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Review

The common bloom-forming cyanobacterium *Microcystis* is prone to a wide array of microbial antagonists

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ABSTRACT

Many degraded waterbodies around the world are subject to strong proliferations of cyanobacteria – notorious for their toxicity, high biomass build-up and negative impacts on aquatic food webs – the presence of which puts serious limits on the human use of affected water bodies. Cyanobacterial blooms are largely regarded as trophic dead ends since they are a relatively poor food source for zooplankton. As a consequence, their population dynamics are generally attributed to changes in abiotic conditions (bottom-up control). Blooms however generally contain a vast and diverse community of micro-organisms of which some have shown devastating effects on cyanobacterial biomass. For *Microcystis*, one of the most common bloom-forming cyanobacteria worldwide, a high number of micro-organisms (about 120 taxa) including viruses, bacteria, microfungi, different groups of heterotrophic protists, other cyanobacteria and several eukaryotic microalgal groups are currently known to negatively affect its growth by infection and predation or by the production of allelopathic compounds. Although many of these specifically target *Microcystis*, sharp declines of *Microcystis* biomass in nature are only rarely assigned to these antagonistic microbiota. The commonly found strain specificity of their interactions may largely preclude strong antagonistic effects on *Microcystis* population levels but may however induce compositional shifts that can change ecological properties such as bloom toxicity. These highly specific interactions may form the basis of a continuous arms race (co-evolution) between *Microcystis* and its antagonists which potentially limits the possibilities for (micro)biological bloom control.

Contents

Abbreviations: MLV, *Microcystis*-lysing viruses; MLB, *Microcystis*-lysing bacteria; MGF, *Microcystis*-grazing flagellates; MGA, *Microcystis*-grazing amoebae.

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1. Introduction

Cyanobacterial blooms are a common phenomenon in lentic freshwater bodies all over the world. Due to their widespread toxicity, high biomass build-up and negative impacts on aquatic food webs and human use of freshwaters (Codd et al., 2005), bloom-forming cyanobacteria are generally considered as pest species (Chorus and Bartram, 1999). As these organisms are favored by hypertrophic conditions and high temperatures, the frequency of bloom formation is expected to further increase due to cultural eutrophication and climate change (Jöhnk et al., 2008; Paerl and Huisman, 2008; Kosten et al., 2012).

Cyanobacterial population dynamics are traditionally believed to be mainly driven by abiotic factors including water temperature, pH, CO_2 and nutrient concentrations (e.g. Ohkubo et al., 1991; Yagi et al., 1994; Shapiro, 1997; Vézie et al., 2002; Huisman and Hulot, 2005; Banares-Espana et al., 2006; Kardinaal et al., 2007; Imai et al., 2009). Top-down control by filter-feeding zooplankton is supposed to be of minor importance since many cyanobacteria are relatively well protected against zooplankton-grazing due to morphological and size constraints (Fulton and Paerl, 1987; Lampert, 1987) and toxin production (DeMott, 1999; Rohrlack et al., 1999, 2001; Lotocka, 2001) and are of relatively poor food quality since they generally lack sterols and polyunsaturated fatty acids (Gulati and DeMott, 1997; Müller-Navarra et al., 2000; Basen et al., 2012). The inability of zooplankton to suppress phytoplankton biomass is believed to be one of the key elements in the formation of cyanobacterial and algal blooms (e.g. Irigoien et al., 2005; Turner, 2014). Smaller and more selective grazers such as rotifers, cyclopoid copepods and small cladocerans are, however, able to coexist with bloom-forming cyanobacteria and their grazing impact might be significant at times (e.g. Davis and Gobler, 2011; Perga et al., 2013; Ger et al., 2014; Urrutia-Cordero et al., 2015). Moreover, eutrophication might lead to the replacement of metazooplankton by microbiota as the most important grazers of phyto- and bacterioplankton (Mathes and Arndt, 1994; Auer et al., 2004). There is a great diversity of microorganisms known that are able to use cyanobacteria as a food source, apparently less hindered by morphological and/or biochemical constraints, and maximal population densities of microbial predators sometimes coincide with strong reductions in cyanobacterial biomass (Cook and Ahearn, 1976; Canter et al., 1990; Rashidan and Bird, 2001; Sigee et al., 2007; Kobayashi et al., 2013; Peduzzi et al., 2014).

Microcystis is one of the most common bloom-forming cyanobacteria worldwide (Visser et al., 2005). In nature *Microcystis* generally appears as colonies, each consisting of a few to several thousands of round cells embedded in a mucilage matrix. About 20 taxa are currently recognized based on cell size and colony morphology (Komárek and Anagnostidis, 1999), of which *Microcystis aeruginosa*, *Microcystis flosaquae*, *Microcystis viridis* and *Microcystis wesenbergii* are most frequently reported to form blooms. The high similarity based on DNA–DNA hybridizations and the lack of phylogenetic structure in ITS rDNA and 16S rDNA phylogenies however suggest that in fact the genus consists of a single, highly variable species, *M. aeruginosa*, with a cosmopolitan distribution (Otsuka et al., 2001; van Gremberghe et al., 2011; da Silva Malone et al., 2014). *Microcystis* is a poor food source for zooplankton due to toxin production (DeMott, 1999; Rohrlack et al., 1999, 2001; Lotocka, 2001) and colony formation (Fulton and Paerl, 1987; Lampert, 1987). Its colonies can, however, harbor an abundant and diverse microbial community (Fig. 1) of viruses, bacteria, microalgae, microfungi and amoeboid taxa of which some establish a mutualistic relationship with *Microcystis* while others exhibit strong antagonistic effects (Pankow, 1986; Imamura et al., 2001; Maruyama et al., 2003; Honjo et al., 2006; Shi et al., 2009; Van Wichelen et al., 2010; Li et al., 2011). These antagonists are mainly predators or parasites that use *Microcystis* as a food source while others, including other planktonic cyanobacteria (Li and Li, 2012), are competitors that reduce exploitative competition by producing *Microcystis* growth-inhibiting compounds.

In this review, we summarize and assess the nature and properties of all known microbial agents with strong antagonistic capabilities toward *Microcystis* described so far in order to estimate their ecological significance for *Microcystis* bloom dynamics. We hereby focus on all components of the microbial food web including viruses, bacteria, cyanobacteria, eukaryotic microalgae, microfungi, hetero- and mixotrophic nanoflagellates, amoebae and ciliates.

2. Overview

2.1. Viruses

The first knowledge on the existence of cyanobacteria-infecting viruses (cyanophages) dates back to more than 50 years ago when Safferman and Morris (1963) described a viral infection of several filamentous cyanobacteria. Rubenchik et al. (1966) and Goryushin and Chaplinskaya (1968) were the first to experiment with the addition of filtered, bacteria-free water, originating from several Ukrainian reservoirs containing severe *Microcystis* blooms, into several *Microcystis* cultures resulting in cell lysis in association with the presence of virus-like particles. Using the same technique, later workers confirmed the presence of *Microcystis*-lysing viruses (MLV) in American (Parker et al., 1977; Phlips et al., 1990), Japanese (Manage et al., 1999; Honjo et al., 2006; Yoshida et al., 2006), Chinese (Ou et al., 2013; Li et al., 2013), Australian (Tucker and Pollard, 2005) and European (Deng and Hayes, 2008) eutrophic waterbodies. Recent genotypic characterization revealed a potentially high MLV diversity in the water column (Honjo et al., 2006; Takashima et al., 2007; Deng and Hayes, 2008) as well as in the sediment (Hargreaves et al., 2013), containing representatives of the three main known families of double-stranded DNA viruses (Myoviridae, Siphoviridae and Podoviridae, see Suttle, 2000). So far, about 7 different MLV taxa are formally recognized, mainly on morphological and autoecological criteria (see Suppl. Table 1). Several field surveys have demonstrated the ecological significance of viral infection for *Microcystis* bloom dynamics since peaks in cyanophage activity or abundance coincided with drastic (temporal) reductions in *Microcystis* abundance (Manage et al., 2001; Yoshida et al., 2008a; Manage, 2009). Other studies, however, did not find such a relationship (Yoshida et al., 2010; Kimura et al., 2012; Xia et al., 2013) which may have been caused by strong strain specificity, a typical feature of many cyanophages. Indeed, growth experiments with cyanophages Ma-LMM01 (Yoshida et al., 2006), MaMV-DC (Ou et al., 2013) and

