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FACTORS PROMOTING THE RECRUITMENT OF BENTHIC CYANOBACTERIA RESTING STAGES: A REVIEW

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ABSTRACT

The sediment-water interface in aquatic systems is an environment connecting bottom sediments with the overlying water column. This transition zone can be easily disturbed by mechanical mixing (bioturbation) caused by foraging fish and/or macroinvertebrates moving around and stirring sediment layers. The sediment of still water ecosystems is largely known as a reservoir of resting stages of various planktonic plants, including cyanobacteria (blue-green algae) and invertebrates. The ecological and evolutionary dynamics of cyanobacteria is in part a function of the numbers and ages of diapausing stages hatching from aquatic sediments. Successful recruitment from this "seed bank" must depend upon the resting stages being present at or near the sediment surface. Often, however, they are found as deep as 15 to 30 cm in the mud. Bioturbation may thus provide a mechanism for the regular return of buried cyanobacteria resting stages to the sediment surface.

INTRODUCTION

Resting stages of water organisms offer a unique possibility of observing gradual functional adaptation in populations, as they can survive in the sediments for decades. Although normally only dormant stages from the uppermost millimeters of the sediments hatch, deeper eggs or algal cysts can be brought back to the surface if the sediment is disturbed (Lampert and Sommer, 2007). Some studies have been considering the physical sediment resuspension (bioturbation) by benthivorous fish and macroinvertebrates as an important mechanism in promoting the recruitment of cyanobacteria. This sediment disturbance could release cyanobacteria resting stages from deep muddy substrate layers acting as inoculation sites for pelagic populations (Brunberg and Blomqvist, 2003). Besides this, new inoculation could participate and trigger the occurrence of cyanobacteria blooms, which can result in serious social, economic and environmental problems (Whitton, 1992) ranging from changes in water quality as oxygen deficiency, production of off-flavor substances, fish kills and release of toxins that affect animal and human health (Smith and Schindler, 2009).

Bioturbation in a broad sense is the biological reworking of soils and sediments by all kinds of organisms, including rooting plants, microscopic animals and macroinvertebrates and vertebrates as food searching and burrowing animals (Meysman et al., 2006). Kristensen et al. (2012) defined bioturbation as all transport processes carried out by animals that directly or indirectly affect sediment habitats. These processes include both particle reworking and burrow ventilation. Furthermore, bioturbation can greatly affect exchange of nutrients between sediments and overlying water. However, the underlying processes that may initiate the development and upward movement of sediment cyanobacteria are still poorly understood (Head et al., 1999).

RECRUITED CYANOBACTERIA RESTING STAGES

Recruited cyanobacteria like e.g. *Microcystis*, which is a widely occurring cyanobacteria genus, often dominate the phytoplankton community in many nutrient-rich still water bodies. The life cycle includes both pelagic and benthic stages, of which the benthic stage is regarded mainly as a physiological rest as the poor light conditions restrict photosynthetic activity (Brunberg and Blomqvist, 2002). The benthic survival of *Microcystis* colonies has frequently been classified as ″overwintering″ when studied in temperate climate zones (Preston et al., 1980; Fallon and Brock, 1981) due to the regular planktonic development of the population during summer. Besides, the benthic biomass may substantially exceed the maximum planktonic biomass in eutrophic lakes (Boström et al., 1989), thus indicating that *Microcystis* colonies are able to survive for longer periods and accumulate in the bottom.

One of the initial surveys about the importance of sediments in the recruitment of cyanobacteria (*Microcystis*) was performed in 1980 by Preston et al. (1980) who studied the movement of *Microcystis* using ^{15}N tracers and showed that overwintered *Microcystis* in the sediments could provide an important inoculum of colonies to epilimnetic surface layers. Additionally, Boström et al. (1989) indicated that large *Microcystis* species (*M. wesenbergii* and *M. viridis*) dominated the microbial biomass in the sediments, constituting 60% to 90% of the total biomass, accounting for a large phosphorus pool in the sediments which eventually can be mobilized. Brunberg and Blomqvist (2003) showed that the "seed bank" of *Microcystis* in the shallow bay of Lake Limmaren (Sweeden) may play an important role in providing inocula for planktonic growth. Likewise, Verspagen et al. (2004) investigated the recruitment of *Microcystis* colonies from the sediment to the water column. Their observations suggested that the recruitment of *Microcystis* is more like a passive process resulting from resuspension by wind-induced mixing or bioturbation. In contrast, Tan (2012) indicated that benthic cyanobacteria recruitment was only accounted for a small portion of pelagic growth, which is similar to that found in deep lakes. These findings suggested that studies on cyanobacterial blooms development should be mainly focused on the pelagic population development.

