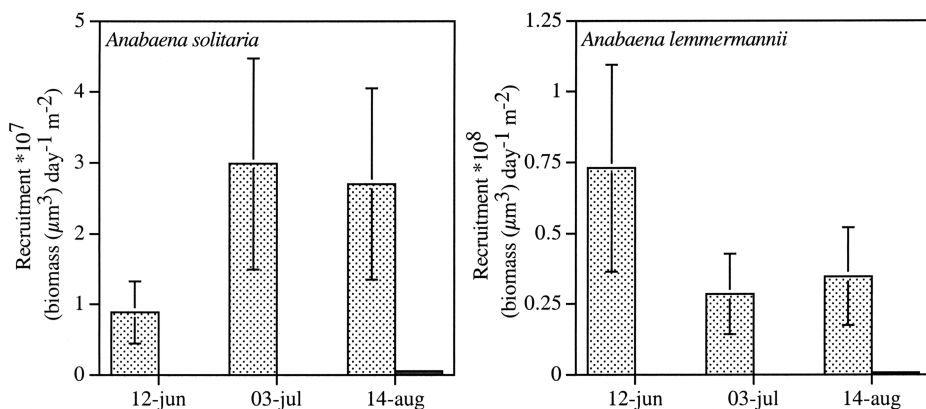

Fig. 2. Recruitment of *Anabaena solitaria* and *Anabaena lemmermannii* at a littoral (light patterned bars) and profundal (dark grey bars) site in eutrophic Lake Erken. Y-bars denote ±1 S. E. Modified from **Paper 4**.

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
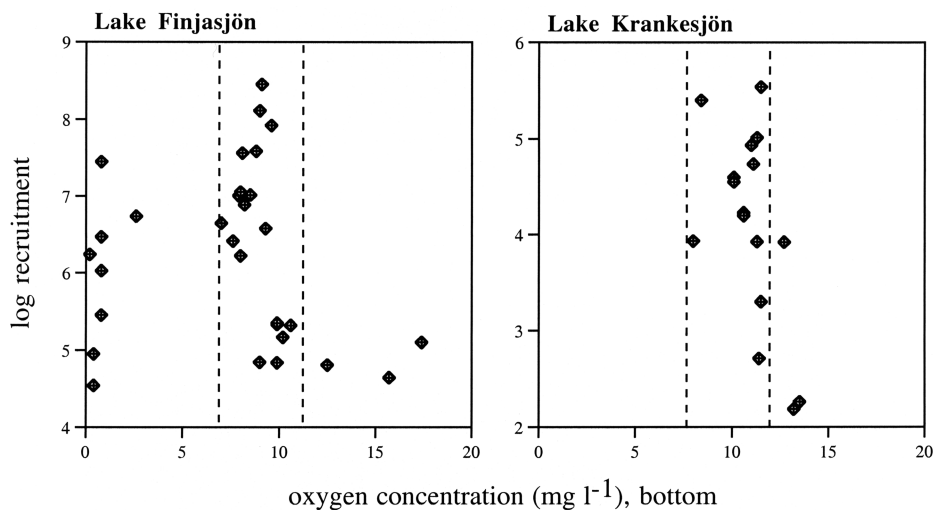
Fig. 3. Recruitment (# m⁻² day⁻¹; log-transformed) of *Microcystis* as a function of oxygen concentrations (mg l⁻¹) at the sediment surface in hypertrophic Lake Finjasjön (left-handed graph) and mesotrophic Lake Krankesjön (right-handed graph). Dashed lines enclose cases where oxygen concentrations were 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 µg 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 µg 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 µg 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**).
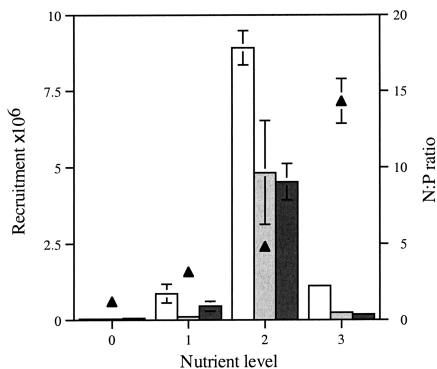
Fig. 4. Recruitment of *Microcystis* (# of colonies enclosure^{-1} day^{-1}) at increasing nutrient (0, 1, 2, 3) and fish (zero, white bar; medium, grey bar; high, black bar) levels. Y-bars denote ±1 S. E. Details in the text. Modified from **Paper 1**.

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 µg 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). Paterson 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 Elfgren (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-
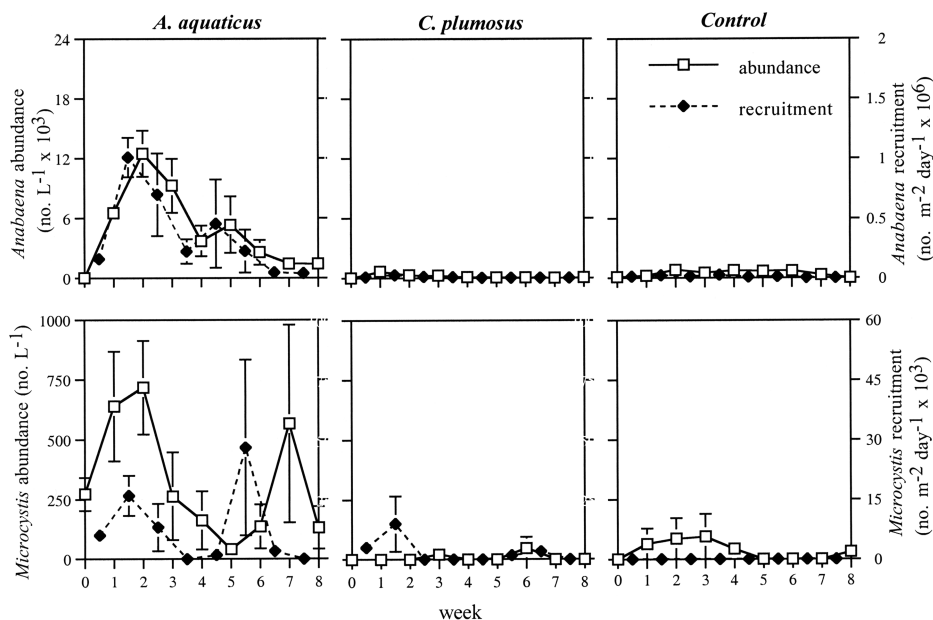

Fig. 5. Differences in recruitment rates (filled diamonds) and abundances (open squares) of *Anabaena* and *Microcystis* at different bioturbation pressures; high, *Asellus aquaticus*; medium, *Chironomus plumosus*; and low, Control. Y-bars denote ±1 S. E. Modified from **Paper 3**.

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 Elfgren 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 µg 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 µg l^{-1}, while the risk is major (80%) at TP concentrations of 100 µg 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 were 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 µg 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 µg l^{-1}), and in the lower nutrient levels (TP<60 µg 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 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 Dagstorpssjön 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.

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