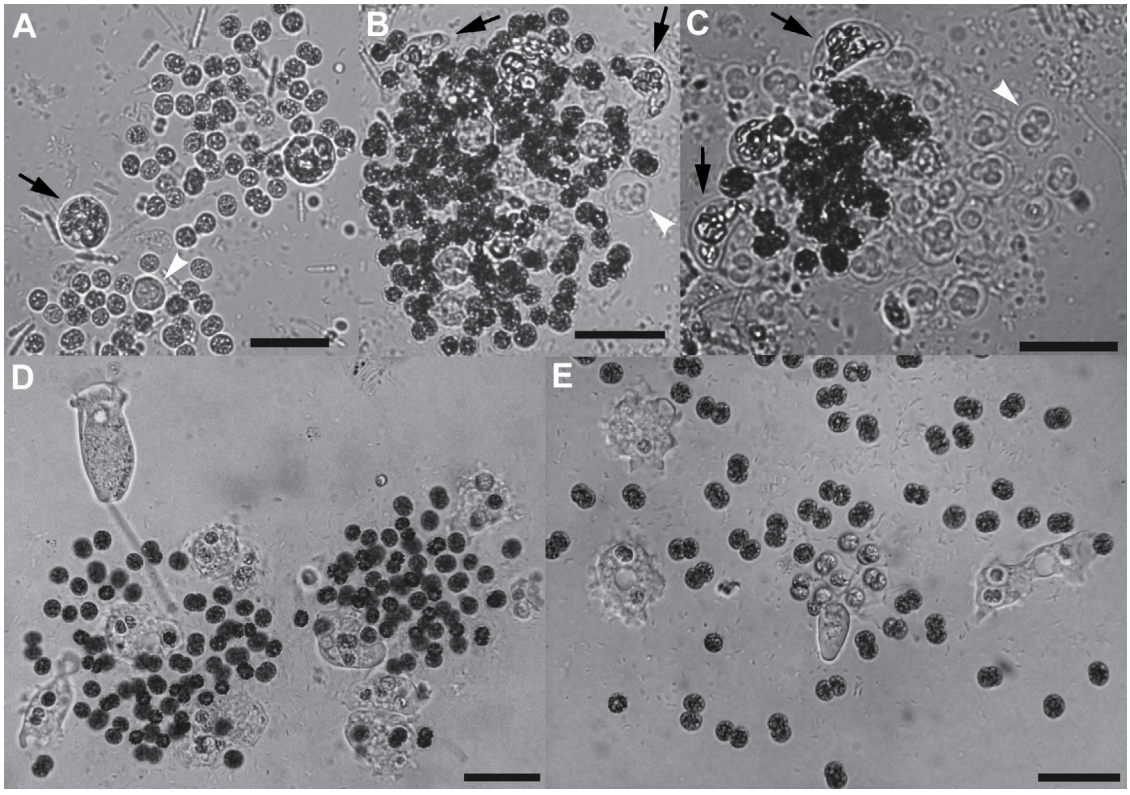

Fig. 1. Diversity of *Microcystis*-associated microbiota in an eutrophic urban pond (Westveld, Sint-Amandsberg, Belgium). (A-C) Infestation with an unknown globular to lunar-shaped amoeboid protist (arrows) ingesting *Microcystis* cells, leaving behind fecal pellets with visible remnants of digested food (arrowheads) (live sample from 20/06/2008). (D-E) Infestation with the *Microcystis*-grazing, naked amoeba *Korotnevella pelagolacustris*, the chytrid parasite *Chytridium microcystidis* and the epiphytic ciliate *Vorticella* cf. *aquadulcis* (live sample from 28/06/2007). All pictures taken by J. Van Wichelen using an Olympus DP50 digital camera mounted on a Leitz Diaplan light microscope (scale bar = 20 μm).

MaCV-L (Li et al., 2013) revealed that these *Microcystis* viruses are highly strain-specific since they caused cell lysis in only 1 out of 11, 1 out of 9 and 1 out of 5 *Microcystis* strains tested, respectively. Also Parker et al. (1977) detected strain specificity of cyanophage SAM-1 for *Microcystis* (only 1 out of 4 tested showed cell lysis), although this virus had a broader host range since it could also infect other cyanobacteria. Since natural *Microcystis* populations generally consist of several to many different *Microcystis* genotypes (Wilson et al., 2005; Yoshida et al., 2008a; Van Wichelen et al., 2010), infection with such highly specific cyanophages might predominantly result in compositional shifts, by replacing cyanophage-sensitive genotypes with cyanophage-insensitive ones, without showing strong (or only very temporal) reductions in total *Microcystis* abundance (Yoshida et al., 2008a, 2010). Also differences in infectivity can be responsible for contrasting effects on *Microcystis* abundance. Cyanophages may adopt a temporal dormant, inactive (lysogenic) state where their DNA is integrated and replicated along with the host chromosome in awaiting the transition to a virulent (lytic) state when the synthesis of virus-encoded proteins results in the destruction of the infected cell and the release of newly formed phages. Although it has been shown that the infectivity of cyanophages is influenced by environmental conditions such as the concentration of nutrients (especially phosphate) and pollutants, temperature and even climate change (reviewed in Jassim and Limoges, 2013), the ecological implications of lysogeny still remain largely unknown (Suttle, 2000). It has been suggested to play an important role, however, in the final stage of recurring cyanobacterial blooms (Sedmak et al., 2008).

Several MLV have a wider host range and are, at least in vitro, also capable of infecting other genera of coccoid (*Anacystis*, *Synechococcus*) and filamentous (*Planktothrix*, *Anabaena*) cyanobacteria (Parker et al., 1977; Deng and Hayes, 2008; Watkins et al., 2014). Since many cyanophages possess several genes similar to cyanobacterial homologues (Yoshida et al., 2008b), such less specific viruses potentially function as important vectors for gene transfer between deeply separated cyanobacterial lineages (Deng and Hayes, 2008).

Recent MLV research has mainly focused on cyanophage Ma-LMM01 and revealed that light plays a crucial role in its relationship with *Microcystis*. By monitoring Ma-LMM01 gene expression in a natural *Microcystis* population, Kimura et al. (2012) discovered a diurnal pattern showing that expression was maximal during the daytime and minimal around midnight. They concluded that Ma-LMM01 proliferation may be dependent on host photosynthetic activity in association with the light cycle. Moreover, Ma-LMM01 is able to influence the photosynthesis of its host since its genome contains a photosynthesis-related gene (*nblA*) essential for the degradation of phycobilisomes, the major light-harvesting complex of cyanobacteria (Yoshida et al., 2008b; Honda et al., 2014). Phycobilisome degradation provides a source of amino acids essential for phage replication (Mann, 2005) and prevents photo-inhibition, a constant stress factor for floating *Microcystis* colonies, by conserving the host's photosystem II. By also maintaining the transcription of the *Microcystis* housekeeping genes upon viral infection and thus reducing drastic changes in host physiology, it is believed that the supply of nucleic or amino acids is guaranteed while at the same time the induction of the host defense system is avoided (Honda et al., 2014). The latter is a constant threat to Ma-LMM01 since *Microcystis* is renowned for the exceptionally large number of antivirus defense genes in its genome (Makarova et al., 2011). Such an extensive *Microcystis* defense system might also explain the large genetic variability observed in natural Ma-LMM01 populations and further indicate the potential existence of a continuous arms race (co-evolution)

between this virus and its host (Kimura et al., 2013; Nakamura et al., 2014; Yoshida et al., 2014).