Furthermore, the temperature has been catalogued as an important environmental factor affecting the recruitment of *Microcystis*. Yamamoto (2009) indicated that the effect of temperature on the recruitment of *Microcystis* colonies was enhanced at above 15 °C and cited that the upward movement of *Microcystis* species is obviously regulated by cell buoyancy. Some studies have suggested a positive effect of temperature on the recovery of buoyancy in *Microcystis* colonies or an increase in the number of buoyant colonies (Tsujimura et al., 2000; Brunberg and Blomqvist, 2003; Verspagen et al., 2005). Otherwise, issues related with genotypic and toxicological dynamics during the benthic life stage of *Microcystis* have been studied, aiming to understand the physiological responses of cyanobacteria benthic resting stages (Latour et al., 2004; Misson et al., 2012). For example, Misson et al. (2011a) reported that benthic *Microcystis* could remain viable and able to initiate microcystin production after more than 6 years of benthic life. This finding also suggests that microcystins could be involved in the benthic survival mechanisms of *Microcystis* (Misson et al., 2011b). The toxic potential of *Microcystis* seems to be well preserved in the sediment (Misson et al., 2012).

What is unclear, however, is whether *Microcystis* recruitment from the sediment is an active process, triggered by internal changes in buoyancy, or whether it is a passive process brought about by resuspension of sedimented *Microcystis* colonies (Verspagen et al., 2004).

BENTHIC MACROINVERTEBRATES

As far as is known, there are few studies related to the cyanobacteria recruitment supported by water-living animals. These studies have demonstrated that bioturbation by macroinvertebrates could be important in creating conditions favorable for algal recruitment (Ståhl-Delbanco and Hansson, 2002) and that it influences the viability and hatching rates of zooplankton benthic eggs (Viitasalo, 2007; Viitasalo et al., 2007).

Such bioturbation can be caused by a variety of benthic macroinvertebrates that forage and burrow various bottom tubes, holes and pits (Adámek and Maršálek, 2013). Thus, the processes involved may either be a result of direct interception by benthic animals, e.g. through bioresuspension of particles or through food ingestion and biodeposition, or of other indirect effects, e.g. changes in the physical properties of sediments or through the constructions mentioned above, along with corresponding changes in pond ecosystem functioning. It has also been suggested that the recruitment of some algal species from the sediment to the water column occurred primarily at shallow depths (<8 m) and often increased total phytoplankton abundance by 10-50% per day (Hansson, 1996).

Ståhl-Delbanco and Hansson (2002) dealt with the effects of different bioturbators on the recruitment of several nuisance algae, namely *Anabaena* spp., *Microcystis* spp. (both Cyanobacteria) and *Gonyostomum semen* (Raphidophyceae). Their recruitment from the sediment to the water column was studied in a long-term laboratory experiment. Results suggested that recruitment rate might be more pronounced in littoral areas, which are often dominated by *Asellus aquaticus* (Isopoda). The activities of *Asellus* increased the recruitment rates of algal groups, whereas chironomids (Chironomidae) showed a less pronounced effect. Also Yamamoto (2010) studied the potential effect of bioturbation by the red swamp crayfish *Procambarus clarki*, suggesting this crayfish could influence the dynamics of cyanobacteria in a pond, where the recruitment process from the sediment is assumed to be especially important in the formation of cyanobacterial blooms.

In addition, Karlson et al. (2012) found that, depending on species-specific traits, deposit-feeding macrofauna – an amphipod, *Monoporeia affinis*, a bivalve, *Macoma balthica* and an invasive polychaete, *Marenzelleria* cf. *arctia* - has the potential to either reduce or facilitate recruitment of the cyanobacterium *Nodularia spumigena* from an anoxic sediment. Their results showed the importance of this, often overlooked, aspect of phytoplankton bloom initiation by macroinvertebrates.

Yu et al. (2012) indicated that some filter-feeding zooplankton species, snails and chironomids can utilize detritus originating from *Microcystis* blooms as a food source, regardless of the exact pathways and mechanisms of this assimilation, and that cyanobacterial scums such as those of *Microcystis* play an important role in both pelagic and benthic food webs of eutrophic lakes.

