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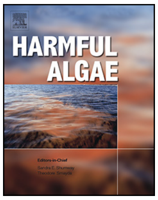

Review

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

Jeroen Van Wichelen [a,*], Pieter Vanormelingen [a], Geoffrey A. Codd [b], Wim Vyverman [a]

[a] *Protistology and Aquatic Ecology, Biology Department, Ghent University, Krijgslaan 281 (S8), 9000 Gent, Belgium*
[b] *Biological and Environmental Sciences, School of Natural Sciences, University of Stirling, Stirling FK9 4LA, Scotland, UK*

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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.

[*] Corresponding author. Current address: Aquatic Management, Research Institute for Nature and Forest, Kliniekstraat 25, 1070 Brussel, Belgium. Tel.: +32 0 2 525 02 77.
E-mail address: jeroen.vanwichelen@inbo.be (J. Van Wichelen).

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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