2.2. Heterotrophic bacteria

The first and most elaborate study on *Microcystis*-lysing bacteria (MLB), by Bershova et al. (1968), showed that more than a quarter of the 2166 bacterial isolates from cyanobacterial bloom samples in Ukrainian reservoirs had an antagonistic effect on a *Microcystis pulverea* strain. Berg et al. (2009) found a much lower fraction of MLB (10 out of 183 analyzed strains) in a similar study of cyanobacterial-affected waters in Finland but they examined a much wider habitat diversity including lakes, rivers, water treatment plants and the Baltic Sea, not all as prone to *Microcystis* bloom development as eutrophic freshwater lakes. The isolation of many MLB strains during recent decades (Suppl. Table 2) however demonstrates their high diversity representing at least 33 genera belonging to the Proteobacteria (19), Bacteroidetes (5), Actinobacteria (5) and Firmicutes (4). The precise ecological role(s) of most of these antagonistic interactions however remain(s) to be elucidated.

The majority of these MLB have a non-selective effect on coccoid and filamentous cyanobacteria while several others were shown to also inhibit the growth of green algae, diatoms and dinoflagellates (Suppl. Table 2). Only a few bacterial strains specifically target *Microcystis* but hardly any information is available yet concerning the strain-specificity of the effects. *Microcystis wesenbergii* however seems less susceptible to MLB. A *Microcystis* bloom infection with a parasitic *Bdellovibrio* species revealed that only *Microcystis aeruginosa* cells were attacked, while no traces of infection were seen in the accompanying *M. wesenbergii* cells (Caiola and Pellegrini, 1984). Tian et al. (2012) also noticed a lack of growth inhibition by an *Exiguobacterium* sp. against *M. wesenbergii*, in contrast to its strong lytic activity against many other cyanobacteria including *M. aeruginosa* and *Microcystis viridis* strains. *M. wesenbergii* was also found to be less susceptible for *Myxococcus fulvus* in comparison with other *Microcystis* morphotypes (Yamamoto and Suzuki, 1990). Such resistance is, however, also known for certain *M. aeruginosa* strains (e.g. Du et al., 2014) and strain-specific differences in susceptibility against MLB are also described for this morphospecies (Yamamoto et al., 1993; Kim et al., 2008).

The natural dynamics of *Microcystis*-lysing bacteria are rarely studied and contrasting effects have been observed. Using a plaque counting technique, Manage et al. (2001) and Manage (2009) obtained a significant positive relationship between the density of MLB (a.o. *Alcaligenes denitrificans*) and *Microcystis* cells during a summer bloom in a hypereutrophic Japanese pond. Zhang et al. (2012) used a joint real-time fluorescence quantitative PCR analysis of *Microcystis aeruginosa* and the *Microcystis*-lysing bacterium *Pseudomonas aeruginosa* in Lake Taihu (China) to reveal a negative relationship between the densities of both. Laboratory experiments made clear that the efficiency of growth inhibition might depend on the physiological state of the host, the initial bacterial densities, pH, temperature and light (e.g. Sugiura et al., 1993; Nakamura et al., 2003; Mu et al., 2009; Liao and Liu, 2014).

At least some MLB have a parasitic lifestyle; they affect their host by either penetrating the host cell prior to cell lysis as shown for *Bdellovibrio* (Caiola and Pellegrini, 1984; Pellegrini et al., 1997) or by adhering to the outside of the host cells (entrapment) causing shadowing, resulting in a reduction in light availability for photosynthesis, or cell aggregation by an increased production of extracellular polysaccharides, before lysis of the host cells finally takes place as observed for several infections by *Bacillus* species (Nakamura et al., 2003; Gumbo and Cloete, 2011a,b; Li et al., 2012). Most MLB however merely affect their host indirectly by excreting growth-inhibitory bio-active compounds including amino acids and derivatives (Yamamoto et al., 1998; Yoshikawa et al., 2000; Liu et al., 2013b; Yang et al., 2013b; Wang et al., 2013a; Du et al., 2014; Yi et al., 2015), (antibiotic) peptides (Reim et al., 1974; Imamura et al., 2000, 2001; Kim et al., 2010; Liu et al., 2013b; Wu et al., 2014; Lin et al., 2015; Guo et al., 2015), enzymes (Chen et al., 2011), steroids (Luo et al., 2013), alkaloids (Kodani et al., 2002), phenol derivatives (Lin et al., 2015), pigments (Yang et al., 2013a; Li et al., 2014) and glycolipids (Kim et al., 2010) into the surrounding water. Also volatile organic compounds might inhibit *Microcystis* growth as shown for several *Bacillus* species capable of producing 3-methyl-1-butanol causing cyanobacterial cell lysis (Wright and Thompson, 1985; Wright et al., 1991). Moreover, Ozaki et al. (2008) demonstrated that even *Microcystis* itself can be induced by a *Brevibacillus* species to produce a lytic volatile compound (β-cyclocitral) thus programming its own cell death by autolysis. Some bacterial compounds affect *Microcystis* in an indirect way. This is the case for siderophores, small iron-chelating compounds produced by certain bacteria (e.g. *Stenotrophomonas maltophilia*), facilitating iron transport into their cells in times of iron deprivation, enabling these bacteria to outcompete *Microcystis* and other cyanobacteria (Liu et al., 2014). In general, a close association between the bacteria and their host cells is still required for optimal functionality of the different compounds, due to their otherwise rapid dilution and subsequent loss of activity (Daft et al., 1985), or when their production is not a constitutive process and is only triggered by the hosts' presence (Choi et al., 2005).

The majority of these compounds cause cell wall destruction and subsequent cell collapse (Yamamoto et al., 1998; Liu et al., 2013a; Yang et al., 2013a) which makes the highly nutritious cell contents more readily accessible to the MLB (Gumbo and Cloete, 2011a). Some MLB additionally induce cell aggregation prior to cell lysis (Xu et al., 2012; Li et al., 2012; Liu et al., 2013b) which can be seen as a very efficient way of food concentration before assimilation takes place (Nakamura et al., 2003). In contrast, other MLB (e.g. *Bacillus mycoides*, *Pseudomonas aeruginosa*) tend to reduce the aggregation of *Microcystis* cells because the mucilage matrix around *Microcystis* colonies might act as a physical barrier preventing cell lysis (Gumbo et al., 2010; Wang et al., 2013b). Oxidative stress is an important factor in the membrane destruction and can be linked with photosynthesis inhibition, the formation of free radicals and changes in the enzymatic activity of superoxidase dismutase, peroxidase and catalyze, thus destroying the antioxidant defense mechanisms of the cell, eventually leading to severe lipid peroxidation (Luo et al., 2013; Kong et al., 2013; Shao et al., 2014; Guo et al., 2015). An *Aquimarina* species is even found to secrete L-amino acid oxidase inducing the production of hydrogen peroxide in *Microcystis* cells and subsequent cell death (Chen et al., 2011). Hydrogen peroxide (H_2O_2) is a reactive oxygen species (ROS) that is biologically produced as by-product of several metabolic processes (photosynthesis, respiration) and is rapidly removed by specific ROS-eliminating enzymes. Cyanobacterial photosynthesis however does not produce H_2O_2 and as a consequence it is believed that cyanobacteria have a lower need for induced expression of ROS-elimination enzymes in comparison with eukaryotic organisms, making them highly sensitive to even low concentrations of H_2O_2 in the environment (Matthijs et al., 2012). Furthermore, the ROS-eliminating enzymes themselves are susceptible to photo-inhibition in *Microcystis* (Whitelam and Codd, 1983a,b). It was shown that the addition of H_2O_2 to *Microcystis* cells consequently leads to a strong decrease of photosynthetic activity and capacity in combination with lysis of the nucleoid zone and membrane deformation, all characteristic for an apoptotic-like cell death (Ding et al., 2012) but also that microcystin-producing strains were less susceptible than non-microcystin-producers due to the radical-scavenging properties of

microcystin (Dziallas and Grossart, 2011). Differential effects of oxidative stress factors generated by heterotrophic bacteria thus might have ecologically important consequences for bloom toxicity. Detoxification can also result from the down regulation of microcystin synthesis induced by the action of certain metabolites (e.g. bacilysin, 4-hydroxyphenethylamine) produced by some MLB (Wu et al., 2014; Yi et al., 2015) or by the degradation of microcystins upon cell lysis by the activity of specific microcystin-degrading bacteria that may be present in the mucilage matrix of the *Microcystis* cells and colonies or in the surrounding water (Maruyama et al., 2003; Kormas and Lymperopoulou, 2013; Zhu et al., 2014).