FISH

It is well known that, in temperate regions, the top-down control based on fish predation could support the larger zooplankton community development, whilst bottom-up control induced by benthivorous fish feeding could release nutrients from the sediments stimulating the phytoplanktonic growth (Jeppesen et al., 2010). Meanwhile, resuspension of settled algal cells by feeding activities of benthivorous fish may be another mechanism but has been little studied (Roozen et al., 2007). Verspagen et al. (2004) mentioned that recruitment of *Microcystis* from the sediment seems to be largely a passive process that is driven by sediment resuspension or bioturbation. Few studies have examined the direct effect of fish bioturbation processes on the phytoplankton community. Roozen et al. (2007) studied the effects of resuspension by common carp (*Cyprinus carpio*) in enclosure experiments where an increase in diatoms and green algae (organisms with a relatively fast sedimentation velocity) was found but only in enclosures where carp could reach the sediment. In addition, Matsuzaki et al. (2007) reported an increase in phytoplankton (dominated by cyanobacteria) in enclosure experiments with small common carp individuals.

On the other hand, Zambrano and Hinojosa (1999) conducted an experiment in five controlled small ponds to determine the effects of common carp on water turbidity, macrophyte and benthic communities in a subtropical shallow system. Results showed that, at densities equal or higher than 0.8 ind.m^{-2}, carp suffer from intraspecific competition. At the same densities, carp produces an increase of water turbidity but the relation is non-linear, suggesting a switch effect from a clear-water-system to a turbid-water-system (Roozen, 2007). They also revealed that a direct effect of carp on macrophytes depends on the susceptibility of each species. Carp affect the abundance of benthic macroinvertebrates directly by predation, but their indirect effects on it remain still unknown. Besides, Kloskowski (2011) suggested that carp predation and its related effects may be primarily responsible for animal diversity loss in affected communities.

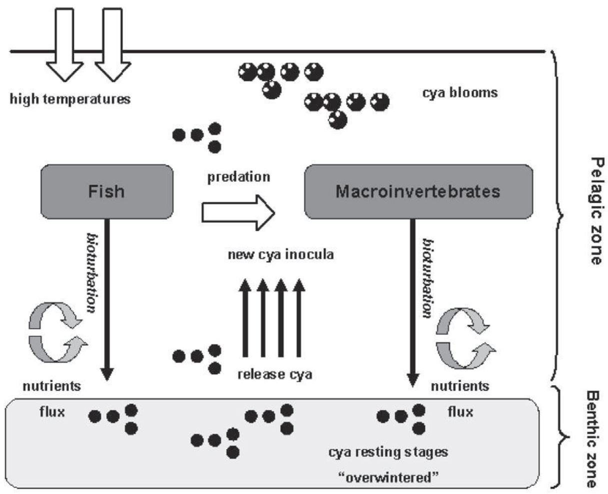

Fig 1. Factors promoting recruitment of cyanobacteria benthic resting stages

Note: cya=cyanobacteria

However, studies about the direct effect of bioturbation by fish and macroinvertebrates on the processes of recruitment of cyanobacteria benthic resting stages are very scarce and so future studies are needed to understand how these processes could promote the recovery of this particular microalgae group. Such research is of especial importance as regards the current interest and support for environmentally friendly fish pond management (Adámek and Maršálek, 2013).

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Sažetak

FAKTORI KOJI POMAŽU IZDVAJANJU BENTOSKIH CIJANOBAKTERIJA IZ FAZA MIROVANJA: PREGLED

Prostor površine bentala (sediment-voda) je okoliš koji povezuje sediment dna i stupac vode iznad. Ova prijelazna zona lako se može uznemiriti mehaničkim miješanjem (bioturbacijom) uzrokovanim ribom koja je u potrazi za hranom i kretanjem makrozoobentosa kroz slojeve sedimenta. Sediment ekosustava stajaćica uglavnom je poznat kao "rezervoar" za mirovanje različitih planktonskih biljaka, uključujući cijanobakterije (modrozelene alge) i beskralježnjake. Ekološka i evolucijska dinamika cijanobakterija ima utjecajnu ulogu za brojne generacijske stadije mirovanja nastale u akvatičnom ekosustavu. Uspješno izdvajanje iz tih "banki stanica" mora ovisiti o fazama mirovanja u/ili blizu površine sedimenta. Međutim, cijanobakterije se često nalaze 15 do 30 cm dubine u mulju. Mehaničko miješanje (bioturbacija) može osigurati povratak ukopanih cijanobakterija iz faza mirovanja na površinu sedimenta.

Ključne riječi: modrozelene alge, dno ribnjaka, bioturbacija, cvjetanje vode

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