2.3. Cyanobacteria

Several cyanobacteria are able to produce secondary metabolites (allelochemicals) with strong inhibitory effects on *Microcystis* growth (Suppl. Table 3) as shown for taxa belonging to the Nostocales (*Anabaena*, *Calothrix*, *Cylindrospermum*, *Cylindrospermopsis*, *Fischerella*, *Nostoc*, *Scytonema*), Oscillatoriales (*Planktothrix*, *Oscillatoria*, *Tychonema*) and Chroococcales (*Microcystis*, *Synechocystis*).

Almost every taxon produces its own specific compound and these generally do not affect *Microcystis* alone but in fact show detrimental effects on a wide range of prokaryotes (cyanobacteria, heterotrophic bacteria) and/or eukaryotes (green algae, diatoms, fungi) (Suppl. Table 3). The production of these compounds is influenced by several parameters. For some, the presence of *Microcystis* is needed to trigger its production (Mello et al., 2012). Experimental work revealed that the production is not necessarily in proportion to the cell density of the producer, but is merely temperature-dependent (Gromov et al., 1991; Issa, 1999) and highly strain-specific (Figueredo et al., 2007). In accordance, the sensitivity of *Microcystis* to these compounds also may vary depending on the *Microcystis* strain. For instance, a study using natural bloom samples revealed that exudates of *Oscillatoria* had a negative effect on all but one of the *Microcystis* genotypes present. In spite of the strong decrease in total *Microcystis* biomass, it was stated that this one insensitive genotype represented a population defence mechanism, further stimulating and explaining the high clonal diversity of natural *Microcystis* populations (Leão et al., 2012). *Microcystis* itself displays such strain specificity both as a producer and as a receiver of *Microcystis*-inhibiting compounds. This was demonstrated by Zhai et al. (2013) and Yang et al. (2012), Yang et al. (2014) who cultivated *Microcystis aeruginosa* in the presence of *Microcystis flosaquae* or *Microcystis wesenbergii* which revealed that *M. aeruginosa* was the best competitor, although they all showed a competitive inhibition toward each other as regulated with specific allelochemicals and depending on their initial cell densities. Competitive inhibition effects are even known to exist between microcystin-producing and non-producing *M. aeruginosa* strains, the first being favored by increasing UV-B radiation levels (Yang et al., 2015).

The allelochemicals mainly act on photosynthesis by distorting the thylakoid membranes and disrupting electron transport, thus inhibiting PSII (Gleason and Paulson, 1984; Gromov et al., 1991; Bagchi et al., 1993; Schlegel et al., 1999; Blom et al., 2006; Figueredo et al., 2007; Shao et al., 2013). As a result, oxidative stress levels can be elevated by the increase of highly reactive oxygen in the cells, eventually resulting in cell death (Shao et al., 2013). Others can inhibit the synthesis of RNA which as a consequence disrupts protein synthesis (Doan et al., 2001; Etchegaray et al., 2004). Some compounds affect *Microcystis* in an indirect way by promoting *Microcystis*-lysing organisms. For instance, Sedmak et al. (2008) discovered that active compounds produced by *Planktothrix rubescens* (planktopeptin, anabaenopeptin) trigger the activation of *Microcystis* lysogens (host cells that harbor the yet inactive viral DNA) thus causing viral infection and massive cell lysis. They linked the difference in susceptibility between the various *Microcystis* strains used (*aeruginosa* and *wesenbergii*) to the amount of lysogens in the cultures and assumed that lysogeny is widespread in cyanobacterial blooms and that the activation of lysogenic host cells might be a very important feature of bloom collapse in nature. Since they mainly disrupt photosynthesis, cyanobacterial allelochemicals active against *Microcystis* can also harm the producing organisms themselves (auto-inhibition). This, however, only happens at much higher values than the *Microcystis*-growth inhibiting concentrations as shown for the production of nostocarbolin by *Nostoc* (Blom et al., 2006). Accordingly, microcystin has growth-limiting effects on *Microcystis* but only at very high concentrations ($25\ mg\ l^{-1}$) (Babica et al., 2007), which can be found in highly concentrated surface scum layers of toxic *Microcystis* blooms however (Wilmotte et al., 2008; Descy et al., 2011) and thus might influence final bloom collapse.

It is argued that allelochemicals are only effective when the competing organisms live in close association with each other, such as in biofilms, due to the otherwise fast dilution of the active compounds in the water column (Schlegel et al., 1999). The production of such substances, however, may help maintain dominance of the producing organism(s) once it reaches a critical (high) density as a result of favorable environmental conditions. This was proposed by Figueredo et al. (2007) who discovered that the production of allelochemicals, causing severe growth inhibition in competing *Microcystis aeruginosa* and *Microcystis wesenbergii* and several green algae, gave the cyanobacterium *Cylindrospermopsis raciborskii* a competitive advantage in a eutrophic Brazilian freshwater lake. Recently, Rzymski et al. (2014) could show that the cyanotoxin cylindrospermopsin and other compounds produced by *C. raciborskii* not only: (1) inhibited growth of *M. aeruginosa*, but also; (2) decreased the production of microcystins, as such diminishing the potential defensive power of toxic *Microcystis* strains, and; (3) upregulated the extracellular alkaline phosphatase activity of the *Microcystis* cells, thereby increasing the bioavailable phosphorus pool for its own account. In both examples, the presence of *Microcystis* was not needed to trigger the production of these bioactive compounds. In contrast, experimental work by Mello et al. (2012) showed the existence of an inducible allelopathic effect of *C. raciborskii* exudates since *Microcystis* cultures were only inhibited when adding filtered culture medium originating from a mixed culture of *M. aeruginosa* and *C. raciborskii*. Moreover, they observed aggregation of *Microcystis* cells into colonies in response to these allelochemicals, although previously unexposed *Microcystis* cells did not aggregate, which they saw as in indication that such a defence strategy is the result of co-evolution between *Microcystis* and *Cylindrospermopsis* (Mello et al., 2012).

2.4. Eukaryotic microalgae

In accordance with cyanobacteria, many planktonic microalgae compete with *Microcystis* for the same resources. Although residence time, nutrient levels, temperature, light limitation and pollutants are all known to influence the competitive outcome (Takeya et al., 2004; Wan et al., 2007; Zheng et al., 2008; Zhu et al., 2010; Lürling and Roessink, 2006; Zhang et al., 2013; Wang et al., 2015), there exists strong evidence that the production and secretion of compounds active against *Microcystis* also play an important role. This was demonstrated mostly for green algae (*Acutodesmus*, *Desmodesmus*, *Scenedesmus*, *Botryococcus*, *Quadrigula*, *Monoraphidium*), dinoflagellates (*Peridinium*) and pennate diatoms (Suppl. Table 4). The metabolites mainly disrupt the thylakoid membranes and electron transport in PSII, causing photo-inhibition, changes in the permeability of the cell membrane, leakage of cell contents, loss

of buoyancy and ultimately complete lysis (Wu et al., 1998, 2011; Vardi et al., 2002; Harel et al., 2013). The production of these compounds is induced by stress, for instance under stationary phase culture conditions, but the presence of *Microcystis* is not needed as a trigger (Harel et al., 2013; Chen and Guo, 2014). Moreover, these metabolites may have a more widespread action, affecting not only many cyanobacteria (Harel et al., 2013) but also green algae, diatoms and even zooplankton (Chiang et al., 2004). On the other hand, Bittencourt-Oliveira et al. (2015) could experimentally demonstrate that *Microcystis* displays intraspecific variability in its susceptibility to growth inhibition by green microalgae, since a *Microcystis aeruginosa* strain was less sensitive than *Microcystis panniformis*. The efficacy of these metabolites in nature largely depends on their concentration and consequently upon the population density of the producer-cells. In this respect, Vardi et al. (2002) considered the patchy distribution of the dinoflagellate *Peridinium gatunense* in Lake Kinneret, which exhibited locally high population densities (and thus high concentrations of *Microcystis*-affecting alellochemicals), a natural defence strategy against competing *Microcystis* populations.

Most experiments however revealed dualistic relationships between *Microcystis* and its microalgal competitors. In response to the presence of microalgae or their allelochemicals, *Microcystis* may activate its own defence mechanism(s) by secreting substances active against its competitors (Vardi et al., 2002; Wan et al., 2007; Harel et al., 2013; Zhang et al., 2013; Bittencourt-Oliveira et al., 2015). Toxic *Microcystis* cells may also increase their microcystin content by upregulating the genes involved in its production (Vardi et al., 2002; Harel et al., 2013; Bittencourt-Oliveira et al., 2015). The presence of extracellular microcystins in nature is known to cause the production of ROS in eukaryotic organisms leading to severe oxidative stress (Vardi et al., 2002) and to induce the production of extracellular polysaccharides in *Microcystis*, thereby enhancing colony formation (Gan et al., 2012). Their allelopathic function however remains questionable since microcystins are not actively secreted by *Microcystis* cells (Rohrlack and Hyenstrand, 2007).

2.5. Mixo- and heterotrophic flagellates

The potential of *Microcystis*-grazing flagellates (MGF) in controlling nuisance algal blooms was first reported by US researchers who observed a fast clearance of *Microcystis* cultures in the presence of several *Ochromonas* species (Prows and McIlhenny, 1973; Cole and Wynne, 1974). It was however not until the 1990s that the importance of MGF was truly realized, which concordantly sparked a lot of research, especially in Asia (Suppl. Table 5). So far, significant grazing on *Microcystis* was demonstrated for MGF belonging to 4 different genera of mixotrophic (*Ochromonas*, *Poterioochromonas*) and heterotrophic (*Monas*, *Paraphysomonas*) chrysophytes, for the heterotrophic chlorophyte *Polytomella* and for two heterotrophic species (*Collodictyon triciliatum* and *Diphylleia rotans*), both with a very specific morphology and belonging to a new lineage in the global eukaryotic phylogeny (Brugerolle et al., 2002; Zhao et al., 2012). All these taxa however seem to be omnivorous grazers not only on various *Microcystis* morphotypes (e.g. Sugiura et al., 1990; Iwami et al., 1996; Zhang et al., 1996; Iwami et al., 1999; Kim et al., 2006), although *M. wesenbergii* seemed less susceptible (Kim et al., 2006), but also on other cyanobacteria, heterotrophic bacteria, yeast and diverse micro-algae (e.g. Klaveness, 1995; Zhang et al., 1996; Zhang and Watanabe, 2001; Kim et al., 2006; Yan et al., 2009; Manage, 2009). The ingestion- and growth rates when feeding on *Microcystis* cells are similar for the different MGF (Suppl. Table 5), and relatively independent of the food items tested or the ability of the flagellates to grow autotrophically. Differences in experimental design could explain the somewhat higher range in observed clearance rates since these are generally inversely correlated with prey abundance (Wilken et al., 2010; Kobayashi et al., 2013). Grazing characteristics might also differ depending on abiotic parameters such as temperature, pH and nutrient concentrations (Sugiura et al., 1991; Kim et al., 2006; Yan et al., 2009; Zhang et al., 2009a). For instance, nutrients can influence the suppression of *Microcystis* in the case of mixotrophic MGF, since MGF can either prey upon or compete with *Microcystis* for the same resources when grown autotrophically, a phenomenon termed intra-guild predation by Wilken et al. (2014a). Such combined effects can lead to a stronger suppression of *Microcystis* by *Ochromonas* but since this flagellate suffers from intraspecific interference at high densities and is not able to use nitrate as nitrogen source, its effectiveness in reducing natural *Microcystis* blooms is limited to relatively less productive, ammonium-rich waters (Wilken et al., 2014a).

MGF seem to be omnipresent in nature especially in association with *Microcystis* (Van Donk et al., 2009). The only environmental study simultaneously exploring the dynamics of MGF and *Microcystis* (Nishibe et al., 2002), however, could not demonstrate a close relationship between *Microcystis* abundance and the grazing characteristics of *Collodictyon triciliatum*. Its effect on the abundance of natural *Microcystis* populations was negligible (<2.5% of the standing stock grazed per day), especially when compared to the high removal rates of *Microcystis* cells by MGF obtained under laboratory conditions (10–60%, see Suppl. Table 5). In comparison with the straightforward and simple design of some laboratory experiments, other biological interactions (e.g. top-down regulation of the MGF by larger organisms) might influence the interaction between *Microcystis* and its flagellate grazers in nature (Nishibe et al., 2002). Also differences in *Microcystis* morphology can be an important variable influencing the flagellate grazing capabilities. *Microcystis* cells in nature are mainly aggregated into colonies, a feature usually lost during cultivation (Reynolds et al., 1981). As demonstrated for *Ochromonas*, flagellate clearance and growth rates are much lower for *Microcystis* colonies compared to single cells. Colony formation can even be induced as a defense mechanism against flagellate grazing (Burkert et al., 2001; Yang et al., 2006, 2008, 2009a,b; Yang and Kong, 2012). Such induced colony formation is apparently not the result of aggregation of already existing *Microcystis* single cells, but rather caused by the inability of the *Microcystis* daughter cells to separate after division due to an increased production of soluble and cell-bound lipopolysaccharides by the cells (Yang et al., 2009b; Yang and Kong, 2012). Colony formation, however, comes with a metabolic cost since *Microcystis* cells in colonies displayed a lower PSII efficiency in comparison with single cells (Yang et al., 2009b). Colony formation thus might be the result of a trade-off between flagellate grazing losses and living under suboptimal physiological conditions. Since small *Microcystis* colonies are easily ingested by *Ochromonas* (Van Donk et al., 2009), *Collodictyon* (Nishibe et al., 2002) and *Polytomella* (Manage, 2009), there also seems to exist a certain threshold in the number of aggregated cells before colony formation is beneficial against MGF. Small-scale aggregation seems also a less effective strategy for *Microcystis* against grazing by *Poterioochromonas malhamensis* since this species is very flexible and is able to expand its volume substantially in order to ingest prey a few times larger than itself (e.g. Zhang et al., 1996).

The presence of microcystins apparently does not protect *Microcystis* against flagellate grazing since both microcystin-producing and non-microcystin-producing *Microcystis* strains are affected (Kim et al., 2006; Baek et al., 2009; Van Donk et al., 2009). *Poterioochromonas* for instance can tolerate microcystins by simply excreting them after the digestion of toxic *Microcystis* cells (Watanabe et al., 1996) or by reducing oxidative stress caused by these toxins by means of an increased production of superoxide

dismutase (Ou et al., 2005). *Diphylleia rotans* is even capable of metabolizing the microcystins during digestion (Mohamed and Al-Shehri, 2013). Because of their microcystin-neutralizing capacity, such MGF potentially play an important ecological role by decreasing the toxicity of *Microcystis* populations and thus facilitate *Microcystis* ingestion by large cladoceran grazers such as *Daphnia* (Bec et al., 2006; Zhang et al., 2009b).

2.6. Amoebae

Free-living planktonic amoebae, mainly associated with suspended mineral particles or detritus (Caron et al., 1982; Rogerson et al., 2003), use colonies of planktonic cyanobacteria as an appropriate habitat (Whitton, 1973; Anderson, 1977; Rodríguez-Zaragoza, 1994) where they can feed on associated microorganisms or on the cyanobacteria themselves (Dryden and Wright, 1987). Whitton (1973) was the first to report the existence of *Microcystis*-grazing amoebae (MGA) but until recently, only a few other amoeboid organisms ingesting *Microcystis* in natural samples were observed (Suppl. Table 6). The lack of observations suggests that *Microcystis* is not a favorable food item for many planktonic amoebae. This is indeed the case for the percolozoan *Naegleria* sp. and the amoebozoan *Acanthamoeba castellanii* which egested grazed *Microcystis* cells immediately upon ingestion (Liu et al., 2006; Urrutia-Cordero et al., 2013). The presence of toxic secondary metabolites in the ingested *Microcystis* cells may be the culprit, since these can cause alterations in the cytoskeleton structure leading to irreversible cell damage of the amoebae (Urrutia-Cordero et al., 2013). The recent description of 8 new MGA of which some displayed strong bloom-reducing capacities, irrespective of the presence of microcystins, however indicates that their biodiversity and ecological significance are much higher than previously appreciated (Van Wichelen et al., 2010, 2016; Berney et al., 2015). About 11 amoeboid taxa capable of sustaining growth on a diet of microcystin-producing *Microcystis* are currently known (Suppl. Table 6) but only the opisthokont *Nuclearia* and the amoebozoans *Penardochlamys* sp. and *Korotnevella pelagolacustris* are relatively well studied. The latter two feed exclusively on *Microcystis* (Nishibe et al., 2004; Van Wichelen et al., 2010, 2016) while *Nuclearia* has a broader food range (Yamamoto and Suzuki, 1984) and is also able to feed on other cyanobacteria (*Anacystis*, *Anabaena*, *Phormidium*) and to a lesser extent also on certain green algae (*Staurastrum*, *Closterium*).

Nuclearia obtained higher growth rates at higher temperatures and pH values (Yamamoto, 1981), conditions typical for *Microcystis* bloom formation, while this amoeba and the testate amoeba *Penardochlamys* had lower growth rates under darkness, indicating that the physiological activity of *Microcystis* is important too (Yamamoto, 1981; Mizuta et al., 2011). Moreover, feeding experiments and field observations have demonstrated that *Microcystis* morphotypes differ in their susceptibility to MGA. For instance, *Nuclearia* induced much smaller plaques in agar cultures of *Microcystis flosaquae* in comparison with *Microcystis aeruginosa* (Yamamoto and Suzuki, 1984) and *Korotnevella pelagolacustris* was shown to preferentially feed on *M. aeruginosa* instead of *Microcystis viridis* in mixed field populations of both *Microcystis* morphotypes (Van Wichelen et al., 2010). *Penardochlamys*, on the other hand, was able to feed on both *M. aeruginosa* and *Microcystis wesenbergii* in the field (Nishibe et al., 2004; Mizuta et al., 2011). Although *M. aeruginosa* and *M. viridis* differ in the amount of mucilage around their cells and colonies, not the mucilage but the constitutive production and secretion of yet unknown grazing deterrents caused resistance against the MGA tested (Van Wichelen et al., 2012).

Regarding the ecological impact of MGA, the only two available field studies showed either a strong (Van Wichelen et al., 2010), or only a very limited (Nishibe et al., 2004) effect on the biomass and population structure of natural (microcystin-positive) *Microcystis* blooms.

2.7. Ciliates

Strong negative effects of ciliate grazing on cyanobacterial populations have been described, but thus far only on filamentous taxa (Canter et al., 1990; Fyda et al., 2010). *Microcystis* grazing by ciliates is only documented for the algivorous heterotrichs *Condylostomum vorticella* and *Stentor roeselii* (Takamura and Yasuno, 1983; Kim et al., 2007; Suppl. Table 7). The first was found to ingest *Microcystis* colonies of up to 40 cells, regardless of the presence of a mucilage matrix, as part of a wide variety of other coccoid cyanobacteria and algal taxa in its natural diet (Takamura and Yasuno, 1983). *S. roeselii* was able to graze away *Microcystis aeruginosa* cultures but its impact was much reduced in the presence of an algicidal bacterium, an antagonistic effect the authors assumed to be attributed to additional anti-ciliate properties of the bacterium (Kim et al., 2007). Gerritsen et al. (1987) and Sanders (1988) performed feeding experiments with the scuticociliate *Cyclidium* sp. on *M. aeruginosa*. However, the much smaller cell dimensions (0.8–1.1 μm diameter) of the *Microcystis* strain used in comparison with *Microcystis* cell dimensions obtained from the literature (Komárek and Anagnostidis, 1999) suggest that this may have actually involved an *Aphanocapsa* or *Aphanothece* species. Peritrich ciliates such as *Vorticella* and *Pseudohaplocaulus* are frequently observed attached to colonies of *Microcystis* and other colonial cyanobacteria (Pratt and Rosen, 1983; Canter et al., 1990; Foissner et al., 1999; own observations). While the feeding currents of these epibionts can cause relocation of the cyanobacterial colonies in the water column, their buoyancy is only disrupted at high densities of attached ciliates per colony and their relationship is supposed to be merely mutualistic (Canter et al., 1992).

2.8. Microfungi

Many phytoplankton species are prone to fungal parasites mainly belonging to the Chytridiomycota (chytrids). These microscopic fungi infect their host by zoospores which, after attachment and penetration, develop a rhizoidal system inside the host cell that digests the cytoplasm to eventually form sporangia that produce and release new zoospores. Fungal infections of phytoplankton can occur at any time of the year (Holfeld, 1998) and infection prevalence can reach 80 to almost 100% (e.g. Canter and Lund, 1953; Anderson et al., 1995; Holfeld, 1998), sometimes resulting in a strong reduction of the host population (e.g. Alster and Zohary, 2007). Several chytrid parasites of cyanobacteria are known of which the majority infect the filamentous taxa *Anabaena*, *Aphanizomenon*, *Cylindrospermopsis*, *Lyngbya* and *Oscillatoria* (Kagami et al., 2007). They were shown to play an ecologically significant role in the termination of blooms by degrading and defragmenting cyanobacterial filaments, thus facilitating zooplankton grazing of otherwise inedible particles (Sime-Ngando, 2012). Two chytrids, *Chytridium microcystidis* (Skuja, 1948) and *Rhizidium microcystidis* (Sen, 1988) appear to be host-specific parasites of *Microcystis* (Sen, 1988; Canter-Lund and Lund, 1995; Suppl. Table 8). A maximal prevalence of 90% was observed for natural *R. microcystidis* infections of *M. aeruginosa* blooms leading to a significant decline in *Microcystis* population densities (Sen, 1988). Van Wichelen et al. (2010) observed a maximal prevalence of 76% for natural *C. microcystidis* infections on *M. aeruginosa*, however without clear effects on *Microcystis* population dynamics. Moreover, the susceptibility to this parasite showed some strain-specificity since the infection prevalences were higher for *M. viridis*

(max. 85%). Since both *Microcystis* morphotypes produced microcystins, these toxins were probably not involved in chytrid resistance. Both studies also demonstrated high interannual variation in *Microcystis* infection percentage by these parasites.

At least one non-chytrid fungus can use *Microcystis* as a nutrient source. The ascomycete *Trichoderma citrinoviride* isolated from a natural *M. aeruginosa* bloom sample was able to completely lyse toxic *M. aeruginosa* cultures within 2 days and to degrade the microcystins within 3 days (Mohamed et al., 2014). These authors could demonstrate that fungal exudates were mainly responsible for the observed degradation and that this species is probably highly specific since green algae and diatoms were not affected.

3. Synthesis

3.1. High diversity of Microcystis-killing microbiota

Microcystis is obviously prone to a wide array of antagonistic microbiota (currently about 120 different taxa known) of which the activities can inhibit or reduce its growth. About 50% of these biota concern heterotrophic bacteria and, especially during the last 15 years, many new taxa of so-called *Microcystis*-lysing bacteria (MLB) have been detected (comprising about 68 papers). Also flagellates (28 published studies in the last 15 years), viruses (19) and competing cyanobacteria (18) are currently well studied. In contrast, studies about competing microalgae (9), amoebae (7), chytrids (3) and ciliates (1) are seriously under-represented or even not existing, as is the case for oomycetes, fungal-like protists phylogenetically related to brown algae and diatoms with known pathogenic effects on (marine) macro- and microalgae (e.g. Carney and Lane, 2014; Scholz et al., 2014). This disparity does not necessarily represent a natural phenomenon but rather reflects technical difficulties in isolation, cultivation and identification, depending on the organism concerned. For instance, viruses and bacteria are rather easily isolated from natural localities and large quantities can be tested simultaneously for their *Microcystis*-lysing capacities using relatively facile techniques (such as plaque formation in *Microcystis* lawns on agar, e.g. Bershova et al., 1968). Micro-predators (flagellates, amoebae, ciliates) and parasites (chytrid fungi) of *Microcystis*, on the other hand, require visual recognition, which, given their fast population turn-over, is merely a matter of chance. The subsequent experimental testing of their feeding habits requires single-cell isolation and co-cultivation in liquid medium followed by specific abundance measurements (e.g. microscopy and/or fluorescence/absorbance analyses). As a result, the diversity of these micro-organisms is still seriously underestimated and careful microscopical observations of *Microcystis* bloom samples may uncover many new *Microcystis*-killing taxa (e.g. Van Wichelen et al., 2016;Fig. 1). Their mainly cryptic lifestyles pleads for careful, high-frequency surveys of natural proliferations of *Microcystis* that could be facilitated by applying next generation sequencing techniques (e.g. Li et al., 2011; Steffen et al., 2012; Cai et al., 2014). The apparent lack of literature about *Microcystis*-grazing ciliates is especially remarkable. As an inherent part of the microbial loop, ciliates often dominate the protozoan biomass in shallow eutrophic waters, thereby exerting a grazing pressure on the phyto- and bacterioplankton comparable to that of metazooplankton (Mathes and Arndt, 1994, 1995; Zingel, 1999) and several are known to be specific grazers of filamentous (toxic) cyanobacteria (Canter et al., 1990; Combes et al., 2013). Although we have never observed *Microcystis*-grazing ciliates during a high frequency monitoring campaign in a eutrophic pond either (Van Wichelen et al., 2010), a small-scale study on their microcystin content gave positive results for two out of five analyzed ciliate cells (Descy et al., 2011) which may indicate at least some *Microcystis*-grazing activity of these ciliates. The importance of ciliate grazers upon natural *Microcystis* bloom dynamics definitely deserves more investigation.

3.2. Main modes of action

The microbiota affect *Microcystis* in two main ways, either directly, always requiring close physical contact, or indirectly by the secretion of allelochemicals. Direct attack is carried out by parasites that attach themselves to and penetrate the *Microcystis* cells in order to biodegrade the cell contents for their own nutrition, a typical feature of all viruses, certain bacteria (e.g. *Bdellovibrio*) and all chytrid fungi. Grazing is also a form of direct attack and ingestion of cells and/or small colonies of *Microcystis* can take place by engulfment, typical for amoebae and flagellates, or filtration which is the main feeding mode for ciliates. Secretion of allelochemicals appears to be the main strategy for most bacteria, cyanobacteria and eukaryotic microalgae to kill *Microcystis* for food (bacteria) or to reduce resource competition (cyanobacteria and eukaryotic microalgae). The majority of these bioactive compounds specifically seem to inhibit PSII and the antioxidant defence mechanisms of the cell, causing membrane destruction by elevated oxidative stress levels (Shao et al., 2013, 2014; Harel et al., 2013). Sometimes however, secretion only takes place after physical contact with the host cell (e.g. Nakamura et al., 2003). These two different modes of action are also reflected in the observed host ranges which tend to be relatively narrow for parasites and some grazers of *Microcystis*, in contrast to the metabolite-producing microbiota that can also affect other cyanobacteria and microalgae.

3.3. Ecological significance

The few studies which have simultaneously monitored natural population dynamics of *Microcystis* and antagonistic microbiota showed a variety of outcomes with either strongly negative effects (Sen, 1988; Manage et al., 2001; Vardi et al., 2002; Van Wichelen et al., 2010) or no obvious effects (Nishibe et al., 2002, 2004; Yoshida et al., 2008a, 2010; Van Wichelen et al., 2010) on bloom biomass. The few positive correlations between the abundance of *Microcystis* and its antagonist that have been noticed in nature (Daft et al., 1975; Stewart and Daft, 1976; Manage et al., 2001; Manage, 2009; Zhang et al., 2012) are mainly caused by the density-dependence of many antagonistic infections (e.g. Vardi et al., 2002; Zhang et al., 2008; Li and Li, 2012; Zhang et al., 2014) and/or the potentially facultative antagonistic nature of some of these microbiota, which can also sustain growth on extracellular compounds of *Microcystis* during bloom conditions (Daft et al., 1985). One reason for the discrepancy between experimental results and field observations could be the relatively low sampling frequency of most field studies, which increases the risk of missing the generally short-lived population maxima of antagonistic microbiota (Van Wichelen et al., 2010). Moreover, local environmental characteristics may substantially influence the magnitude of antagonistic effects of microbiota against *Microcystis* populations in nature, where such organisms are part of a complex foodweb and are concordantly influenced by abiotic conditions such as nutrients, light and temperature (e.g. Sugiura et al., 1993; Wilken et al., 2014a,b) and biological interactions such as predation (e.g. Brabrand et al., 1983; Canter et al., 1990; Nishibe et al., 2002). The physiological state of the antagonists or the host cells might be of importance too. For instance, the effects of viral infections might be obscured by the prevailing amount of lysogeny (Suttle, 2000; Jassim and Limoges, 2013), and the temporally weaker cell walls of fast-growing *Microcystis* cells (during exponential growth) make them easier targets for parasites or bio-active compounds, in comparison with stationary phase cells (Liao and Liu, 2014).

A feature that seems widespread among the antagonists of *Microcystis* is the strain specificity of their interactions. For instance, cyanophages SAM-1, Ma-LMM01, MaMV-DC and MaCV-L all caused cell lysis in only 1 out of many *Microcystis aeruginosa* strains tested (Parker et al., 1977; Yoshida et al., 2006; Ou et al., 2013; Li et al., 2013). Feeding experiments showed that a *Microcystis flosaquae* strain was less sensitive for grazing by the amoeboid *Nuclearia* sp., but however was highly inhibited by exudates from the bacterium *Pseudomonas*, in contrast to *M. aeruginosa* (Yamamoto and Suzuki, 1984; Du et al., 2014). *Microcystis wesenbergii* especially seems less susceptible than other *Microcystis* morphotypes to antagonistic bacteria (Caiola and Pellegrini, 1984; Yamamoto and Suzuki, 1990; Tian et al., 2012) and heterotrophic flagellates (Kim et al., 2006). It seems therefore justified to assume that different *Microcystis* genotypes are susceptible to different specialized antagonist species (and genotypes?) whose actions can cause compositional shifts in bloom populations. Intraspecific differences in susceptibility leading to compositional shifts in natural *Microcystis* populations have so far only be described for cyanophage infections, causing the replacement of microcystin-producing by non-microcystin-producing subpopulations (Yoshida et al., 2008a, 2010) and for predatory amoebae, by provoking a shift from grazing-sensitive to grazing-resistant *Microcystis* populations (Van Wichelen et al., 2010). Highly specific grazing on the most abundant *Microcystis* types might even promote *Microcystis* diversity by making less abundant *Microcystis* types more competitive (Prowe et al., 2012).

The inclusion of less visible indirect effects of antagonistic microbiota would reveal a much better estimation of their ecological significance for *Microcystis* bloom dynamics. The microbial fragmentation and degradation of particles that are too large and toxic to become ingested may facilitate zooplankton grazing, thus making otherwise inedible biomass available for higher trophic levels, a phenomenon called trophic upgrading (Bec et al., 2006; Zhang et al., 2009b; Gerphagnon et al., 2013, 2015). The production of non-toxic compounds by competing cyanobacteria that activate lysogenic *Microcystis* cells to eventually culminate in the massive production of lytic particles causing ultimately bloom collapse (Sedmak et al., 2008) is another indirect effect and a good example of 'the enemy of my enemy is my friend'-principle.

3.4. Microcystis *defence mechanisms*

Microcystis displays a high morphological variability rendering, depending on the enemy, protection as single cell or colonial morph. The aggregation of single cells into colonies or the increase in colony size is efficient against flagellates (Yang et al., 2006, 2009a,b), predatory bacteria (Xu et al., 2012) and even competing cyanobacteria (Mello et al., 2012) but not against grazing amoebae (Van Wichelen et al., 2012). The increase in colony size is an inducible process, requiring the presence of the antagonist (Yang et al., 2006, 2009a,b), and is mainly carried out by an increased production of extracellular polysaccharides (Yang et al., 2008, 2009b) leading to an elevated stickiness of the cells and an increased inability of newly divided cells to separate (Yang and Kong, 2012). Interestingly, some predatory bacteria can induce a reduction in *Microcystis* colony size (Gumbo et al., 2010; Wang et al., 2013b) thus negating the protective role of colony formation. The additional metabolic costs due to a lower PSII efficiency of colonial cells compared to single cells (Yang et al., 2009b) are probably outweighed by the benefits given the almost exclusive occurrence of colonial *Microcystis* morphs in nature (Reynolds et al., 1981). Besides morphological variability, *Microcystis* also maintains a high genomic plasticity (Lin et al., 2011). Its genome hosts the highest known abundance and diversity of anti-virus defense genes of all Archaea and Bacteria tested (Makarova et al., 2011).

Also the production of specific grazing deterrents might offer protection against certain microbiota (Van Wichelen et al., 2012) as well as against metazoan grazers (e.g. Jüttner et al., 2010). The production of microcystins generally does not prevent microbial ingestion and/or digestion of *Microcystis* (Kim et al., 2006; Van Donk et al., 2009; Van Wichelen et al., 2010) but may however be effective against competing microbiota (Vardi et al., 2002; Bittencourt-Oliveira et al., 2015) in accordance to its protection against metazoan grazing (DeMott, 1999; Rohrlack et al., 1999, 2001; Lotocka, 2001). The production of a wide variety of grazing deterrents, active against many microbial and metazoan antagonists, can be regarded as a positive feedback mechanism that may contribute to the maintenance of *Microcystis* dominance as an alternative stable state in shallow eutrophic lakes.

Its strong flexibility and adaptability could have been largely influenced by – and perhaps forms the basis of – a continuous arms race (co-evolution) between *Microcystis* and its antagonists as already been suggested for *Microcystis*-cyanophage relationships (Parker et al., 1977; Kimura et al., 2013; Kuno et al., 2014; Yoshida et al., 2014). Oscillations in the genotypic composition of cyanophage populations tend to happen both on short-(days) and long-(years) term scales in nature and can be an important driver for the maintenance of a high genotypic diversity of *Microcystis* and its cyanophages by negative frequency-dependent selection (Kimura et al., 2013). Co-evolutionary effects are also suggested for chemical interactions between *Microcystis* and its cyanobacterial competitor *Cylindrospermopsis raciborskii* (Mello et al., 2012) or potential metazoan grazers such as *Daphnia* (Lemaire et al., 2012).

3.5. *Potential for biological control of* Microcystis *blooms*

The currently strong restrictions on the use of chemical treatment (e.g. with $CuSO_4$) of waterbodies affected by cyanobacterial blooms, and of the limitations of expensive physical/mechanical control mechanisms of uncertain efficiency (e.g. Lürling and Tolman, 2014) have ignited renewed interest in the search for microbiological tools to combat *Microcystis* bloom development, a potential already considered since the earliest investigations of *Microcystis*-killing microbiota (e.g. Goryushin and Chaplinskaya, 1968; Prows and McIlhenny, 1973; Parker et al., 1977). The successful application of *Microcystis*-killing microbiota in nature is however far from certain. A general lack of knowledge on the natural effectiveness for most antagonistic microbial taxa makes any valid conclusion about their potential use as a biological control agent premature. Most studies have rarely gone further than the observation of a lytic effect on laboratory cultures of only one *Microcystis aeruginosa* strain (in most cases originating from a culture collection). Besides, several antagonistic microbiota are non-indigenous organisms, even from marine or terrestrial origins (e.g. Chen et al., 2011; Jia et al., 2013; Somdee et al., 2013), which make their potential use as biological control agents against *Microcystis* at least questionable. The in vivo application of *Microcystis*-killing microbiota is hardly explored. So far only anecdotal information is available about the use of certain cyanophages (Padan and Shilo, 1973) and heterotrophic bacteria (Fogg et al., 1973) in order to attempt to control natural *Microcystis* blooms. Moreover, *Microcystis*' extreme resilience, largely the reason why it behaves as a real pest and harmful species in nature (Cray et al., 2013), forms the main challenge for successful application of any large-scale biological control mechanism. Given the high potential for co-evolution between *Microcystis* and its microbial antagonists, the application of any microbial control mechanism will probably induce only short-term effects.

For long-term maintenance, more structural measures like restoring and improving submerged vegetation stands are probably more appropriate to combat *Microcystis* bloom formation (Hilt and Gross, 2008). Macrophytes are natural and crucial components of the aquatic foodweb in undisturbed freshwater lakes and known to induce and stabilize clear water conditions (Scheffer et al., 1993). Apart of competing with microalgae and cyanobacteria for dissolved nutrients, they are also natural producers of allelopathic compounds inhibiting algal and cyanobacterial growth (Nakai et al., 2000; Li and Hu, 2005; Zhang et al., 2009c). The best and probably only long-lasting way to re-establish submerged vegetation in deteriorated waterbodies is by halting and reversing the eutrophication process. This is however a common responsibility that calls for a significant change in current land- and water-use management on a global scale (e.g. Rockström et al., 2014).

4. Conclusions

In spite of the uneven attention given to the different microbial antagonists of *Microcystis*, several generalities can be deduced from what has been studied so far:

(1) The diversity of *Microcystis*-killing microbiota in nature is high. This is not only documented for relatively well-studied groups such as cyanophages and heterotrophic bacteria but seems also to be true for rarely studied antagonists such as predatory amoebae. Undoubtedly, many antagonists remain to be discovered which, given their mainly cryptic lifestyles, pleads for careful, high-frequency surveys of natural *Microcystis* bloom events.
(2) Many antagonists of *Microcystis* have a very restricted host range, since they fail to grow on other potential hosts/prey. This is especially the case for most cyanophages, chytrid parasites and most predatory amoebae and is also documented for several predatory bacteria.
(3) The interactions between *Microcystis* and its microbial antagonists are highly strain-specific which may prevent lasting declines in bloom biomass but may, however, lead to compositional shifts, potentially influencing bloom characteristics such as toxicity.
(4) There are strong indications that some of these highly specific interactions form the basis of a continuous arms race (co-evolution) which potentially limits the possibilities for (micro)biological control of *Microcystis* in accordance to what is expected for metazoan grazers (Ger et al., 2014).

Conflict of interest

The authors declare no conflict of interest.

Contributors

JVW gathered and evaluated all available literature, wrote the first draft and adapted the manuscript based on discussions with and valuable comments from PV, GAC and WV. The submitted version of the manuscript was approved by all authors.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.hal.2016.02.009.

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